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The Functional Morphology and Evolution of the Primate Auditory System

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Abstract of the Dissertation

The Functional Morphology and Evolution of the Primate Auditory System

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Primates express numerous modifications on the fundamental mammalian ear morphology, and these differences have proven useful for phylogenetic classification at various taxonomic levels. However, the functional consequences related to diversity in primate auditory structure remain speculative and unproven. Although a considerable amount of research on the functional morphology of the ear has been done in other vertebrate groups, primates remain poorly studied. This dissertation sought to help fill this void by exploring the form-to-function relationships of the primate auditory system.

To address this problem, numerous structures from the outer, middle, and inner ears were measured in a broad sample of primates with known hearing capabilities. The structures investigated included the size and shape of the pinna, the areas of the tympanic membrane and stapedial footplate, the masses and lever arm lengths of the ossicles, the volumes of the middle ear cavities, and the length of the cochlea. In total, over 1400

specimens representing more than 50 genera were assayed. The methods used to obtain these data included traditional morphometric measurement techniques, high-resolution computed-tomography (CT), digital photography, latex casting, and dissections of cadaveric specimens. By identifying specific form-to-function relationships it was possible to test current theories on auditory function, evaluate inter-specific differences in hearing performance, and predict the hearing sensitivity in extinct primate taxa.

The results from these investigations demonstrate that a variety of auditory structures show significant correlations with particular aspects of hearing sensitivity. The majority of these relationships agrees with expectations from acoustic theory but some fundamental theories were not supported. For example, the idea that longer ossicular lever arms result in increased hearing sensitivity was rejected. By applying the functional relationships that are theoretically sound, hearing sensitivity was estimated in four fossil species representing pivotal nodes in primate evolution. These estimations suggest that primates have been steadily reinvading the "low-frequency niche" by progressive modification of various auditory structures. They also show that these adaptations were not present in our closest extinct relatives. The data provided by this dissertation present many opportunities for future research and will help shed light on the adaptive significance of differences in hearing performance.

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CHAPTER 1

The ear is the most mechanically complex sensory system of the head comprised of a multiplicity of structures including moveable bones, membranes, muscles, ligaments, sinuses, resonating canals and sensory neurons (efferent and afferent), to name a few (Figure 1.1). It is generally recognized that these structures act as a series of filtering mechanisms to help localize and amplify incoming sound waves. Yet, the intricacy and

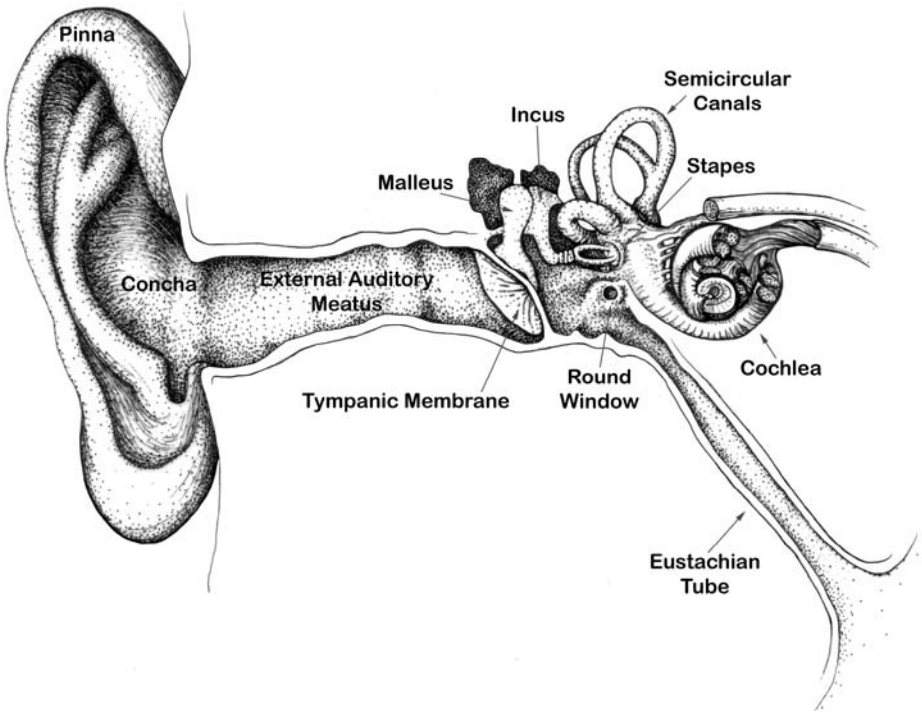

Figure 1.1 - Illustration of a coronal section through the human auditory apparatus showing the major components of the outer, middle and inner ears.

diminutive nature of the auditory apparatus has led to an inadequate knowledge about the precise functional qualities and adaptive nature of the ear. Despite a wide range of research in numerous mammalian groups, we are still a long way from having a complete understanding of auditory functional anatomy.

Structures associated with the auditory region have proven to be touchstone phylogenetic indicators used by numerous investigators to help sort out relationships among various extant and extinct mammalian groups (Gregory 1910; Archibald 1977; Novacek 1977, 1980, 1986; Novacek and Wyss 1986; Wible 1986, 1987; Wible and Martin 1993; McKenna *et al*. 2000). This is particularly true in primates and closely related taxa (Figure 1.2), where major adaptive radiations were often associated with shifts in auditory structure (Gregory 1915; Szalay 1972, 1975; Cartmill 1975; Szalay and Wilson 1976; MacPhee 1977, 1979, 1981; Cartmill *et al.* 1981; Novacek *et al*. 1983; Rosenberger 1985; MacPhee and Cartmill 1986; MacPhee 1987; Wible and Covert 1987). However, the functional consequences related to diversity in primate auditory structure remain speculative and unproven. In the words of one prominent primatologist, "Although we know much about the anatomy of the auditory system, the physiological significance of many anatomical differences among primate ear regions is poorly understood" (Fleagle 1999).

In addition to functional relationships, the adaptive and evolutionary implications of differences in auditory structure have yet to be fully grasped. Although it is obvious that the basic role of the ear is hearing (and possibly thermoregulation in some groups), differences in sensitivity may be largely controlled by selective factors such as group communication, prey detection and/or predator avoidance (Stebbins 1975, 1978, 1980).

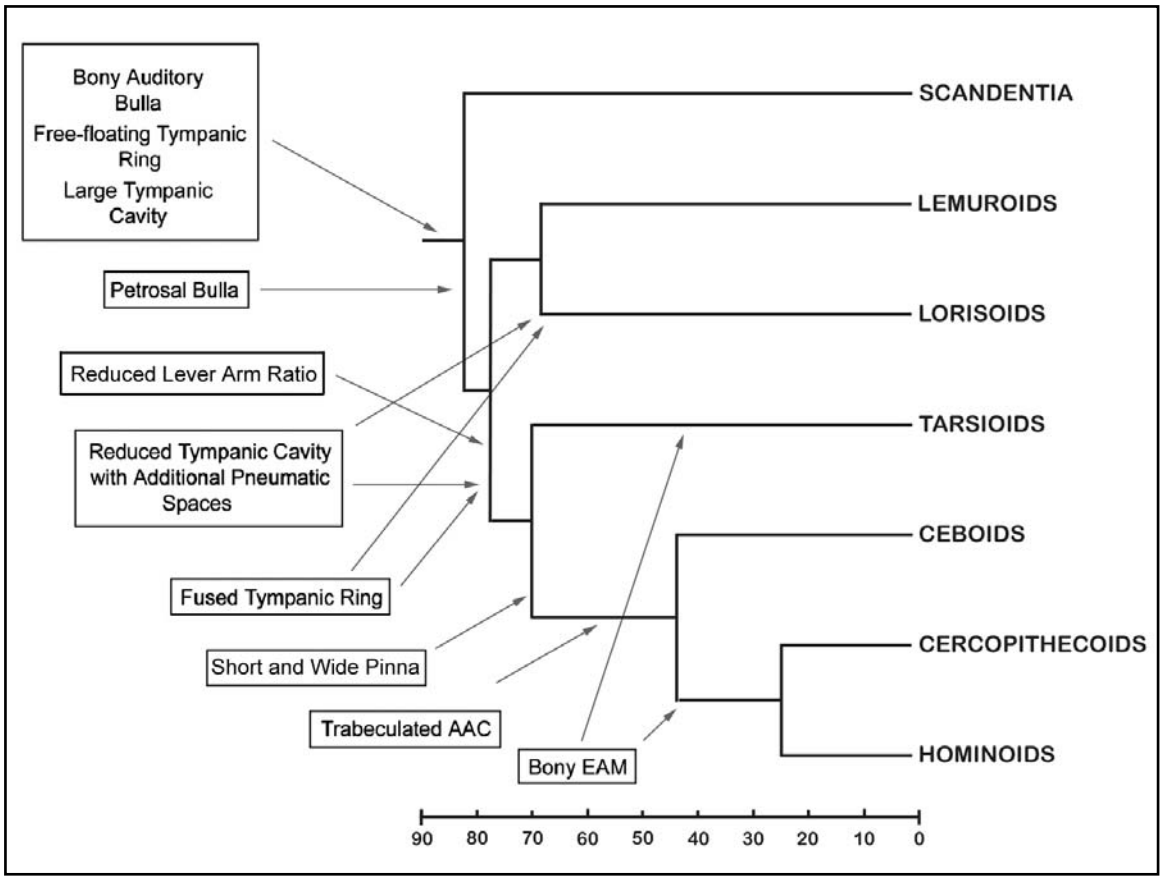

Figure 1.2 - Evolutionary development of selected auditory features in primates and tree shrews. Numbers are in millions of years. Dates for time since divergence taken from the literature and described in chapter 7. AAC refers to the anterior accessory cavity and EAM refers to the external auditory meatus. See chapter 2 for more details.

In other words, the ecology of an animal plays a large role in shaping its hearing sensitivity. The interactions between form, function and ecology can be visualized as an "adaptive triangle" (Figure 1.3), whereby each factor influences the others.

One approach towards understanding the adaptive significance of hearing is simply to note associations between anatomical structure (form) and specific behaviors or environmental stimuli (ecology). However, this "back-door" approach can lead to

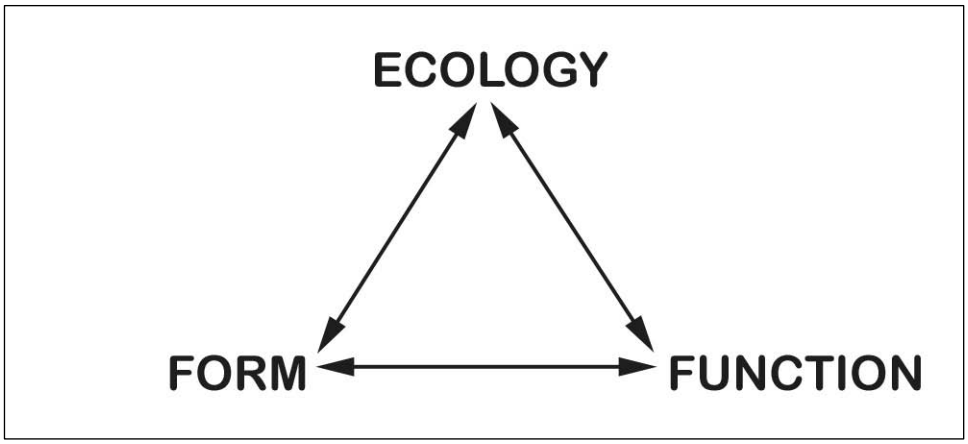

Figure 1.3 - The "adaptive triangle" showing the interrelated nature between form, function and ecology.

correlation without understanding causation, and could possibly result in spurious conclusions. Another, arguably more sound approach, is to build a strong foundation between structural variation (form) and differences in hearing performance (function). Currently, only a handful of studies have been targeted at directly linking form to function in the auditory system, and none of these have been focused on primates (see Chapter 2). The dearth of such first principles research was best expressed by Fay, a leading authority on the subject, when he stated:

> "The field would be greatly advanced by a comprehensive detailed analysis of several carefully selected species with the aim of understanding general principles. These general principles will provide a context for understanding species differences and specializations or adaptations" (1994:15).

The aspiration of this statement encapsulates the primary objective of this dissertation: to undertake a comprehensive analysis of several carefully selected species

of primates with the aim of understanding general principles and species adaptations. The remainder of this chapter outlines the basic approach that was used in this endeavor to gain a better understanding of the functional morphology and evolution of the primate auditory system.

The next (second) chapter provides an overview of previous studies related to anatomical variation and functional morphology of the mammalian auditory system, with a particular spotlight on primate-related studies. The opening section deals with the basic anatomy of the ear and highlights differences that have been noted by various authors in phylogenetic and morphological comparisons. The subsequent section presents a synopsis of the principal models and theories that have been used to investigate and test auditory function of various structures. It also demonstrates the lack of such studies focused on primates.

The third chapter reviews all previously published data dealing with primate hearing thresholds (audiograms) and attempts to synthesize these data to produce reliable datasets for further analyses. This chapter is the longest of the dissertation but its length is justified because audiogram data represent roughly half of the final comparative dataset, and the author was not involved in any of the actual data collection. Therefore, in order to gain some understanding of the quality and limitations of individual audiograms, detailed examination of each study was necessary. The first section gives a brief summary of the methods used in animal psychophysics to produce audiograms and validates the method used here for extracting threshold data from published reports. The second section then proceeds to scrutinize each individual audiogram study, paying particular attention to details that could influence the results (*e.g.*, type of transducer, conditioning technique,

etc.). The third section addresses methodological problems that need to be considered before comparing audiograms. The three main problems that were tackled were error due to intra-individual variability, intra-specific variability, and inter-laboratory variability. The final section uses these meta-analyses to establish final audiogram datasets on which 14 audiometric measurements were taken.

The forth chapter lays out the research design for the primary analysis including the hypotheses tested, morphological measurements taken, and validation experiments for the methods. The next (fifth) chapter investigates the influence of using different types of size variables (for allometric comparisons) in functional comparisons involving the orbit and mandible. The aim of this chapter was to use empirical biomechanical models to establish the most stable and statistically powerful scaling (size) variable for use in auditory allometric analyses. The sixth chapter examines ontogenetic, sexually dimorphic, and phylogenetic differences in auditory morphology as well as head and body size in a relatively broad sample of primate taxa. The goal was to determine the degree to which subgroups of data could be pooled in order to increase sample sizes and potentially eliminate problems associated with taxonomic uncertainty. These data should also be of general scientific interest since these topics (ontogeny and sexual dimorphism) have rarely been addressed in functional auditory research.

The seventh chapter embodies the real heart of the dissertation and examines the associations between auditory sensitivity (audiometric variables) and auditory structure (morphological variables). This chapter also investigates the influence of different statistical approaches on the results (*i.e.*, traditional comparative methods versus phylogenetic corrective procedures). These results are then compared with findings from

previous research and expectations from auditory theory. The eighth and final chapter uses the form-to-function relationships identified in the previous chapter to evaluate and predict the hearing sensitivity in fossil taxa. Three extinct groups of primates[1] were examined using CT data, each representing a pivotal node in the evolution of the order. The closing remarks comment on the possible adaptive role(s) of hearing in primates and point to future directions for research.

[1] One of the groups is actually Plesiadapiformes which is currently considered a sister-group to Primates.

CHAPTER 2

SECTION I: ANATOMY OF THE EAR

The basic structures that comprise the outer, middle and inner ears were first recognized and named by numerous anatomists of the sixteenth century[2] (Versalius 1543 – malleus and incus; Ingrassia 1546 – stapes, oval and round windows; Fallopius 1561 – differentiated inner ear into cochlea and labyrinth; Eustachius 1564 – tensor tympani muscle and Eustachian tube; Varolius 1591 – stapedius muscle). In the following centuries it was discovered that the inner ear was completely filled with lymphatic fluids (Cotugno 1774) and finally, with the aid of the microscope, the auditory hair cells were discovered (Corti 1851). Detailed descriptions of the auditory region in numerous species soon followed and we now have a solid understanding of ear morphology in most major taxanomic groups (Hyrtl 1845; Doran 1878; Parker 1886; Van Kampen 1905; Cockerell *et al*. 1913; van der Klaauw 1931, Segall 1943, 1947, 1969, 1971a, 1971b, 1973, 1974; Hill 1953, 1955, 1957, 1960, 1962, 1966, 1970; Kobrak 1959; Hinchcliffe and Pye 1969; Schultz 1969; Lay 1972; Fleischer 1973; Henson 1974; Hershkovitz 1974, 1977; Hunt 1974; Saban 1975; Webster and Webster 1975; Pye and Hinchcliffe 1976; Hunt and

[2] Most of the references for the early anatomists (1543-1851) were taken from Wever and Lawrence 1954.

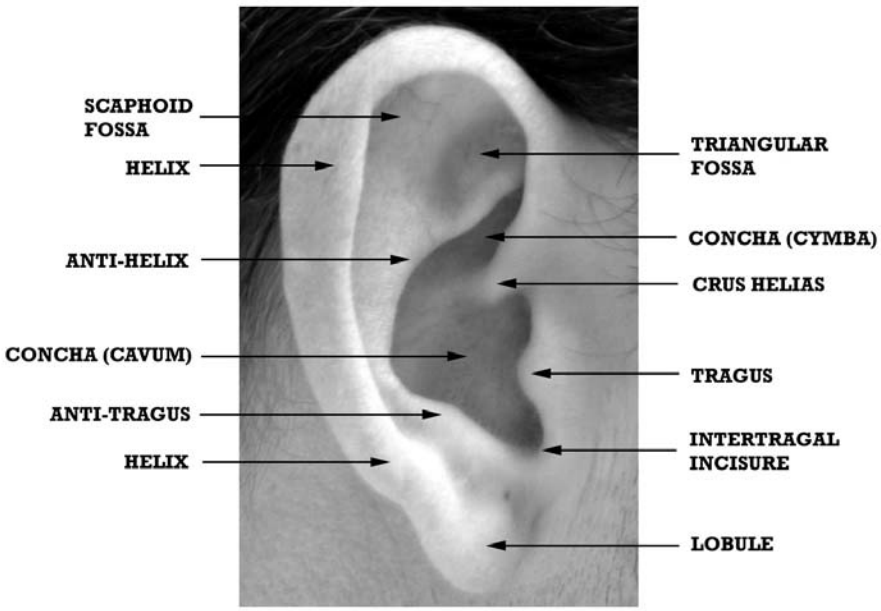

Figure 2.1 - Human outer ear showing the major components of the auricle and concha.

Korth 1980; MacPhee 1981; MacPhee and Cartmill 1986; Wible 1986; Wilkens *et al*. 1999). The following sections present an overview of basic auditory anatomy with a special focus on diversity in primates.

Outer Ear

The **outer ear** is unique to mammals and three primary sections are recognized, the pinna flange, concha, and external auditory meatus, although the transition between these sections may not be as easily distinguished in other mammals as in the human ear (Shaw 1974). In humans, the *pinna flange* or auricle includes the helix, tragus and lobule in addition to several other folds and fossae (Figure 2.1). According to Schultz (1969), a "true" ear lobe is not present in orangutans, gibbons, New World monkeys, or prosimians.

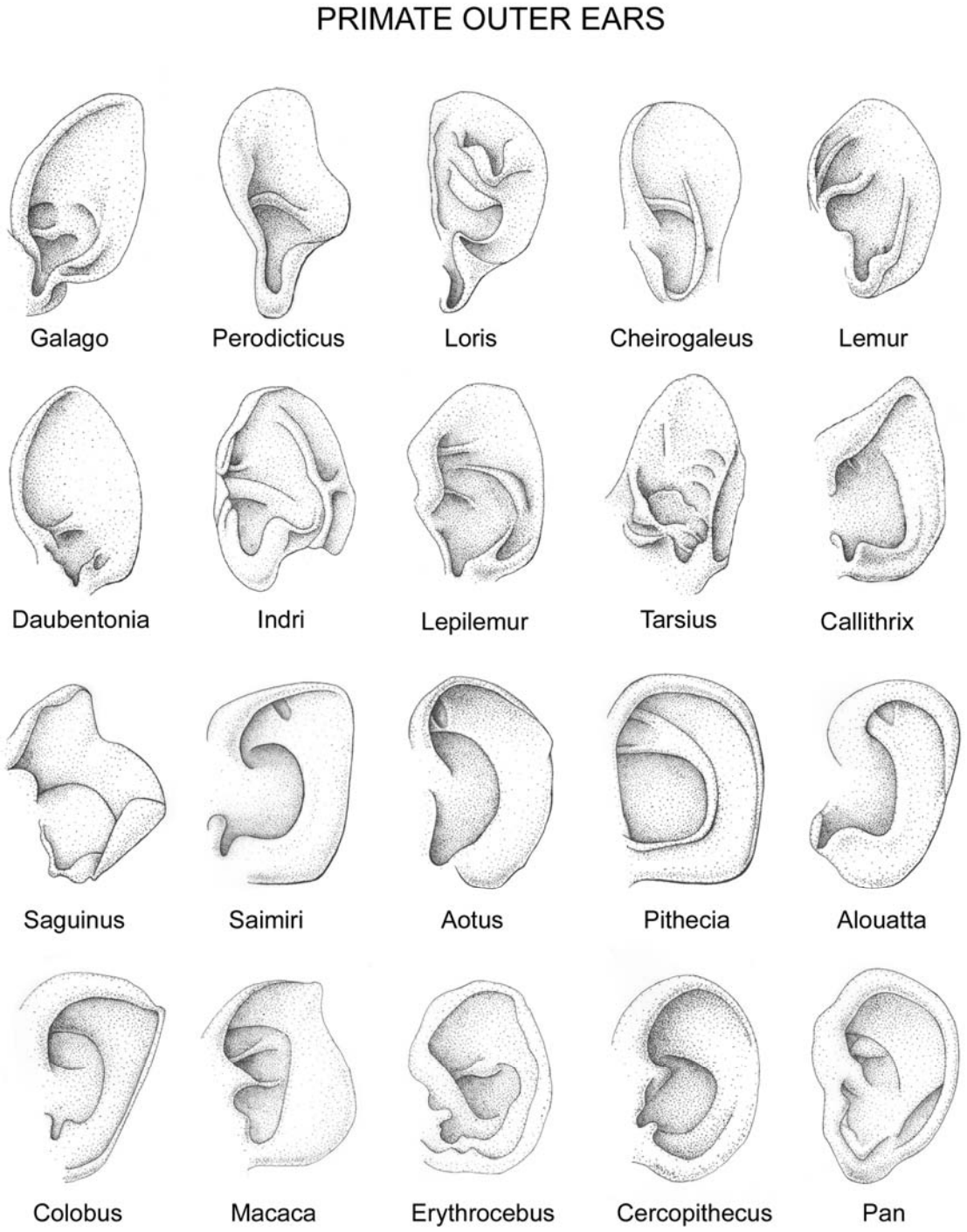

Figure 2.2 - Primate outer ears showing the differences in shape of various species. From Coleman and Ross (2004).

Primate pinnae (Figure 2.2) are highly variable in shape and size but can generally be classified into one of two major morphotypes. The first type (*e.g.*, tarsier) has an elongated auricular lamina (helix, antihelix, and scaphoid fossa) that is often ovate or conical in shape with a pointed or rounded tip. The second type (*e.g.*, chimpanzee) has a relatively shorter long axis resulting in a more subquadrate outline, and has an involuted helix which may act to increase the stiffness of the structure. Most prosimians resemble the first type while most anthropoids have the second type (Coleman and Ross 2004), although some primates show an intermediate form. For example, the helix of many baboons and macaques is involuted on the anterior and anterodorsal border only, leaving a pointed flange on the posterodorsal edge. Many callitrichids show a similar design and Hershkovitz noted that the callitrichid external ear is less complex than that of other platyrrhines and anthropoids but more complex than that of prosimians (1977). He also remarked that the ears of *Saimiri*, *Aotus*, and *Callicebus* resemble the callitrichid subtype more than that of other New World monkeys. Darwin envisaged a transition from the conical type to the more human-like type (1874) and consequently, the point formed in the intermediate types where the helix is not completed involuted is often referred to as a "Darwin's tubercle".

Schultz (1969; 1973) calculated an index[3] of ear size to head size for over 100 species of primates and found that the majority of prosimians have relatively larger ears than all anthropoids. Tarsiers (*Tarsius*) averaged a value of 50, indris (*Indri*) 53, galagos (*Galago*) 66, and the aye-aye (*Daubentonia*) had the largest relative ear size with a value

[3] The index expresses the product of pinna height times pinna width as a percentage of the product of head length times head height.

of 89. Only slow lorises (*Nycticebus*) and pottos (*Perodicticus*), with a value of 15, overlapped the anthropoid range. Old World monkeys had indices that range from 8 in proboscis monkeys up to 19 in patas monkeys. In contrast, the highest value for any ape was 17 in chimpanzees (*Pan*). Gibbons and siamangs (*Hylobates*) had the next largest ape ears with values of 13 and 8, respectively. Humans (*Homo*) had a diminutive value of 5, gorillas (*Gorilla*) even less with 4, and orangutans (*Pongo*) had the smallest ears of any primate with an index value of only 3. Although little is known about sexual dimorphism in pinna size, a 9% difference in the linear dimensions between male and female humans is common (Shaw 1974), roughly paralleling total body size dimorphism.

The *concha* can be subdivided into cavum and cymba sections although the concha is commonly included as part of the pinna *sensu stricto*, but is considered separately here because these two parts of the outer ear appear to have different functional qualities (see below). The *external auditory meatus* (EAM) is a sinuous tubular structure that provides a restricted entrance to the eardrum that presumably serves to help protect it from external injury (DuVerney 1683; Sinyor and Laszlo 1973). Extant primates have an EAM consisting of a bony part medially and a cartilaginous part laterally. In strepsirrhines and platyrrhines, the bony portion is comprised primarily by the ectotympanic and does not extend far beyond the lateral surface of the tympanic membrane. In catarrhines and *Tarsius* however, the ectotympanic is expanded into a U-shaped structure that is completed dorsally by the squamous temporal. Packer (1983) suggested that the bony meatal tube is an adaptation that reduces noise produced by the mandible during mastication but is replaced by cartilage in species where there is room

for the imposition of a substantial postglenoid process between the jaw joint and the meatus.

The development of the auricular musculature in primates follows similar phylogenetic lines as differences in the shape and size of the outer ear. Primates generally have three pairs of extrinsic auricular muscles (*attrahens auriculam***,** *retrahens auriculam*, and *attollens auriculam*) and six pairs of intrinsic auricular muscles (*helicis major, helicis minor, tragicus, antitragicus, transversus auriculae, obliquus auriculae*). There appears to be a gradual decrease in the development and differentiation of both the intrinsic and extrinsic musculature as one proceeds from prosimians to hominoids. For example, lemuroids and tarsiers have a well developed *retrahens auriculam* which consists of three muscular bellies, whereas in marmosets this muscle is apparently fully functional yet represented by only a single muscular belly (Lightoller 1934). The *transversus auriculae* and *obliquus auriculae* are also degenerated in callitrichids compared with the condition found in lemurs and tarsiers (Huber 1930). The auricular muscles of lorisoids have been less well studied, but they appear qualitatively similar to those of lemuroids, although considerable inter-specific differences occur (Burrows and Smith 2003). In contrast, the "higher platyrrhines" (*Aotus*, *Pithicia*, *Cebus*, *Alouatta*, and *Ateles*) and presumably other anthropoids as well, show less development of the muscles of the outer ear (Huber 1930). It has even been reported that the ears of orangutans are completely devoid of intrinsic muscles (Schultz 1969). Furthermore, at least some prosimians (although not tarsiers) retain the primitive marsupioplacental condition by possessing an additional extrinsic muscle named the *auriculo-mandibularis* (Lightoller 1934). The degree of movement of primate pinnae (Darwin 1874; Hill 1955; Schultz

1969; Charles-Dominique 1977; Hershkovitz 1977) seems to be generally correlated with the development and differentiation of the auricular muscular.

Middle Ear

The main structures that make up the **middle ear**, or *tympanum*, include the tympanic membrane, the ossicular chain (the three auditory ossicles, two intratympanic muscles, and numerous ligaments), the cochlear promontory, and the middle ear cavity itself. The *chorda tympani* (a branch of the facial nerve) and the internal carotid artery or one of its braches also commonly course through the middle ear region. The tympanum is separated from the EAM by the tympanic membrane, from the inner ear by the round and oval windows, and from the nasopharynx by the Eustachian tube which generally remains closed except during swallowing or yawning. The oval window (*fenestra ovalis*) opens into the vestibule of the inner ear while the round window (*fenestra rotunda*) communicates with the opening into the cochlea. Both pierce the internal wall of the tympanic cavity (*paries labyrinthica*), but are effectively closed by the stapedial footplate (see below) and the *secondary tympanic membrane*, respectively. Therefore, under normal conditions, the middle ear cavity is sealed off from the external environment except when the Eustachian tube is patent.

The middle ear cavity originates as an evagination of the endoderm of the pharynx called the first pharyngeal pouch. This becomes the *Eustachian tube* which expands distally to produce the tympanic cavity (*cavum tympani*). This expansion eventually meets with the first pharyngeal cleft, an invagination of the ectoderm on the side of the embryonic head that ultimately develops into the EAM. A thin film of

mesoderm persists between the endodermal and ectodermal linings with all three layers collectively constituting the tympanic membrane. The bony tympanic roof separates the tympanic cavity from the endocranium and is formed by the *tegmen tympani*, a dorsal outgrowth of the petrosal (MacPhee and Cartmill 1986). The floor of the tympanic cavity (auditory bulla) is unique in primates in that it is composed almost exclusively by the petrosal element of the temporal. The advantage of having a middle ear with an ossified floor is that it prevents adjacent soft tissue structures from applying pressure to the lining of the cavities during mastication, swallowing, and head movements which could alter their acoustic properties (see below) (Henson 1974).

The tympanic cavity can be divided into two parts, the tympanic cavity proper and the epitympanic recess which is a small alcove positioned dorsal and just medial to the tympanic membrane. The epitympanic recess often communicates posteriorly, via the *foramen pneumaticum*, with an extensive network of pneumatized regions collectively termed the epitympanic sinus (Hunt and Korth 1980). This sinus can constitute up to five distinct major air cell groups. Three of these, the dorsal squamosal, postglenoid (including the zygomatic arch), and the occipital groups are confined within the squamosal. The other two, ventral and lateral mastoid air cells, occur in the mastoid.

Among primates, there is considerable diversity in the development of the epitympanic sinus although in many cases the degree of expression follows phylogenetic patterns. Most Malagasy primates appear to be devoid of any cellular pneumatization in either the mastoid or squamosal portions of the temporal bone. *Allocebus trichtis* presents one exception to this trend among extant lemurs by displaying development of the epitympanic sinus in both the mastoid and squamosal in a pattern similar to that seen

in lorisiforms (Major 1899; Petter-Rousseaux and Petter 1967), while other cheirogaleids have a smaller, less developed sinus in this position (Cartmill 1975). *Lepilemur* and *Daubentonia* are also reported to show significant development of the epitympanic sinus (Saban 1975). *Tarsius* aligns itself with the majority of lemuroids in the absence of an identifiable epitympanic sinus (MacPhee and Cartmill 1986). On the other hand, all Old and New World monkeys appear to develop substantial sinuses, but the exact contribution of individual air cell groups remains poorly documented. Within hominoids, pneumatization is limited primarily to the mastoid in humans but infiltrates most regions of the temporal in chimpanzees and gorillas (Sherwood 1999). Sherwood (1999) found there to be only minimal variation in the areas which become pneumatized in the African apes compared with the high variability expressed in humans.

The anteromedial portion of the tympanic cavity is sometimes partitioned off by a septum to produce an additional cavity called the hypotympanic sinus (van der Klaauw 1931). In haplorhines, this space originates as a diverticulum of the Eustachian tube and is referred to as the *anterior accessory cavity* (AAC) (MacPhee and Cartmill 1986). The opening that connects the AAC to the tympanic cavity proper is called the *apical aperture*. In anthropoids, the AAC is filled with trabecular bone while tarsiers are distinctive in that they completely lack cellules in this location. Lorisoids possess a hypotympanic sinus that occupies essentially the same position as the AAC but is referred to instead as the *medial accessory cavity* (MAC) (MacPhee 1981). This distinction is warranted since the MAC begins as a diverticulum of the epitympanic recess called the supracochlear duct. In other words, the AAC and MAC are non-homologous structures. No matter how complicated the arrangement of diverticuli, all

related spaces and the structures contained within them are lined by an epithelium continuous with the mucosal lining of the tympanic cavity.

The eardrum or **tympanic membrane** (*membrana tympani*) is attached along the majority of its perimeter to the C-shaped ectotympanic ring, either on the inner border of the *sulcus tymapnicus* or along the medial crest of this sulcus (*crista tympanica*). In nearly all lemuroids (except *Allocebus*), the ectotympanic ring is suspended within the tympanic cavity with only the crural tips being fused to the roof of the tympanic cavity (actually the anterior crus is in contact with but not fused in most specimens). The non-articulated central arc of the tympanic ring retains a connection to the petrosal (lateral bullar wall) by a cartilaginous annular membrane that is continuous with the EAM. In all other extant primates, the entire ectotympanic is more or less fused to the lateral bullar wall (petrosal and squamosal) in variable positions (Hershkovitz 1974; MacPhee 1977).

The center of the tympanic membrane is drawn medially to give the membrane an overall conical shape with the apex being called the *umbo*. As previously mentioned, the membrane is composed of three primary layers and the middle fibrous layer consists of two groups of fibers (radial and circular) that give the eardrum its structural stability (Dallos 1973). These fibers result in the majority of the membrane being taut and consequently named the *pars tensa*. However, many mammals also exhibit a loose component of the tympanic membrane called the *pars flaccida* (of Shrapnell) in the region between the two crura of the ectotympanic (the *notch of Rivinus*). The *pars flaccida* lacks radial and circular fibers and is roughly triangular in shape with the apex at the short process of the malleus and the base at the *notch of Rivinus*. The presence of a

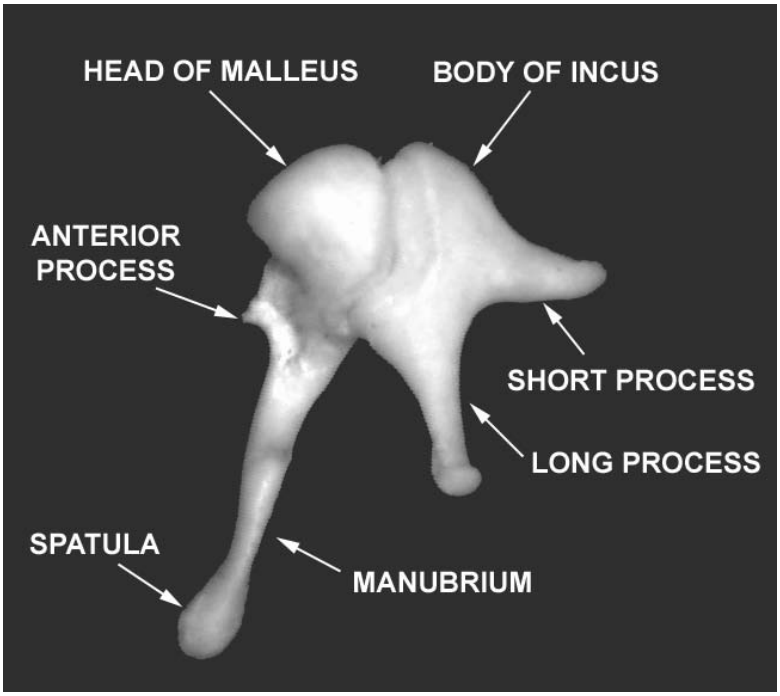

Figure 2.3 - Basic structures of the malleus and incus (*Varecia variegata* pictured here).

pars flaccida portion remains poorly documented in primates and may be completely absent in those taxa lacking a short process of the malleus (see below).

The **malleus** occupies a lateral position in the ossicular chain and consists of a head, manubrium, and several processes (Figure 2.3). The head (*capitulum mallei*) is an expanded and rounded extremity of the malleus that articulates with the incus. The articular surface is generally divided into a pair of medial and lateral facets that are separated by a small ridge. The delicate superior ligament of the malleus connects the head to the roof of the epitympanic recess. The manubrium (*manubrium mallei*) is embedded in the *pars tensa* of the tympanic membrane along the superior radius, with its spoon-shaped apex (*spatula mallei*) attached to the *umbo*. All catarrhines and some prosimians also possess a constricted area of the manubrium between the head and lateral

process referred to as the neck (*collum mallei*). The neck is undefined in nearly all platyrrhines except for a few species of *Callithrix* which also illustrate a well developed *orbicular apophysis*, a spherical protuberance on the posterior side of the manubrium that is rare in primates but common among marsupials, insectivores, bats, rodents, and carnivores (Hershkovitz 1977).

An anterior process is found in all primates and extends anteriorly from the inferior angle of the head. It provides attachment for the anterior ligament which continues rostrally to connect to the petrotympanic fissure. The lateral or short process (*processus brevis*), on the other hand, is absent in platyrrhines but well developed in prosimians and catarrhines, reaching its maximum development in hominoids (Hershkovitz 1977). This blunt process projects from the root of the manubrium to attach on and often project into the upper part of the tympanic membrane, forming the *prominentia mallearis*. Many primates (except most hylobatids and humans) also have a muscular process for attachment of the tensor tympani muscle which manifests as a short tubercle situated about midway along the manubrium.

The intermediately positioned ossicle, the **incus,** resembles a bicuspid tooth with double roots (Helmholtz 1885), and consists of a body and two processes (Figure 2.3). The body (*corpus incudis*) bears medial and lateral facets for articulation with the malleus. Although this connection has been described as having a V shape, with the incus forming the wedge and the malleus having the notch (Fleischer 1978), in truth the articular surfaces are quite complex in shape and are more accurately described as a double saddle (Wever and Lawrence 1954). The incudomalleolar joint (*articulatio incudomallearis*) formed by this junction appears to be of the synovial type in the few

primates that have been examined (Hinchcliffe and Pye 1969). Although this joint was traditionally considered to be essentially immobile (Dallos 1973; Fleischer 1978; Møller 1974; Moore 1981), recent research suggests that the incudomalleolar joint is actually "mobile" allowing considerable movement between the bones, even at moderate intensity levels (Marquet 1981; Hüttenbrink 1988; Willi *et al*. 2002; Nakajima *et al*. 2004).

The two processes of the incus diverge from each other at approximately right angles and differ in shape and function as much as length. The short process (*crus breve*) is conical in shape and is attached to the *fossa incudis* on the lower posterior wall of the epitympanic recess by the posterior incudal ligament. The long process (*crus longum*) is generally slightly longer with an overall slender profile and terminates in a rounded globular projection, the lenticular process (*processus lenticularis* or *os orbiculare*), which articulates with the head of the stapes in a ball and socket-like joint. The long process may be grooved along its length by the *sulcus incudis* and its orientation is roughly parallel to the manubrium of the malleus. The junction with the stapes, the incudostapedial joint, also appears to be of the synovial variety in primates (Hinchcliffe and Pye 1969), but has been found to be fibrous in other mammals with increased high frequency sensitivity such as the bat (Moore 1981; Lombard and Hetherington 1993).

The **stapes** is the most medially positioned of the ossicles, and is comprised by a head, neck, two crura, and a footplate. As previously stated, the head (*caput stapedis*) articulates with the incus laterally and is constricted medially to form a neck. The crura (*crus anterius*, *crus posterius*), which are normally hollow, diverge from the neck and connect at their medial extremities to the oval-shaped footplate (*basis stapedis*). The divergence of the crura produces the intercrural (obturator) foramen which may

occasionally be filled with a thin lamina of bone on its dorsal aspect in those species not possessing a stapedial artery as an adult. The circumference of the footplate is affixed to the medial rim of the fenestra vestibuli by the annular ligament, which is essentially a belt of radially running fibers. Although the stapedovestibular joint is generally fibrous in most mammals, Hinchcliffe and Pye (1969) reported that *Callithrix geoffroyi* instead has a synovial joint at this junction. Moore (1981) states that the anterior fibers of the annular ligament are generally longer and thinner than those situated posteriorly. Until recently, the exact plane of movement was poorly understood and it was thought that the stapes vibrates in a piston-like fashion (Høgmoen and Gandersen 1977). However, recent research on humans has shown that above about 1 or 2 kHz, the movement becomes more complex with increasing anterior-posterior "rocking" motions (Heiland *et al*. 1999; Hato *et al*. 2003). Nevertheless, as long as the force exerted by the incus is predominately in line with the axis of the stapes, the total volume displacement of the footplate will be the same regardless of the actual plane of movement (Wever and Lawrence 1954).

The two middle ear muscles are of the striated-pennate type which allow for the production of great tension with minimal displacement (Dallos 1973). The **tensor tympani** muscle is usually the larger of the two and lies in a bony sulcus just above the canal for the auditory tube. It terminates in a tendon that makes a sharp bend before inserting on the malleus. Contraction of the tensor tympani pulls the malleus medially, perpendicular to the axis of rotation of the malleus-incus complex, thus suppressing rotation (Fleischer 1978). Because this direction is also perpendicular to the tympanic membrane, another result is to increase the tension of the membrane. The **stapedius** muscle attaches to the neck of the stapes and in anthropoids and strepsirrhines arises from

a groove or canal in the posterior wall of the tympanum while in tarsiers and tree shrews the muscle takes origin outside of the tympanic cavity on the side of the skull (MacPhee 1981). This muscle pulls the stapes parallel to the long axis of the footplate forcing one side into the vestibule and the other side laterally, increasing the tension of the annular ligament. Contraction of both muscles results in a stiffening of the entire ossicular chain (Dallos 1973) which may have the result of decreasing sensitivity to low-frequencies while providing a slight increase (< 10 dB) at the mid-frequency range and even less at higher frequencies.

Inner Ear

The **inner ear** is found within the petrous portion of the temporal bone and is comprised by a series of fluid-filled bony canals (bony labyrinth) and membranous ducts (membranous labyrinth). The central cavity of the *bony labyrinth* is the vestibule which communicates with the middle ear at the oval window and is flanked posteriorly by the semicircular canals and anteriorly by the small spiral-shaped cochlea. The *membranous labyrinth* is made up by the cochlear duct (spiral canal), the semi-circular ducts, the utricle, and the saccule. Since, the structures related to hearing are confined to the cochlea, the following descriptions will be limited to this region.

The mammalian cochlea is distinguished by its spiral configuration which winds around a central pillar of cancellous bone called the *modiolus*. The coiling of the cochlea minimizes space (West 1985) and apparently creates favorable conditions for the pressure waves that travel through it (Wysocki 2001). The number of turns ranges from1.5 to 4.5 in mammals, with primates generally falling in the middle of this range (macaques ≈ 2.5

– 2.75, humans and marmosets ≈ 2.75, baboons ≈ 2.75 – 3.25) (Hill 1970; Nadol 1988; West 1985). The size of the cochlea shows only a loose relationship with the overall size of the individual (Wysocki 2001).

The cochlea is divided internally by the membranous cochlear duct to form three compartments: the *scala tympani*, which follows the outer contours of the cochlea; the *scala vestibuli*, which follows the inner contours; and the *scala media* which constitutes the space within the cochlear duct itself (Figure 2.4). The scala tympani and the scala vestibuli are connected just beyond the end of the cochlear duct by an aperture called the *helicotrema* and are filled with perilymph. The geometry of the perilymphatic space of the cochlea is characterized by alternating dominance in the dimensions of the scala vestibuli and the scala tympani. The reversal of dominance takes place on average

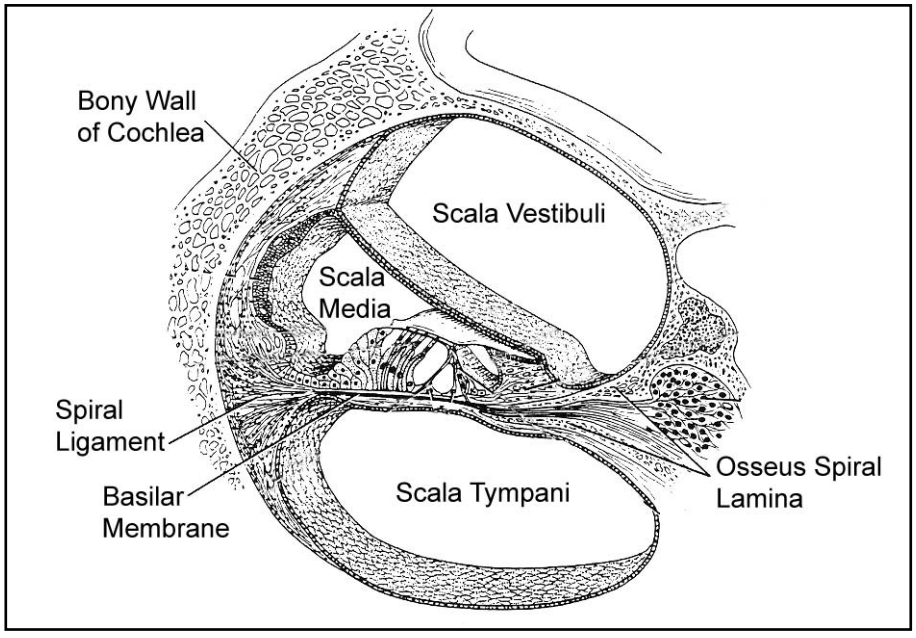

Figure 2.4 - Internal view of cochlea. Modified from Bloom and Fawcett (1975).

three to four times, roughly equivalent to the number of turns of the cochlea (Wysocki 2001). The *scala media* is continuous with the saccule via the *ductus reuniens* and is filled with endolymph as are all spaces of the membranous labyrinth.

The cochlear duct is roughly triangular in cross-section with the medial edge anchored to a thin crest of bone projecting laterally from the modiolus called the osseus spiral lamina and the lateral wall affixed to the spiral ligament lining the bony cochlea. The walls of the cochlear duct are comprised of three histologically distinct epithelial membranes. The roof is formed by the vestibular (Reissner's) membrane, the floor by the basilar membrane, and the lateral wall by the stria vascularis (which produces endolymph). The basilar membrane increases in width but decreases in thickness from the base to the apex of the cochlea and in humans it is approximately 1 μm wide at the basal end and 5 μm wide at the far end with a total length of 35 mm (Nadol 1988).

Projecting into the scala media and intimately applied to the floor of the basilar membrane is an epithelial ridge called the **spiral organ of Corti**. This “organ” is comprised of a specialized series of columnar cells referred to as cochlear hair cells because their apical surfaces are capped with bundles of 30-120 stereocilia. The tips of individual stereocilia are joined to their next tallest neighbor by thin filaments dubbed tip-links. The organ of Corti has one row of inner ‘hair cells’ situated close to the osseus spiral lamina and three rows of outer ‘hair cells’ located more peripherally, all of which extend in longitudinal rows along the greater part of the cochlear duct. The number of inner hair cells varies depending on the length of the basilar membrane. Humans have approximately 3500 per ear but the mouse cochlea (*Mus musculus*), with a basilar membrane measuring 6.8 mm, possesses only 765 (Ehret and Frankenreiter 1977). The

number and length of stereocilia on each inner hair cell increase from the base to the apex of the cochlea. The outer hair cells are much more numerous than the inner hair cells (approximately 12,000 per cochlea in humans), yet their total number is also governed by the size of the cochlea. The number and length of the outer hair cell stereocilia also change with longitudinal location. There are fewer but longer cilia at the apex compared with those at the base. Situated above both the inner and outer hair cells is an acellular flap called the tectorial membrane. The lateral region of the tectorial membrane (referred to separately as Hardesty's membrane) attaches directly to the tallest stereocilia of the outer hair cells while the medial region (Henson's stripe) simply overlays the inner hair cells, leaving their stereocilia freestanding (Lim 1986).

In addition to the cochlear hair cells being differentiated by their topological organization and physical characteristics, they can be further distinguished by their pattern of innervation. The cell bodies of the auditory neurons are found in the spiral ganglion which is housed in a bony cavity (Rosenthal's canal) running between the modiolus and osseus spiral lamina. The dendrites of these neurons travel through radial canals in the osseus spiral lamina and emerge through small foramina called *habenula perforata*. The axons for these neurons leave the medial edge of Rosenthal's canal to travel through the center of the modiolus, eventually emerging from the cochlea to coalesce into the auditory component of the vestibulocochlear nerve (CN VIII). Each inner hair cell is innervated by approximately 10 spiral ganglion cells but several outer hair cells are innervated by a single spiral ganglion cell. Therefore, even though the outer hair cells are more numerous than the inner hair cells, they receive only about 10% of the afferent innervation. However, the outer hair cells are unique in that they also receive

efferent innervation originating from the superior olivary complex within the auditory brainstem (Warr 1992).

SECTION II: AUDITORY FUNCTION

Once the major structures of the ear had been unveiled, the first models of the sounds transmission were developed (*e.g.*, Coiter 1573). The most perceptive ideas were presented by Joseph Guichard DuVerney in a book titled *Traité de l'organe de l'ouie* (1683). DuVerney envisioned the outer ear as a trumpet-like structure that collects and amplifies sound waves as it directs them towards the primary receiver, the tympanic membrane. He thought the tympanic membrane to be tuned by the actions of the intra-tympanic muscles so that it can be tensed for the reception of high-frequency sounds and slackened for the reception of low-frequency sounds. Once the membrane is set into motion, these vibrations are transferred to the malleus, which in turn moves the incus, which ultimately results in the stapes communicating the oscillations to the cochlea. Although DuVerney, like all of his contemporaries, thought that the inner ear was filled with air, he realized that the tapered nature of the bony spiral lamina (and the basilar membrane which he considered a support for the thin edge of the bony spiral lamina) caused it to be differentially tuned to a range of frequencies.

We now know that many of DuVerney's basic conceptions were correct. Research in the twentieth century revealed that the acoustic gain afforded by the human outer ear

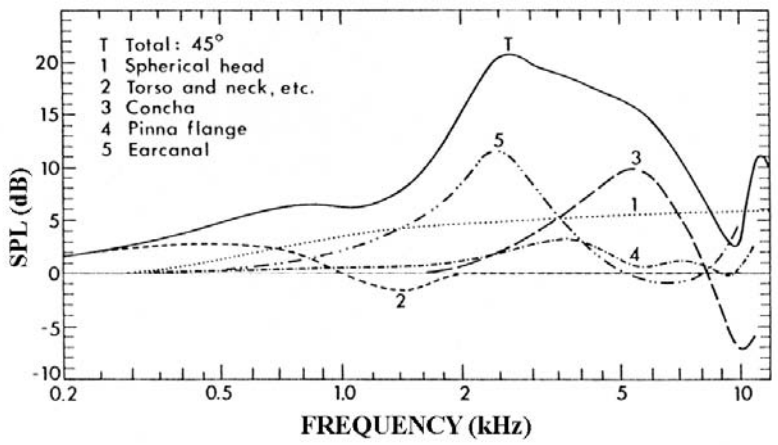

Figure 2.5 - Contribution of individual components to the total transformation of sound from the free-field to the eardrum at an angle of 45°. Modified from Shaw 1974a.

can be as much as 20 dB[4] SPL, centered around 3 kHz (Wiener and Ross 1946). Figure 2.5 shows that the external auditory meatus contributes up to 15 dB to this increase (at 2.7 kHz), the concha adds just over 10 dB (between 4 and 5 kHz), and the pinna flange, head and torso impart an overall gain of around 5 dB (Shaw 1974a, 1997). Similar pressure gains from the outer ear have been found in cats (Wiener *et al*. 1966), chinchillas (von Bismark and Pfeiffer 1967), model rabbit ears (Fattu 1969), guinea pigs (Sinyor and Laszlo 1973), and ferrets (Carlile 1990). Even higher levels of gain were reported for wallabies (Coles and Guppy 1986) and bats (Guppy and Coles 1988). In addition to amplification, the outer ear aids in localizing the position of a sound source. It is now well established that the many folds and crevices of the outer ear (Figure 2.1) produce unique spectral cues as a function of frequency and angle of incidence that are used in localization (Shaw 1974a, 1974b; Shaw and Teranishi 1967; Teranishi and Shaw 1968; Batteau 1967; Fisher and Freedman 1968; Blauert 1969; Gatehouse and

[4] A decibel (dB) is the logarithmic unit of measure for sound pressure level (SPL), usually based on the standard reference level of 0.0002 dynes per centimeter^2.

Oesterreich 1972; Navarro 1972; Gardner 1973; Bulter 1975; Kuhn 1979; Brown 1982; Butler 1986, 1987; Butler and Belendiuk 1977; Middlebrooks *et al*. 1989; Rice *et al*. 1992).

The transmission of vibrations through the middle ear is essentially as DuVerney had proposed although we now know that the motions of the malleus and incus are not as simple as once believed. The traditional view held that the malleus and incus rotate as a unit about an axis that runs through the anterior process of the malleus and the short process of the incus (Dahmann 1929; Bárnáy 1938; Wever and Lawrence 1954; Békésy 1960; Møller 1974), propelling the stapes in a predominately piston-like fashion at the oval window (Guinan and Peake 1967; Høgmoen and Gandersen 1977). However, as mentioned previously, the coupling between the malleus and incus in humans is generally not fixed, allowing relative motions between the bones, and the stapes moves like a piston only at lower frequencies (Marquet 1981; Hüttenbrink 1988; Heiland *et al.* 1999; Willi *et al*. 2002; Hato *et al*. 2003; Nakajima *et al*. 2004). Furthermore, recent studies have shown that the rotational axis is not fixed and varies considerably with frequency (Decraemer *et al*. 1991; Decraemer and Khanna 1995, 2004; Kelly and Prendergast 2001). Therefore, the traditional axis of rotation can be considered only a rough first approximation.

Although the middle ear muscles (tensor tympani and stapedius) do not appear to actively "tune" the tympanic membrane as suggested by DuVerney, the "acoustic reflex" has been shown to selectively attenuate loud external and internal sounds (> 70 dB) (Möller 1974; Borg *et al*. 1984; Rodriguez and Gerhardt 1988; Gelfand 1998). The total attenuation can be as much as 20 dB for low frequency sounds (Borg *et al*. 1984), but

there is a general decrease in attenuation with increasing frequency and very little reduction above 2 kHz for most animals (Möller 1984). However, in animals with “stiffer middle ears” such as bats, the middle ear muscles can become activated in response to stimuli as high as 80 kHz (Rosowski 1994).

The pressure waves created by the stapes travel from the vestibule into the spiral-shaped cochlea resulting in the displacement of the basilar membrane in a pattern that has been described as a “traveling wave" (Békésy1960). This traveling wave originates at the base and moves towards the apical end of the basilar membrane exhibiting a peak displacement at a specific location determined by the frequency of the stimulus (Turner and Muraski 1981). The frequency tuning of the basilar membrane is related to the tapered nature of the bony spiral lamina, as put forward by DuVernry, but in a manner different than he envisaged. This passive tuning is due to the fact that the basilar membrane increases in width but decreases in thickness from the base to the apex, producing a stiffness gradient on the order of 10^3 in humans (Békésy 1960). Movements of the basilar membrane (and the attached organ of Corti) cause displacement of the stereocilia of the inner hair cells at their apical ends which initiates an electrical potential at their basal ends. This electrical potential causes a chemical discharge that results in an electrical potential in CN VIII, relaying these neurological impulses to neurons located in the cochlear nuclei of the auditory brainstem.

Once it was discovered that the inner ear is filled with fluid (Cotugno 1760; Meckel 1777), it was realized that there will be an impedance mismatch between the lower acoustic resistance of air (41.5 dynes sec/cm^3) compared to the much higher acoustic resistance of cochlear fluid (≈ 11,200 dynes sec/cm^3) (Zwislocki 1975). Thus, it

was proposed that the ear (primarily the middle ear) acts as a mechano-acoustic transformer that helps to minimize this impedance mismatch by increasing the pressure presented at the oval window over that occurring at the eardrum. The first mechanical principles to be applied to this problem were offered by the next great luminary of auditory science, Hermann L. F. Helmholtz, in a book titled *On the Sensations of Tone* (1863). Helmholtz proposed three processes that could be responsible for increasing the pressure of the signal: 1) the conical lever action of the tympanic membrane; 2) the lever action of the malleus-incus complex; and 3) a hydraulic action that results from the smaller surface area of the stapedial footplate compared to that of the tympanic membrane.

The tympanic membrane as a conical lever hypothesis. Helmholtz believed that a catenary principle was at work with the tympanic membrane due to its unusual shape. He realized that the interaction of the circular and radial fibers of the middle layer of the eardrum causes its surface to curve slightly outward (convexly), despite the overall concave form that results from the umbo being drawn medially by its attachment to the spatula of the malleus. Therefore, vibrations of larger amplitude but smaller force occurring in the middle parts of the radial fibers will be transformed into movements of smaller amplitude but greater force at the ends of the radial fibers. Since one end of the radial fibers attach to the umbo, the forces acting on the malleus will be greater than those acting on the tympanic membrane itself.

However, experimental evidence from research by Békésy (1941) and Wever and Lawrence (1954) found no support for the conical lever hypothesis and were thought to largely invalidate the application of the catenary principle to the tympanic membrane.

Yet more recently, holographic experiments in cadaveric humans and cats have shown the displacement amplitude of the malleus to be smaller relative to the adjacent portions of the membrane, which agrees with expectations predicted by Helmholtz (Khanna 1970; Tonndorf and Khanna 1970, 1972, 1976; Khanna and Tonndorf 1972). Tonndorf and Khanna (1976) found this mechanism to provide a mechanical advantage of 2:1 in cats. Despite their findings, few other auditory scientists (if any) have embraced the conical lever hypothesis in studies investigating the transformer mechanism of the ear.

The ossicular lever hypothesis. The second means of impedance matching advocated by Helmholtz was the lever action provided by the uneven lengths of the manubrium of the malleus and the long process of the incus. The basic concept is relatively straightforward and proposes that the malleus and incus act as a simple first-class reducing lever with the manubrium of the malleus acting as the effort arm and the long process of the incus acting as the resistance arm (Helmholtz actually proposed a compound and simple lever model). One of the major difficulties in applying this model relates to determining the axis of rotation, which as previously discussed, varies with frequency. Various axes of rotation have been proposed but the most commonly used axis runs from the short process of the incus through the anterior process of the malleus, as suggested by Dahmann (1929) and Bárnáy (1938).

The effective lever arms are determined by measuring the perpendicular distances from the rotational axis to the point of operation of the force. Traditionally, the center of force acting on the tympanic membrane was considered to occur at the umbo. Thus, the mallear lever (effort) arm would extend to the tip of the manubrium while the incudal lever (resistance) arm would extend to the lenticular process. However, Khanna and

Tonndorf (1972) have suggested that because the manubrium is embedded in the tympanic membrane for almost its entire length, the force transferred to it will also be along its entire length. Therefore, each point along the manubrium will have an associated effort lever arm, substantially reducing the total effective lever arm. In cats, they calculated the effective lever arm ratio as providing a mechanical advantage of ≈ 1.15:1 compared with the "full length" value of ≈ 2.35 (Khanna and Tonndorf 1972; Tonndorf and Khanna 1976). The consequences of this supposition may be somewhat lessened by the fact that there is variation across mammals in the degree of attachment of the malleus to the tympanic membrane (Funnell and Laszlo 1982). In cats, the manubrium is firmly attached to the membrane as stated by Tonndorf and Khanna (1976) while in humans there is a strong attachment only at the umbo and the lateral process (Graham *et al*. 1978).

Determining the effective ossicular lever arm ratio may be further complicated because the movements of the malleus may include both translation and rotation (Decraemer *et al*. 1991), the linkage between the malleus and incus may begin to slip at moderately high intensities (Huttenbrink 1988, 1996; Willi *et al*. 2002; Nakajima *et al*. 2004), and the axis of rotation appears to change with frequency (Kelly and Prendergast 2001). In a study of ossicular motion using finite element modeling, Kelly and Prendergast (2001) found that the "instantaneous axis of rotation" changed across the frequency range and the resulting calculated lever ratio for humans rarely exceeded a value of 1 (although it was slightly higher than the traditional value of 1.3 just above 1 kHz). They took this to conclude that the function of the malleus and incus is not to

provide a lever advantage, but instead supported the idea of Huttenbrink (1996) that they act as a protective mechanism against high pressures (*i.e.*, loud sounds).

The areal convergence hypothesis. The areal convergence hypothesis is based on the principle that *pressure equals force per unit area*. Since the area of the tympanic membrane is larger than the area of the stapedial footplate, forces acting on the tympanic membrane will result in a pressure increase when transferred to the stapedial footplate, and this realization was not lost on Helmholtz. He concluded that this hydraulic-like principle (pneumatic lever) would produce a mechanical advantage in humans of between 15:1 to 20:1. In fact, recent research has revealed that the areal convergence ratio of a wide range of tetrapods is approximately 20:1 (Rosowski 1992; Rosowski and Graybeal 1991), although the values can vary from 14:1 to 60:1 among different taxa (Henson 1974).

The main problem in estimating the areal convergence ratio lies in determining the vibrational patterns of the tympanic membrane. Since the membrane is attached along its circumference to the tympanic ring, it is unlikely that the entire membrane will vibrate in response to auditory stimuli. Several studies have attempted to reveal the exact modes of tympanic membrane vibration but have often arrived at somewhat conflicting results. The most commonly cited of these are the experiments by Békésy (1941) which used a capacitive probe to measure extremely small vibratory amplitudes (10^{-5} mm). He found that for frequencies up to 2.4 kHz, the central portion of the membrane moved as a unit that rotated around a hinge located at the superior margin (following the rotational axis of the ossicles). The stiff central portion had an area that was around 65% the total area of the tympanic membrane which was taken as the "effective" area. Above 2.4 kHz, Békésy

found that “the conical portion of the eardrum loses its stiffness, and the manubrium in its motion lags behind the motion of the adjacent portion of the membrane” (1960:102). Wever and Lawrence arrived at a similar value for cats and concluded that the effective area was between 60 and 72% of the anatomical area (1954).

In contrast, the previously mentioned holographic experiments by Khanna and Tonndorf (1972) and Tonndorf and Khanna (1972) were interpreted to indicate that below 3 kHz, the vibratory pattern of the tympanic membrane is uniform and therefore the entire membrane contributes to displacement of the malleus (*i.e.*, the anatomical area is equivalent to the effective area). Above this frequency, the uniform pattern begins to breakup and grows continuously more complex as frequency increases. Above 4 kHz, they suggested that only the area immediately adjacent to the manubrium is effective in transmitting movements to the ossicular chain while the other portions of the tympanic membrane may act as an acoustical baffle (Tonndorf and Khanna 1970). The discrepancy between these two interpretations of tympanic membrane vibratory mode(s) has yet to be satisfactorily resolved.

The overall transformer ratio. After deriving estimates of the mechanical advantage provided by various structures (and ignoring the potential problems associated with each mechanism) it is possible to calculate the overall transformer ratio. Traditionally, two different transformer ratios have been utilized although they overlook the effects of the outer ear and the possible advantage afforded by the conical lever (curved membrane). The first of these is the pressure transformer ratio (PTR) which is a measure of the greatest degree of pressure attainable by the middle ear. The PTR can be

computed by multiplying the areal convergence ratio by the ossicular lever ratio, given by the formula:

(2.1) $$PTR = (A_d / A_s) * (L_m / L_i)$$

where A_d is the effective surface area of the tympanic membrane, A_s is the surface area of the footplate, L_m is the lever arm off the malleus, and L_i is the lever arm of the incus. This formula was initially in popular usage because of the view that the ear is essentially a pressure detector (Békésy 1960). However, since the transformer action does not increase hearing efficiency in direct proportion to an increase in pressure (Dallos 1973) and the widely held notion that the middle ear functions primarily as an impedance matching device, greater stress has been placed on the impedance transformer ratio (ITR). The ITR places more emphasis on the ossicular lever ratio than does the PTR[5] and is calculated by the formula:

(2.2) $$ITR = (A_s / A_d) * (L_i / L_m)^2$$

where the symbols are as stated above. Note that ITR = PTR * (L_i / L_m), and that since PTR and ITR are both dominated by the areal convergence ratio, PTR and ITR are inversely correlated.

The PTR and ITR are often called "ideal transformer ratios" (Dallos 1973) because they ignore the mechanical and acoustical characteristics of the outer, middle,

[5] Although it should be noted that the areal convergence ratio will still have the largest impact on the final transformer ratio values.

and inner ears themselves. Models that take the characteristics of the auditory system into account have been termed "peripheral filter" hypotheses (Rosowski 1994). All vibrating bodies have limitations placed on their movements related to their "mechanical impedance" which is controlled by three factors: mass, stiffness, and frictional resistance (Wever and Lawrence 1954). Multiplying the mass by the angular frequency ($2\pi f$) yields a quantity termed *mass reactance* which represents the inertial opposition of an object to changes in velocity. This value increases with mass and as a function of frequency. The *elastic reactance* is a measure of the opposition of an object to displacement (stiffness) and is derived by dividing the stiffness by the angular frequency. This term is also frequency dependent but in an inverse fashion: the higher the frequency the smaller the elastic reactance. The frictional resistance is not frequency-dependent but is simply proportional to friction, which results in a loss of energy from the dissipation of heat. At lower frequencies the impedance is dominated primarily by the elastic reactance while at higher frequencies the effects of mass reactance prevail (Møller 1974). The result is that the transmission of both high- and low-frequency sounds will be attenuated compared with mid-range frequencies. It has been proposed that it is only in the intermediate range where the two reactive components cancel each other out that the performance of the middle ear approaches that predicted by the "ideal transformer ratio" (Dallos 1973).

Measurements of the *actual* pressure gain imparted by the middle ear (middle ear transfer ratio) have provided support for the idea that the middle ear does not function as a frequency-independent ideal transformer. The middle ear transfer ratio is derived by measuring the pressure in the perilymph of the vestibule produced by controlled stimulation of the tympanic membrane. Figure 2.6 shows the functions obtained for cats,

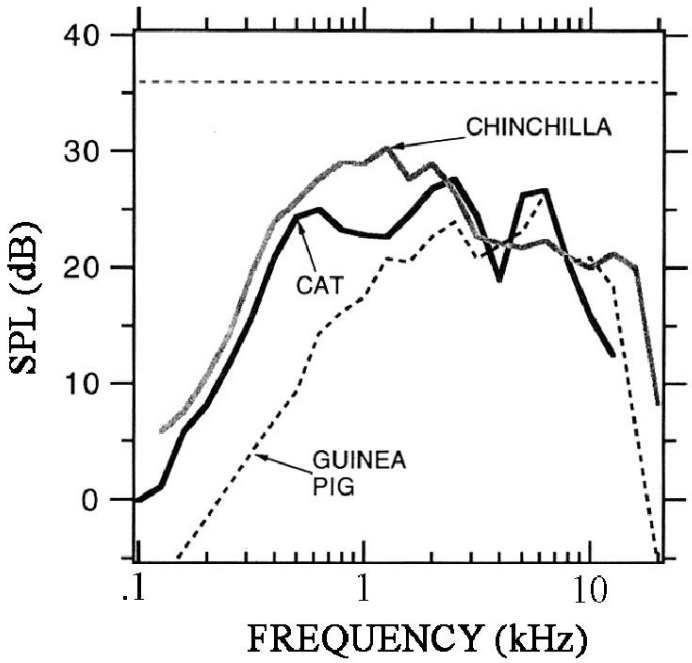

Figure 2.6 - Middle ear pressure transfer ratio for the cat, guinea pig and chinchilla. Dotted line represents the predicted transfer ratio (PTR) for the cat based on anatomical measurements. Modified from Rosowski 1994.

chinchillas, and guinea pigs (taken from Rosowski 1994). These functions demonstrate that in the mid-frequency range the middle ear produces a pressure gain of 25-30 dB, but that the maximum amplification is still at least 6 dB below that predicted by the "ideal transformer ratio" (dotted line). They also show that the pressure gain is substantially reduced at both lower and higher frequencies. All of these facts taken together indicate that the impedance matching function of the middle ear is both frequency-dependent and somewhat dampened when compared with ideal values predicted from anatomical measurements.

The overall similarity between the transformation functions of the outer and middle ears and hearing sensitivity curves (audiograms) has led several researchers to

propose that absolute auditory thresholds are largely controlled by the frequency-filtering properties of the outer and middle ears (Khanna and Tonndorf 1969; Dallos 1973; Fleischer 1973; Saunders and Summers 1982; Shaw and Stinson 1983; Rosowski *et al*. 1986, Relkin 1988; Rosowski 1991, Long 1994; Rosowski 1994; Dallos 1996; Zwislocki 2002). The conventional view states that the main components that contribute to the mass reactance are the ossicular chain and eardrum, while the majority of elastic resistance comes from the effective volume of the tympanic cavity, the stiffness of the eardrum, and the degree of fixation of the ossicles (Wever and Lawrence 1954; Dallos 1973; Fleischer 1978; Hunt and Korth 1980). The frictional resistance of the ear appears to be mostly confined to the cochlea (Möller 1974: Zwislocki 1975), suggesting that the rotation of the ossicles produces little friction. The lack of a significant frictional component in the middle ear seems partially explained by the finding that the center of mass of the malleus-incus complex by and large coincides with the traditional rotational axis and therefore moves very little with oscillations of the ossicles at most frequencies and intensities (Baranay 1936; Békésy 1960).

Often ignored, however, is the fact that the impedance of the cochlea is frequency-dependent at lower frequencies (Lynch *et al*. 1982). In fact, it had been proposed that the cochlea shapes both the upper and lower ends of the audiogram (Ruggero and Temchin 2002; Overstreet and Ruggero 2002). In truth, the ear is probably best described as "a cascade of interdependent acoustical and mechanical processes" (Rosowski 1994) which collectively modify an acoustic signal during its course from the free-field to the auditory nerve. Specializations for a particular hearing pattern (*e.g*., heightened low-frequency sensitivity) are likely to be reflected in all three regions of the

ear (Manley 1971, 1972; Kermack and Musset 1983). Furthermore, "while the inner and middle ear are co-specialized for certain ranges of hearing, you can learn a lot about the range of hearing by looking at one, the other or both" (pers. comm. Rosowski 2002).

Some of the best examples of how the different regions of the ear appear to be "co-specialized" to specific hearing patterns are found among the Old and New World desert rodents. Measures of hearing sensitivity have been evaluated in numerous species of both heteromyid and gerbilline rodents (Lay 1972; Webster and Strother 1972; Webster and Webster 1972; Ryan 1976; Heffner and Masterson 1980) and many of these species show unusually good low-frequency sensitivity for animals of their size. This is at least partly related to the freely mobile ossicular system found in all heteromyids and many of the gerbilline rodents (Oaks 1967; Webster and Webster 1975), in contrast to the tightly-bound "micro-type" ossicular system common to most rodents (Fleischer 1978) which is correlated with relatively poor low-frequency sensitivity (Rosowski 1992). The intra-family differences in desert rodent hearing also show strong correlations with other aspects of ear morphology. For example, the species with the greatest low-frequency sensitivity (*e.g.*, *Microdipodops* and *Pachyuromys*) have extremely large middle ear cavity volumes and tympanic membrane areas as well as large ossicular lever ratios and areal convergence ratios. In addition, these species show modifications in the cochlea by having short but relatively wide basilar membranes with prominent concentrations of hyaline material within the zona pectinata[6] (Lay 1972; Webster and Webster 1977). Curiously, members of both rodent families appear to have relatively small pinna compared with the inflated size of their auditory bulla (Pavlinov and Rogovin 2000).

[6] The zona pectinata is the space between the hair cells and the spiral ligament.

Numerous studies have investigated the relationship between individual structures and aspects of hearing sensitivity although the results have been varied. One of the more commonly examined auditory parameters is the area of middle ear structures (tympanic membrane and stapedial footplate). In general, the larger the middle ear areas, the better the low-frequency sensitivity and the smaller the middle ear areas, the better the high-frequency sensitivity. Rosowski and Graybeal (1991) and Rosowski (1992) found significant correlations ($p < 0.001$) between tympanic membrane area and low-frequency limit ($r^2 = 0.43$), high frequency limit ($r^2 = 0.56$), and the frequency of best sensitivity ($r^2 = 0.76$) in a sample of around 20 mammalian species. Similar relationships were found when comparing stapedial footplate area, except that the frequency of best sensitivity explained the least amount of variance ($r^2 = 0.32$), followed by low-frequency limit ($r^2 = 0.67$) and high frequency limit ($r^2 = 0.68$). No correlations were found between middle ear areas (or the areal convergence ratio) and threshold values (*e.g.*, threshold of the best frequency), which is counter to expectations based on the ideal transformer models (Rosowski and Graybeal 1991; Rosowski 1992).

However, Khanna and Tonndorf (1978) did find a relationship between tympanic membrane area and threshold of the best frequency in a small sample of mammals ($n = 7$) ranging from rats to humans. In contrast, Heffner (1983) determined the audiograms in five breeds of dogs and found no apparent patterns between animal size (and presumably auditory structure size) and low-frequency sensitivity, high-frequency sensitivity, or best sensitivity (frequency or threshold). The breed with the best overall sensitivity and low-frequency sensitivity was the mid-sized poodle, while the largest and smallest breeds (Saint Bernards and Chihuahuas) had very similar thresholds at most frequencies.

Although, eardrum size was not measured in the poodle, the St. Bernard had a membrane area nearly twice as large as the Chihuahua, leading Heffner to propose that there is no correlation among dogs between tympanic membrane size and hearing sensitivity (1983).

One of the most conspicuous differences between the middle ear morphology of birds and reptiles compared with mammals is the one-bone versus three-bone ossicular system. Since mammals have a greatly expanded audible range compared with other vertebrates and are the only group to perceive frequencies above about 12 kHz (Fay 1988), the middle ear bones have figured prominently in theories explaining differences in auditory sensitivity (Masterson *et al* 1969; Fleischer 1973). Yet, only a few studies have actually demonstrated the functional consequences of qualitative and quantitative differences in the ossicular system.

The most obvious aspect of ossicular morphology that should theoretically result in differences in sensitivity is the lever arm ratio. Although the aforementioned research on desert rodents is suggestive of such a pattern, since the species with the larger lever and areal ratios had the best low-frequency hearing, it is difficult to disentangle their influence from that of other low-frequency adaptations (*e.g.*, increased bullar volume). On the other hand, sensitivity (measured using cochlear potentials) in the middle-frequency range (1-4 kHz) of four species of gerbilline rodents (*Tatera indica*, *Gerbillus pyramidum*, *Meriones crassus*, *Pachyuromys duprasi*), does generally follow the predicted pattern of larger lever ratios being associated with better hearing (data taken from Lay 1972). However, this pattern can be obscured by differences in the larger areal convergence ratio since the areal convergence ratio varies between 20 and 40 while the ossicular lever ratio varies by only 2 or 3. Obviously, more conclusive evidence is needed

before lever arm and areal convergence ratios can be used as direct proxies of hearing efficiency.

Another aspect of the middle ear bones that has factored into hearing sensitivity is the stiffness of the ossicular chain which is governed by the degree of rigid attachment to the surrounding bones. Fleischer (1973, 1978) proposed that mammals can be classified into three basic middle-ear types based upon their degree of torsional stiffness. The first type is called the "microtype" and is characterized by having a malleus that is fused to the tympanic bone, via the gonial process, resulting in high torsional stiffness. The manubrium is parallel to the rotational axis and is separated from the articular surface (for the incus) by a "transversal part" that is roughly perpendicular to the manubrium. There is often an additional bony mass called the orbicular apophysis found at the junction between the manubrium and the transversal part. In this type the incus is very small in comparison to the size of the malleus. Due to the small size of the incus and the additional mass of the orbicular apophysis, the center of mass[7] for the malleus-incus complex is off-set in relation to the axis of rotation. The microtype is thought to be similar to the "ancestral type" but is restricted to small mammals such as bats, shrews, and many rodents (Fleischer 1978). Although Fleischer did not consider any primates as possessing a microtype middle ear, the presence of an orbicular apophysis was reported by Hershkovitz for several species of *Callithrix* (although absent in other species of this genus) and possibly (although rudimentary) in some pithecines (1977).

At the other end of the stiffness spectrum is the "freely mobile" type which has a low torsional stiffness due to the lack of fusion between malleus and tympanic. In this

[7] It should be noted that the actual center of mass for any middle ear type has been determined for only a few species.

type, the malleus is supported by its attachment to the tympanic membrane and the incus, but the only attachment to the tympanic is via the anterior ligament which arises from the anterior process. The freely mobile type is also distinguished by the fact that the manubrium is perpendicular to the rotational axis, the transversal portion is absent although there is a well developed mallear head, and the incus is enlarged (relative to the malleus) with a mobile posterior ligament. This is the ear type described above for humans and, as previously stated, the center of mass generally coincides with the rotational axis. The freely mobile type is also found in a variety of other terrestrial mammals including some rodents (*Chinchilla*, *Dipodomys*), elephants (*Loxadonta*), and other "higher" primates (*Pan*, *Macaca*).

In between these two types is the "transitional" type which has an intermediate degree of torsional stiffness (Fleischer 1978). The gonial is greatly reduced compared with the microtype but may still show partial fusion to the tympanic. The manubrium is obliquely oriented relative to the rotational axis and the transversal portion is present although no orbicular apophysis is noticeable. In this type, the center of mass is close to but not exactly in line with the rotational axis. The transitional type is found in horses (*Equus*), cats (*Felis*), squirrels (*Sciurus*), tree shrews (*Tupaia*), and apparently "lower" primates such as bushbabies (*Galago*).

Fleischer suggested that the microtype ear is found in those taxa with exceptionally good high-frequency hearing (*e.g*., bats) while the freely mobile type is found in those with expanded low-frequency hearing (*e.g*., humans). Peterson *et al*. (1974) set out to test this association by comparing hearing sensitivity (using cochlear potentials) in groups with different ear types. They compared sciurid rodents, which were

described as having an ear type intermediate between the transitional and freely mobile types, with representatives of the transitional type (ringtails – *Bassariscus astutus*) and the freely mobile type (guinea pigs – *Cavia porcellus*). These researchers found that, although the sensitivity functions were similar between the three groups, the region of greatest sensitivity was shifted slightly higher in ringtails and slightly lower in guinea pigs compared with the sciurids (1974), generally supporting Fleischer's views.

Even more illuminating was the analysis by Rosowski (1992) that compared hearing sensitivity data (taken from audiograms) for 19 species representing all three ear types (five with microtype, five with transitional type, and nine with freely mobile type). This investigation revealed that there were significant differences in high- and low-frequency sensitivity between the three types although considerable overlapping in their respective distributions did occur (Rosowski 1992). Furthermore, the greatest separation between groups was in their low-frequency sensitivity which supports the idea that the ancestral mammalian pattern was primarily limited to high-frequency sensitivity if indeed the microtype represents the ancestral condition as suggested by Fleischer (1978).

An additional factor to be considered relates to ossicular mass[8]. As stated above, the masses of the ossicles (and eardrum) are traditionally considered to be the main components contributing to the impedance at higher frequencies, although the evidence supporting this idea is limited (for a *contra* view see Rosowski 1994). Using a simple isometric model, Hemilä *et al*. (1995) attempted to predict the high frequency limit for a large group of mammals (with all three middle ear types) with known behavioral

[8] Although not discussed here, Rak (1994) suggested that ossicular morphology might be pleiotropically linked to the mandible due to a common evolutionary origin. If true, the size of the mandible could influence the size (and mass) of the ossicles. This idea was investigated but no supporting evidence was found (Coleman 2005a).

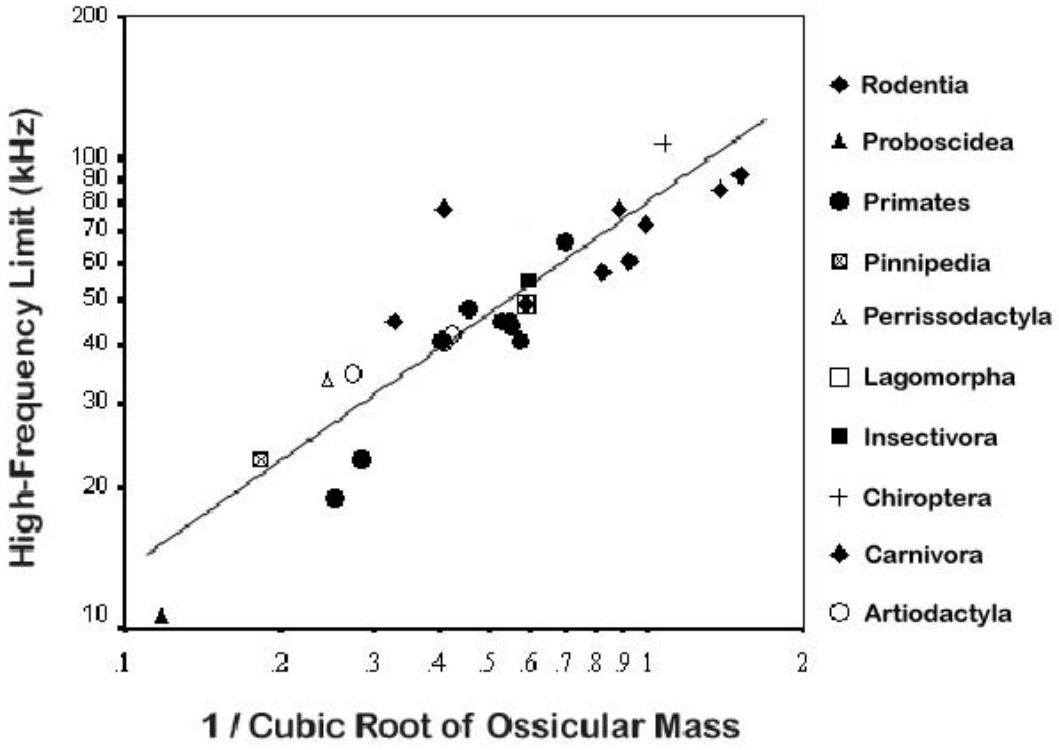

Figure 2.7 - Regression of the combined mass of the malleus and incus versus high frequency limit. Data taken from Hemilä *et al*. 1995.

thresholds. As can be seen from Figure 2.7, the cubic root of the combined mass of the malleus and incus shows a reasonably strong correlation with the actual high frequency limit having a prediction accuracy of ± 0.2 log units ($r^2 = 0.80$). The conclusion drawn by the authors from these findings was that the inertia of the malleus and incus is partly responsible for the rise in threshold intensity at higher frequencies (Hemilä *et al*. 1995).

Returning again to the work of Fleischer (1978), we see that he put forth a model that considered both the mass and the stiffness of the ossicular chain. Building on the finding by Onchi (1961) that the malleus-incus complex in human cadavers has a lower resonant frequency than the stapes, Fleischer (1978) proposed that the resonant

frequencies of the middle ear bones determine the basic shape of the audiogram. The single ear-bone configuration of birds and reptiles results in an audiogram with only a single peak and narrower overall range while the three bone configuration of mammals produces a double resonance that broadens the overall range. The resonant frequency of the malleus-incus complex depends on the stiffness, mass, and distribution of the mass. In the freely mobile ear, the last factor can be ignored since the mass appears to be more or less balanced around the rotational axis but in the microtype ear[9] the off-set center of mass greatly increases the moment of inertia as described by the parallel axis theorem (Fleischer 1978). The slightly off-set center of mass for the transitional type probably also results in a slight increase in the moment of inertia.

The resonant frequency of the stapes is determined by its mass and the stiffness of the annular ligament. No exact figures are available for the stiffness of the annular ligament, although Fleischer suggested that different ear-types generally have similar attachment patterns (thickness and width of the annular membrane) and that in cetaceans the resonant frequency is mainly tuned by increasing or decreasing the mass (1978). The finding by Rosowski (1992) presented above, that the main difference between the ear types is in low-frequency sensitivity could be interpreted to support Fleischer's idea that the resonant frequency of the malleus-incus complex (governed by its stiffness and mass) shapes that audiogram at lower frequencies. Then again, Johnstone and Taylor (1971) measured the effect of increasing the mass of the stapes (by one-third) and found there to be little difference in the amplitude response at 10 kHz and 15 kHz (the only two frequencies they investigated). It is possible that measuring the response at higher

[9] Fleischer also proposed that the microtype has two rotational axes and therefore two primary modes of vibration. This proposal received support from a study by Saunders and Summer (1982) on mice.

frequencies may have shown significant differences. Regardless of these conflicting results, it is clear that this concept deserves further consideration.

One of the most intensively investigated aspects of middle ear function relates to the volume of the tympanic cavity and its affect on hearing sensitivity. The size of the tympanic cavity is important because it is one of the main factors controlling the responsiveness of the tympanic membrane at different frequencies (Henson 1974). Small cavities provide fewer air molecules able to be compressed by movements of the tympanic membrane and are therefore "stiffer" and better suited for high-frequency hearing. Conversely, larger cavities provide a bigger cushion of air that helps reduce the stiffness of the membrane and increase sensitivity to low frequency sounds. Numerous studies on a wide variety of taxa have documented the relationship between cavity volume and sensitivity but no group has received as much attention as rodents.

Enlarged bullae have been noted in certain species of rodents since the early part of the last century and it was quickly realized that they facilitate low-frequency hearing (Howell 1932; Legouix and Wisner 1955; Webster 1960). The influence of cavity volume on sensitivity has been demonstrated in a series of experiments by Legouix and Wisner (1955), Webster (1962), Webster and Webster (1972) and others where they showed that reducing the cavity volume resulted in reduced sensitivity, particularly at lower frequencies. Specifically, Webster and Webster found that reducing the overall cavity volume by 75% in kangaroo rats (by injecting plasticene in the mastoid sinuses) raised the auditory thresholds at 1 kHz and below by 10 dB SPL or more (1972). Likewise, a similar reduction in sensitivity was reported for *Cebus capucinus* (next chapter) when the middle ear cavity was filled with fluid from an infection after surgery (Bragg and Dreher

1969). As early as 1963, Mundie noted that the impedance of the guinea pig middle ear increased when the volume was reduced (by about one-third) by adding mercury to the cavity. More recently, Zwillenberg *et al*. (1981) found that the responsiveness (admittance magnitude) of the hamster tympanic membrane decreased as the volume of the tympanic cavity was reduced by injecting small amounts of water into the bulla.

However, the mechanical stiffness of the cavity is determined not only by the volume of air enclosed within it but also by the size of the surface that is compressing the air (the tympanic membrane). Fleischer (1978) gave the following formula for determining the mechanical stiffness of the cavity volume:

$$E_{vol} = (c^2 * \rho * A^2) / V_e \quad (2.3)$$

where c is the velocity of sound, ρ is the density of air, A is the area of the tympanic membrane, and V_e is the volume of the cavity. This formula shows that the stiffness of the volume increases with the square of tympanic membrane area, so that a larger membrane will have a higher mechanical stiffness than a smaller membrane in two ears with the same middle ear air volume. Therefore, taxa with relatively large tympanic membranes will have to have exponentially large cavity volumes to realize a decrease in the mechanical stiffness of the cavity. This appears to be exactly the strategy employed by the specialized desert rodents with large membranes (*Microdipodomys* and *Pachyuromys*) in which the combined volume of their middle ears is larger than their endocranial volume (Webster and Plassmann 1992).

Another complicating factor arises when one considers the configuration of the tympanic cavity and the additional spaces that are connected to it. As mentioned above,

even within a single order such as Primates, cavity configurations can range from the simple single-compartment cavity found in *Lemur catta*, to the multi-compartment arrangement (some of them highly trabeculated) characteristic of monkeys and apes. Mundie (1963) found that the two-cavity arrangement of guinea pigs functioned as a system of coupled cavities where at lower frequencies the impedance was determined by the sum of both cavity volumes whereas at higher frequencies the impedance was determined by the main cavity only. The transition between these two impedances is determined by the resonance of the accessory cavity which can be estimated using the formula for a Helmholtz resonator (F_h):

$$F_h = (c / 2\pi) * (A_o / (l_o * V_a))^{1/2} \quad (2.4)$$

where c is the velocity of sound, A_o is the area of the connecting orifice, l_o is the length of the orifice, and V_a is the volume of the accessory cavity. At frequencies just below the resonance frequency the total cavity impedance reaches a minimum, but as the resonant frequency is reached the cavity impedance quickly rises to a maximum. Above the resonant frequency, the impedance *of the opening* between the cavities increases rapidly and acoustically closes off the accessory cavity from the main cavity. The cavity impedance again drops to a minimum and is now determined solely by the volume of the main cavity (Mundie 1963). Such an arrangement will stiffen the middle ear at higher frequencies and may act to broaden auditory sensitivity by enhancing the reception of both high- and low-frequency sounds (Henson 1974; Moore 1981).

In general, the inner ear (specifically the cochlea) has been the target of less investigation than the middle and outer ears. Still, a couple of functional principles have

been proposed and are supported by a limited amount of comparative data. As previously mentioned, the reactive component of the cochlear impedance is thought to decrease sensitivity to low-frequency sounds. This reactance seems to be mostly explained by the combined effects of the elasticity of the secondary tympanic membrane (round window), the annular ligament of the stapes, and possibly the helicotrema (Lynch *et al*. 1982). It has also been proposed that the high-frequency limit of hearing is determined largely by the cochlea (due to the high-frequency limits of the auditory nerves fibers) (Ruggero and Temchin 2002). Thus the cochlea seems to have a substantial impact on both the upper and lower bounds of the audiogram.

The structure that has been the subject of most inner ear research is the basilar membrane. The basilar membrane is organized tonotopically in that frequency sensitivity is mapped along its length. Therefore, the length of the basilar membrane will place limits on the range of frequencies to which it is receptive. Comparative studies in mammals have shown an inverse relationship between basilar membrane length and high-frequency sensitivity (West 1985, Rosowski and Graybeal 1991; Echteler *et al*. 1994). A similar discovery was made in archosaurs (birds, crocodilians, and dinosaurs) where the highest and most sensitive frequencies in a species were inversely related to the length of the basilar papilla (Gleich *et al*. 2005). However the pattern is reversed in non-archosaur reptiles where shorter basilar membranes are correlated with less high-frequency hearing (Manley 1971, 1986). Regardless of the pattern, the length of the basilar membrane (or papilla) seems to have a strong impact over the range of frequencies that can be detected.

In addition to length, basilar membrane width has been implicated as influencing hearing limits. Like length, several researchers have suggested that there is an inverse

relationship between basilar membrane width and high-frequency sensitivity (Fleischer 1973, Pye and Hinchcliffe 1976, Ketten 1984). This seems supported by the research on desert rodents referred to previously where the animals with extended low-frequency hearing have a wide (and relatively short) basilar membrane. Apparently, both length and width can have an impact on overall hearing ranges. This has led to the suggestion that it is the interplay between length and width that ultimately determines frequency tuning of the basilar membrane (Manley 1972). However, comparative studies between mice and men have shown that species with the essentially the same length-to-width ratios (termed the "membrane value" by Manley 1972) can have substantially different hearing limits (Ehret and Frankenreiter 1977). In fact, as mentioned in the first section of this chapter, humans have a basilar membrane that is over five times longer than that of mice and this allows for a much greater number of hair cells (approximately five times more). This seems to suggest that basilar membrane length may be the dominant factor controlling the overall range of frequencies that an animal can hear.

Final Comments

Despite this growing awareness that one must consider all of the components of the auditory system in order to fully understand its function, several investigators have continued to use the simple "ideal transformer ratios" as direct measures for comparing hearing performance in various taxa (Wever and Lawrence 1954; Hunt and Korth 1980; Masali *et al*. 1992). In addition to the inherent problems associated with measuring lever arms (confounded by determining the axis of rotation, the effective lever arm length, slippage between the joints, etc.) and determining the effective area and vibrational mode

of the tympanic membrane, these models ignore effects related to the mass reactance, elastic reactance, and frictional resistance of the middle ear structures themselves (Figure 2.6). Furthermore, they do not consider the frequency selectivity of the cochlea, the effects of cochlear input impedance or the amount of pressure presented to the tympanic membrane (which is affected by the pressure gain produced by the outer ear).

This misusage of the PTR and ITR stems partly from a misunderstanding of the presumed function of the middle ear transformer mechanism. The middle ear does not function as an acoustic amplifier, as often perceived, but instead as a *transformer* which attempts to match the input and output impedances. For example, a species with a larger cochlear impedance will require a larger PTR[10] just to maintain equal auditory sensitivity with an animal with a smaller cochlear impedance and matched PTR. This dependence on the cochlear load impedance greatly complicates the predicted effects of variations in PTR or ITR when the cochlear load is unknown. In other words, middle ear transformer ratios can be directly compared only if all of the other factors (listed above) are approximately equal. This is a questionable assumption to make and to my knowledge, no one has yet to test the correlation between transformer ratio values and absolute hearing thresholds. Consequently, testing this association will be one of the primary goals of this dissertation. The following chapter will examine hearing sensitivity in primates and prepare these data to be compared with morphological diversity.

[10] Or smaller ITR.

CHAPTER 3

SECTION I

Introduction

An animals hearing performance can be tested in many ways (absolute thresholds, critical bands and ratios, localization acuity, amplitude, temporal and frequency difference limens), but determining the lowest absolute threshold that an animal can detect at a given frequency is often considered the most fundamental (Harris 1943; Stebbins 1975; Lonsbury-Martin and Martin 1981; Jackson *et al*. 1999; Heffner 2004). Absolute threshold values are often presented as bivariate graphs called audiograms. An audiogram plots threshold values measured in decibels (dB) along the ordinate and frequency values measured in hertz (Hz) along the abscissa. Information on primate hearing sensitivity[11] has been steadily accumulating for the last 70 years and audiograms are now available for nearly 30 species of non-human primates (Table 3.1). However, there have been nearly as many variations in testing procedures as there have been species investigated. Only a handful of studies have sought to investigate the effects that different procedures have on estimating thresholds (Fujita and Elliot 1965; Dalton 1968; Bragg and Dreher 1969; Heffner *et al*. 1969; Stebbins 1970; Green 1971, 1975), and these studies have rarely focused on more than one species. The main goals of this

[11] Throughout this dissertation sensitivity will refer to measures of absolute auditory thresholds.

Investigators	Year	Species	Technique	Transducer	Ages
Elder	1934	*P. troglodytes*	PR	Headphones	3-7
Wendt	1934	*A. paniscus, C. torquatus, H. sapiens, M. mulatta, P. anubis*	PR	Speaker	?
Elder	1935	*H. sapiens, P. troglodytes*	PR	Speaker	Children,3-7
Harris	1943	*M. mulatta, M. sinica*	NR	Speaker	< 2
Seiden	1957	*C. jacchus, H. sapiens*	NR	Speaker	Juvenile-Adult, ?
Clack & Herman	1963	*M. mulatta*	NR	Speaker	Adult
Semenoff & Young	1964	*H. sapiens, M. nemestrina*	GSR	Headphones	Y. Adult, Adult
Fujita & Eliot	1965	*M. fascicularis, M. mulatta, S. sciureus*	NR/PR	Speaker	Y. Adults
Behar *et al.*	1965	*H. sapiens, M. mulatta*	NR	Speaker	17-26, Adol.-Adult
Farrer & Prim	1965	*H. sapiens, P. troglodytes*	NR	Headphones	4-6,5-34
Stebbins *et al.*	1966	*M. fascicularis, M. nemestrina*	PR	Headphones	Y. Adol.
Clack	1966	*H. sapiens, M. mulatta*	NR	Headphones, Speaker	?
Dalton	1968	*C. capucinus, M. mulatta*	CS, GSR, ECR	Headphones, Speaker	?
Dalton *et al.*	1969	*M. mulatta*	CS	Headphones	Adol.
Bragg & Dreher	1969	*C. capucinus*	NR	Earphones	Adult
Heffner *et al.*	1969	*G. senegalensis*	CS	Speaker	Adult
Heffner & Masterson	1970	*N. coucang, P. potto*	CS	Speaker	Y. Adults, Y. Adults
Gourevitch	1970	*M. nemestrina*	PR with shock	Headphones	?
Mitchell *et al.*	1970	*E. fulvus, E. macaco, L. catta*	PR with shock	Speaker	3 Adult, 3 Adol.
Mitchell	1970	*L. catta*	NR	Speaker	3-7
Mitchell *et al.*	1971	*L. catta*	NR	Speaker	Adol.-Adult
Green	1971, 1975	*S. sciureus*	NR/PR	Headphones	Adult
Gillette *et al.*	1973	*L. catta*	NR	Speaker	3-6
Pugh *et al.*	1973	*M. nemestrina*	PR	Headphones	?
Stebbins	1973	*C. aethiops, E. patas, M. arctoides, fascicularis; mulatta; nemestrina, P. papio*	PR	Headphones	3-7
Beecher	1974	*S. sciureus*	PR	Speaker	?
Beecher	1974	*A. trivergatus*	PR	Speaker	?
Pfingst *et al.*	1975	*H. sapiens, M. mulatta*	PR	Headphones	27-35,3-5
Pfingst *et al.*	1978	*M. mulatta*	PR	Headphones	?
Lonsbury-Martin & Martin	1981	*M. mulatta*	PR	Headphones	Adult
Hienz *et al.*	1982	*P. cynocephalus*	PR	Speaker	Adult
Bennett *et al.*	1983	*M. mulatta*	PR	Speakers	9-31
Brown & Waser	1984	*C. mitis, H. sapiens*	PR	Speaker	Juvenile, Y. Adults
Brown	1986	*L. albigena*	PR	Speaker	Adult
Smith *et al.*	1987	*E. patas*	PR	Headphones	Juvenile
Bennett *et al.*	1988	*C. aethiops, C. neglectus, H. sapiens, M. fuscata*	PR	Headphones	Juvenile
Owren *et al.*	1990	*H. sapiens, P. troglodytes*	PR	Headphones	4,2,5-7
Kojima	1997	*M. fuscata*	PR	Earphones	Juvenile
Smith & Olszyk	1999	*H. sapiens, M. fuscata*	CS	Speakers	13-17
Jackson *et al.*	1999	*M. mulatta*	PR	Speakers	Adult
Lasky *et al.*	1999	*E. fulvus*	N/A	Speaker	N/A
Heffner	2004				

TABLE 3.1 – All species for which behavioral audiograms have been determined. PR = positive reinforcement, NR = negative reinforcement, CS = conditioned suppression, GSR = galvanic skin response, ECR = evoked cortical response.

chapter are threefold. First, summaries of each study are presented with a focus on the individuals that were tested, the methods and apparati that were used to determine the auditory thresholds, and the relevant conclusions reached by the authors. Second, the extracted threshold values from these audiograms are analyzed in an attempt to identify the effects that different procedures have on absolute values. Third, lists of "good" audiograms are compiled for the purpose of evaluating inter-species differences[12]. In later chapters, these sets of hearing sensitivity data will be compared with morphological structures to investigate relationships between morphology and hearing sensitivity.

Animal Psychophysics

Audiograms (auditory threshold data) have been produced almost exclusively by psychologists in a subfield known as psychophysics. Psychophysics measures the absolute and difference thresholds in various sensory modalities and was initially applied only to humans. Therefore, language was used to communicate the task being investigated and to register the responses of the subjects. However, when non-human animals began to be investigated it became necessary to incorporate elements from other branches of psychology, namely conditioning procedures used in learning and behavior experiments. Classical conditioning developed out of the work of Pavlov (1927) and allowed researchers for the first time to examine correlations between stimuli and responses that are not strictly reflexive. In classical conditioning, a new reflex (conditioned reflex) is established by pairing an existing unconditioned reflex (an unconditioned response to an unconditioned stimulus) with a neutral stimulus

[12] Initial results from these comparisons were presented at the Acoustical Society of America 149th Semi-annual Meeting, New York (Coleman 2004a).

(conditioned) that initially has no detectable response. After a number of pairings, the conditioned stimulus is capable of producing a conditioned reflex in the absence of the unconditioned stimulus. Classical conditioning has seen limited usage in the exploration of primate auditory thresholds but two studies that employed this technique are described in section II (Semenoff and Young 1964 and Dalton 1968).

By far the most pervasive conditioning technique used with primates has been operant conditioning, first established in mainstream psychology by Skinner (1938). In operant conditioning, behaviors in response to stimuli are shaped by either reinforcing a positive response (responding to the detection of a stimulus) with positive reinforcement (*e.g*., food or water) or discouraging a negative response (not responding to an unmistakably detectable stimulus) with negative reinforcement (*e.g*., shock). Occasionally, both reinforcement types have been used in combination (Gourevitch 1970; Mitchell *et al*. 1970). A third approach, called conditioned suppression, takes a somewhat intermediate approach. In conditioned suppression, the desired action is the cessation of an operant behavior (such as licking a water spout) in response to a stimulus in order to avoid receiving shock. While all three techniques are fairly common, positive reinforcement has been the method most often employed in studying primate auditory sensitivity (Table 1).

Once an animal has been trained using one of the conditioning methods described above and meets certain performance criteria, standard psychophysical techniques are used to test the subject. The general approach is to vary the presentation of a stimulus along some physical parameter (intensity, duration, or frequency) and record the responses. Responses are usually binary in nature and equate to “yes, I detect the signal”

(a hit) or “no, I do not detect the signal” (a miss). During normal stimulus trials, a “hit” is referred to as a true positive and a “miss” is referred to as a false negative. Catch trials, where no stimulus is presented but all other aspects of the trial are the same as during a stimulus trial, are often intermixed with stimulus trails and are used to estimate the guess rate of the subject. A hit during a catch trial is referred to as a false positive and a miss is referred to as a true negative. A response during an inter-trial period is also sometimes called a false positive although the “punishment” for false positives during a trial may be different than false positives during an inter-trial period.

One of the traditional techniques used to vary stimuli is the method of limits. In determining absolute auditory thresholds, the method of limits is applied by presenting the subject with a series of different intensities at a single frequency whereby the intensity level is changed in regular intervals on consecutive presentations until the subject changes their response. A standard trial generally consists of one descending and one ascending series of intensities (although either series can be presented first) with the starting points being either well above or well below the threshold of detection. After a number of trials the percentage of correct detections (for stimulus trials only) is plotted against the sound pressure level to produce a perithreshold function which is generally ogival in shape (Figure 3.1). The threshold is interpreted from these graphs as the intensity level at which a tone is detectable 50% of the time. A guess rate is also calculated using the false positive and true negative values and if the percentage is above a certain level (usually 10-20%) the data for that session are not used in calculating the final threshold. This procedure is repeated for all frequencies to be tested. Variations on the method of limits and an alternative approach called the method of constant stimuli are

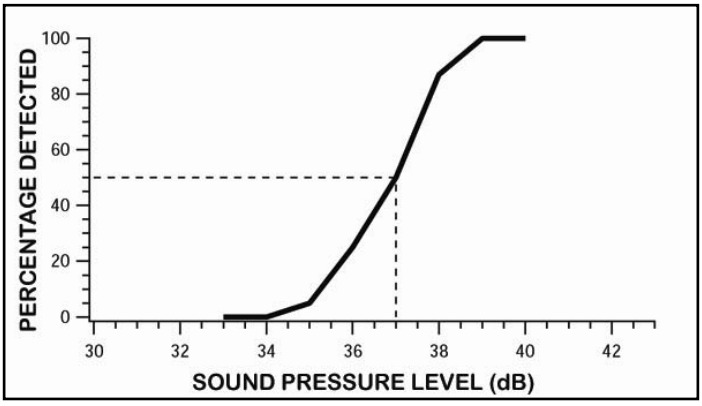

FIGURE 3.1 – Perithreshold function used to determine threshold values using a 50% correct response criterion.

described in section II in the relevant studies that utilized them. For more in depth discussions on animal psychophysics in general and the procedures used to test primate hearing sensitivity and acuity specifically, the reader is referred to the works by Gourevitch 1970, Stebbins 1970a, 1970b, 1971, and Green 1971.

Extracting Threshold Values from Audiograms

Threshold values were extracted from audiograms taken from the literature using the following method. Audiograms were digitally scanned and then imported into Sigma Scan Pro 5 image measurement software. The images were first rotated so that ordinate and abscissa were as close to perfectly vertical and horizontal, respectively, as possible. Next intensity was calibrated by setting the measurement distance equal to the dB levels along the ordinate. This calibration was checked and had to be less than 1 db different from the expected value (*e.g.*, 80 dB) before measurements were taken, otherwise the calibration procedure was repeated. In practice, the difference was usually on the order of

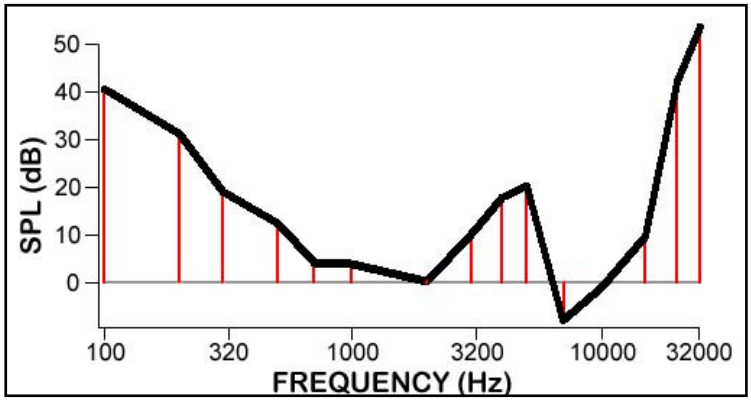

FIGURE 3.2 – Threshold values were extracted from published audiograms by measuring deviations from 0 dB SPL at individual frequencies.

0.1 dB. A horizontal line was then drawn along the 0 dB point and thresholds were measured for each frequency as either positive or negative deviations from this line (Figure 3.2). Threshold values were converted into 0.0002 dynes cm^{-2} when necessary. For certain comparisons presented below, threshold values were interpolated for intermediate frequencies that were not tested in the original study using the formula:

$$(3.1) \qquad dB_{int} = dB_l + ((Freq_{int} - Freq_l) / (Freq_h - Freq_l)) * (dB_h - dB_l)$$

where dB_{int} is the intensity and $Freq_{int}$ is the frequency for the threshold to be interpolated; and dB_l is the intensity of the lower frequency ($Freq_l$) and dB_h is the intensity of the higher frequency ($Freq_h$) with known values. This calculation was only performed when a study did not test a common frequency (*e.g.*, 500 Hz) but tested frequencies that were very close to the desired frequency (*e.g.*, 256 and 512 Hz).

To evaluate the accuracy of this method, extracted threshold values were compared with values from tables in 14 published audiograms. Extracted threshold values

were the same as published values in 74 % (124/168) of the measurements. In 24% of cases (40/168) the values deviated by 1 dB and in 2% of cases (4/168) the difference was 2 dB. Since published (final) threshold values represent the average of several values that deviate by a margin of ± 1.5 to ± 2.5 dB from the mean (see below), this level of measurement accuracy was considered acceptable.

SECTION II

Previous Research on Primate Hearing Acuity

The first scientific investigation aimed at determining auditory sensitivity in non-human primates was conducted by Shepherd in 1910 and concluded that rhesus macaques can discriminate tones of different pitch played on a harmonica as well as variations in intensity produced by slapping boards together with differing degrees of force. A few years later, Kalischer (1912) found that monkeys (the species was not specified) could respond to their names and other commands in order to receive a food reward. In 1929, Yerkes and Yerkes stated that the hearing ability of apes was "virtually a *terra incognita*" (1929:322) despite reviewing numerous accounts from the literature, naturalists and hunters. Under the auspices of Dr. Yerkes, two groundbreaking studies on primate hearing were initiated at Yale University to help fill this void.

ELDER 1934,1935

The first study of auditory acuity to produce an audiogram was the pioneering work of James Elder in 1934 which examined three young common chimpanzees (*Pan troglodytes)* in the Comparative Psychobiological Laboratory at Yale University. The

procedure used to determine threshold values for different frequencies was as follows: The subjects were first trained to press a telegraph key in response to tonal stimuli for the reward of a piece of fruit. The tones were presented in octaves using headphones (both monaurally and binaurally) ranging from 64 to 8192 Hz. During testing, the chimps were given a visual signal to signify the start of a trial which was then followed in half of the trials (3 seconds later) by a 5 second tone. If the subject pressed the key in the presence of a tone it resulted in food reinforcement but if there was a key press during the absence of a tone (false positive) the reward was withheld. Food reinforcement was also given when there was not a key press in the absence of a tone (true negative); a procedure known as the "double-reward" system (Vernon 1967:5). Tone intensity was presented using a psychophysical procedure that is a variant of the method of limits known as the method of serial groups. For each intensity level the stimulus was presented a number of times. If there were positive responses on more than half the trials, the intensity level was lowered for the next series but if the response level is less than half, the intensity level was raised. This procedure deviated from traditional psychophysical methods in that it used only descending intensities levels to determine thresholds.

The final threshold values represent the interpolated 50% correct values and are presented in Figure 3.3 and given in Appendix 1. These results are based on a minimum of 240 trials for each individual at each frequency. Elder noted that the chimpanzee thresholds tended to be lower (more sensitive) than the average human values but suggested this may be related to the favorable testing conditions of his subjects and the fact that the chimpanzees benefited from much more practice than the average human when having their hearing tested. The most interesting finding

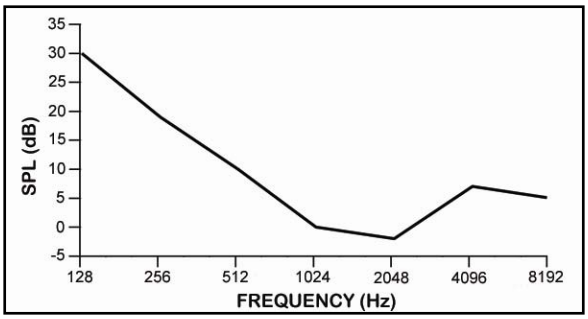

FIGURE 3.3 – Audiogram for *Pan troglodytes* from Elder 1934.

from this study was the "peculiar dip" at 4096 Hz (Elder 1934:182) in the chimpanzee audiogram.

In a second study the following year Elder (1935) sought to determine the upper limit of hearing in chimpanzees. This study used the same testing procedures as the previous study but tested frequencies ranging from 14.4 to 37.4 kHz. The subjects were three chimpanzees (two from the previous study) and three children. The results indicated that the chimpanzees could hear frequencies ranging from 26 to 33.3 kHz while the upper limit for the children was between 22.6 and 23.7 kHz. He concluded that non-human primates are superior to humans in high frequency sensitivity and suggested that valuable insight could be obtained by investigating correlations between high frequency sensitivity and morphological and physiological observations. The major limitation of this report was that the exact intensity levels of the stimuli were not given.

WENDT 1934

Around the same time Elder was working on ape hearing, Wendt (1934) was investigating monkey auditory sensitivity at the Yale Laboratory of Neurophysiology.

This study sought to determine thresholds for four genera of monkeys as well as five young adult human subjects. Although the study began with 11 monkeys, the results were presented for only five; one female baboon (*Papio anubis*), one female rhesus macaque (*Macaca mulatta*), one female mangabey (*Cercocebus torquatus*), and one female and one male spider monkey (*Ateles paniscus*[13]). The experimental technique used was similar to Elder's double-reward system except that the monkeys would open a small drawer below the speaker in front of them to acknowledge having heard the test stimulus (the food reward was delivered in the same drawer). Also similar to Elder, Wendt tested the animals using only descending intensity steps (although using the standard method of limits technique). However, Wendt diverged even further from standard psychophysical methods by determining the absolute threshold as the intensity to which the subject last made a correct response, not the traditional 50 percent response point. Additional differences were that a 12-inch loudspeaker was used to produce the tones instead of headphones and the test frequencies ranged from 64 to 16384 Hz in one octave steps.

Perhaps the largest drawback of Wendt's study is the fact that he did not determine intensity levels in terms of actual physical units, only as the number of decibels introduced into the circuit between the oscillator and the loudspeaker. However, Wendt was able to approximate the actual values by assuming that his human subjects had equivalent thresholds to those obtained in a study by Sivian and White (1933) which measured the true sound pressure level in the region of their subject's heads. By subtracting the values of his human subjects from those of Sivian and White, Wendt developed a correction factor that was then applied to the monkey thresholds in his study. These adjusted threshold values are presented in Appendix 2, along with values that

[13] Originally designated as *Ateles ater* but noted by Stebbins 1971 as *Ateles paniscus*.

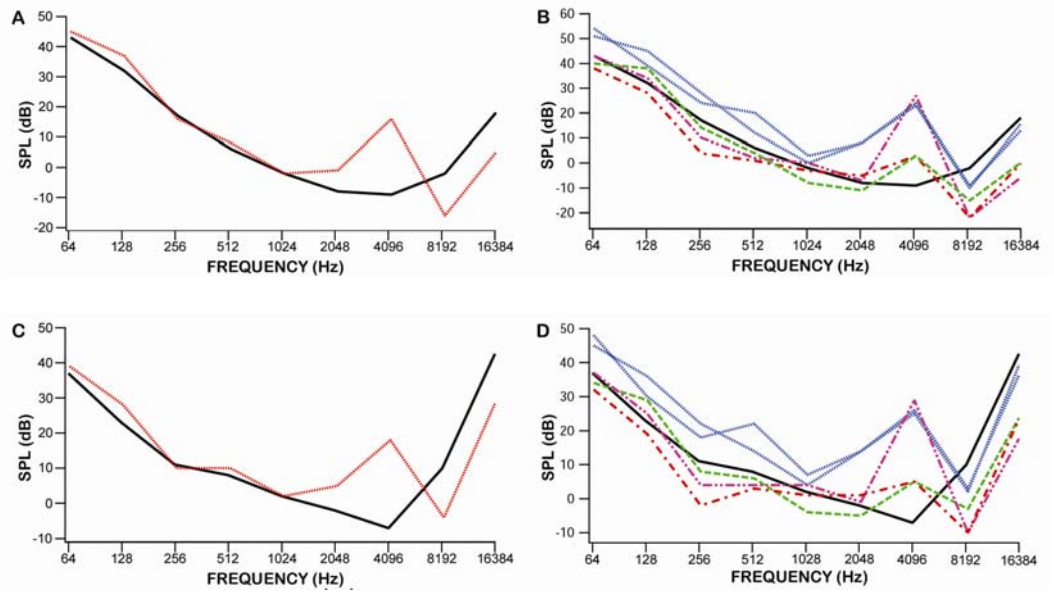

FIGURE 3.4 – Audiograms from Wendt 1934. **A**. Mean human (———) and monkey (▪▪▪▪▪▪) audiograms derived using the corrective factor based on human data from Sivian and White 1933. **B**. Individual audiograms using the same corrective factor: humans (———), *A. paniscus* (▪▪▪▪▪▪), *C. torquatus* (— — —), *M. mulatta* (— ·— ·—), and *P. anubis* (— ··— ··). **C**. Mean human and monkey audiograms derived using ISO corrective factor: same species coding as in Figure 3.4A. **D**. Individual audiograms derived using ISO corrective factor: same species coding as in Figure 3.4B.

have been adjusted using the more recent ISO (International Organization for Standardization) human threshold values (ISO 1961).

When comparing the monkey group as a whole (mean) with humans, Wendt found that there was very little difference in sensitivity at 1 kHz and below (Figure 3.4A). However, in the mid-frequency range humans appeared to be more sensitive, particularly at the "4096 dip" (Wendt 1934:47). Wendt commented that monkeys would be favorable subjects for anatomical and physiological work aimed at explaining the 4 kHz dip (1934:48). At the higher frequencies tested, the monkeys showed better sensitivity than the human subjects. To explore the high frequency range of monkeys, the rhesus monkey was tested further and found to be able to hear frequencies as high as 33.6 kHz, although

the loudness level of the test tones was not specified (relative or absolute). Comparing the monkeys individually (Figure 3.4B), the spider monkeys have the highest thresholds and averaged almost 9 dB higher than the humans while the rhesus monkeys generally had the lowest thresholds averaging 5.7 dB lower than the humans. The baboon and mangabey were only slightly more sensitive overall than are the humans, averaging 1.6 and 3.3 dB lower, respectively. Based on these data, all of the monkeys showed their greatest sensitivity at 8192 Hz and had lower (or equal in one case) thresholds at the frequency of greatest sensitivity compared with humans. Wendt speculated that the reduced sensitivity of the spider monkeys could have been related to their poor health during testing but two facts argue against this possibility. For one, the male spider monkey received a rating of B+ for its performance during testing (in the middle of the ratings range) which was higher than the macaque (B) that had the overall best sensitivity. Second, the two spider monkeys have threshold values that are remarkably similar with a mean range for all frequencies of 3.2 dB, which would seem unlikely if their values were aberrant.

Figures 3.4C and 3.4D present the same sensitivity data except in this case adjusted using the ISO human free-field standard (note that only the frequencies of the original study are used in the correction even though the ISO audiogram contains values for lower and intermediate frequencies). In general, most of Wendt's original observations hold true (Figure 3.4C): the curves are very similar at the lower frequencies, there is still a pronounced 4 kHz dip in the monkey data, and the humans are less sensitive at higher frequencies. However, the mean threshold of the frequency of greatest sensitivity (at 8192 Hz) is now higher than the corresponding value for humans (at 4

kHz). The trend for the individual data (Figure 3.4D) is also generally the same as in the previous graph: spider monkeys typically are less sensitive than the other monkeys and humans (except at high frequencies) and the other monkeys have the same order of sensitivity as before (although with slightly different relative intensities). In contrast, most of the monkey audiograms now have a more pronounced first peak of sensitivity (to the right of the 4 kHz dip). This is partly accounted for by the reduction in the values for the second peak of sensitivity but also because of less relative reduction in the first peak. For example, the first peak (2048 Hz) is now 2 dB lower than the second peak (8196 Hz) in *C. torquatus*, the first peak (1024 Hz) is only 3 dB less than the second peak (8196 Hz) in the average for *A. paniscus*, and there is now a conspicuous first peak (250 Hz) in *M. mulatta* instead of a more gradual decrease on the low frequency side of the graph. The validity of these audiograms will be considered in more detail in section III of this chapter.

HARRIS 1943

The next study to test primate hearing acuity was that of Harris (1943) which sought in part to test some of the conclusions reached by Wendt using more orthodox psychophysical techniques. Wendt tested eight macaque subjects that were all less than two years of age. They included five *M. mulatta*[14], two *Macaca sinica*, and one indeterminate macaque species. Harris tested his subjects with the method of serial groups using both descending and ascending test stimuli in 4 dB intervals to determine threshold (using the 50 percent correct criterion). Unlike Elder and Wendt, Harris avoided the double-reward technique and instead employed a shock avoidance method

[14] Two were referred to as *Macaca rhesus* which is now synonymous with *Macaca mulatta*.

(the first negative reinforcement procedure used to test primate hearing). The animals were trained to elicit a jumping response while a tone was presented in order to avoid receiving a mild shock that occurred concurrently with a buzzer. During the actual testing the shock was only rarely used, although the buzzer always sounded when the animal did not respond to a sound to inform the subject of a miss. Harris considered shock avoidance to be preferable to the technique used by his predecessors, primarily because it requires much less time to produce stable results and appears to reduce false positive rates. He reported that it was sometimes possible to produce an audiogram for a single individual in as little as a week while the positive reinforcement method could take anywhere from two to over five months (Harris 1943:256). The transducer used to deliver the tones was a loudspeaker and the tones ranged from 62.5 to 8000 Hz in one octave steps. The sound pressure levels were measured in actual physical units and calibrated at each frequency to adjust for the particular acoustic properties of the testing chamber. The calibrations were calculated by taking the mean intensity level of a large number (12-67) of representative positions in the testing cage and varied by 1.8 to 6.1 dB for different frequencies. This allows for the results to be directly comparable to other studies with minimal variation due to differences in the testing environments.

The thresholds for the individual subjects as well as the species and genus means are presented in Appendix 3. Harris used the values of all the subjects to produce a single audiogram (Figure 3.5) since the monkey's individual thresholds did not differ appreciably, the animals were within a few months of the same age, and were all from the same family (and genus) (Harris 1943:262). These mean values were compared to the results of the previous primate studies as well as a sample of 18 young men tested by

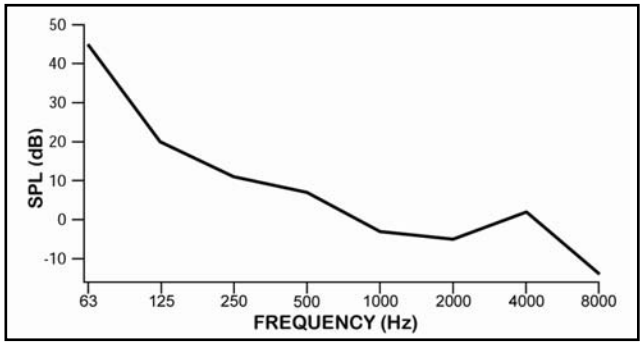

FIGURE 3.5 – Mean macaque audiogram from Harris 1943.

Lipman and Grassi (1942). Harris found relatively good agreement with the results produced by Elder 1943 and Wendt 1934. The mean audiogram shows a fairly strong roll-off (decrease) at the lower frequencies, there is a dip in sensitivity at 4 kHz, and the greatest acuity occurs at 8 kHz. However, it was stated that the 4 kHz dip in his study was not as pronounced as in the monkey audiogram (mean of all specimens) of Wendt (1934). Harris suggests that this may be an age-related phenomenon since his monkeys were all pre-adolescent while those of Wendt were two to eight years older, and that there may be "some unknown peculiarity of structure or function" which accentuates the dip with increasing age (Wendt 1943:263). However, it should be noted that when compared with only the macaque from Wendt's study (the baboon and spider monkeys strongly elevate the mean threshold at 4 kHz), the difference is no more than 3 dB regardless of which corrective factor is used to estimate the Wendt values. This is less than the 4 dB incremental steps Harris used to determine the individual threshold values. Harris concluded by suggesting that the heightened acuity in the high frequency range may be related to the "high-pitched, piercing screams" of their vocal repertoire (Wendt 1943:265).

SEIDEN 1957

In 1957, Seiden undertook a study of the acuity and range of *Callithrix jacchus*[15], the common marmoset, in order to investigate hearing abilities at the lower end of the primate phylogenetic scale. Reflecting popular notions of the time (*i.e.*, *scala naturae*), Seiden considered apes to be at a superior position, most monkeys at a middle position, and lemurs, tarsiers, and callitrichids to be at an inferior position within the primate order. Despite this outdated misconception, this study produced an audiogram for the smallest primate tested to date (and still the smallest tested anthropoid) using rigorous and well established methods. A total of five marmosets were evaluated including one male and four females of both young and mature ages.

The operant conditioning technique was a negative reinforcement procedure similar to that used by Harris. The animals were trained to avoid a shock after the onset of a tone by moving to the opposite side of a double grid (grill) testing cage. The two grids were wired separately so that electric shock could be applied to either side independently. When the subject moved to the opposite side it caused the cage to tilt slightly activating a switch which registered the position. This allowed for automated control of the testing cycle and unequivocal registering of responses. Once the subject had reached the training criterion (20 consecutive avoidance responses) the shock was suspended and testing began. However, unlike Harris no buzzer was used to signal a miss to the test animal.

The psychophysical technique used was another variant of the method of limits called the "up and down" method also known as the tracking, or staircase, procedure. The method was used in this study by starting with an intensity that was known to be above

[15] Originally designated as *Hapale jacchus* but subsequently renamed *Callithrix jacchus*.

the threshold limit and then reduced in 5 dB steps until the subject no longer responded. Then the order was reversed (ascending) until an affirmative response occurred at which time the sequence was reversed again. This procedure continued until there were threshold determinations for two descending and two ascending series (two trials) at each frequency tested. Mathematical and empirical observations have shown that this method can produce reliable threshold estimates in as few as five trials (Dixon and Mood 1948; Brownlee *et al*. 1953) and is unaffected by dB interval size (Stebbins 1970). Seiden determined a total of 16 ascending and 16 descending (16 trials) thresholds for each individual at each frequency. The frequencies tested were: 0.1, 0.2, 0.3, 0.5, 0.7, 1, 2, 3, 4, 5, 7, 10, 15, 20, 25, 30, 35, 40, 50, 60, 70, and 80 kHz. The tones were delivered in a free-field environment through one-of-two speakers depending on the frequency. The sound field was calibrated and the calibration tested by measuring the auditory sensitivity of five human subjects and comparing it to the American Standards Association (Licklider 1951) reference curve. The two audiograms (Figure 3.6A) were found to be in close agreement validating the calibration (Seiden 1957:11).

The individual thresholds, species means and ranges are presented in Appendix 4 and the individual audiograms are presented in Figure 3.6B. The standard deviations for individual animals ranged from 1.25 to 4.73 dB (mean = 3.38), attesting to the consistency of performance of the subjects. Figure 3.6C shows the mean audiogram for all five animals as well as the audiograms for the ascending and descending series threshold determinations. The first point of interest illustrated in this figure is that the descending series thresholds are consistently lower than the ascending series (and necessarily the mean which was determined from these two series). This phenomenon has

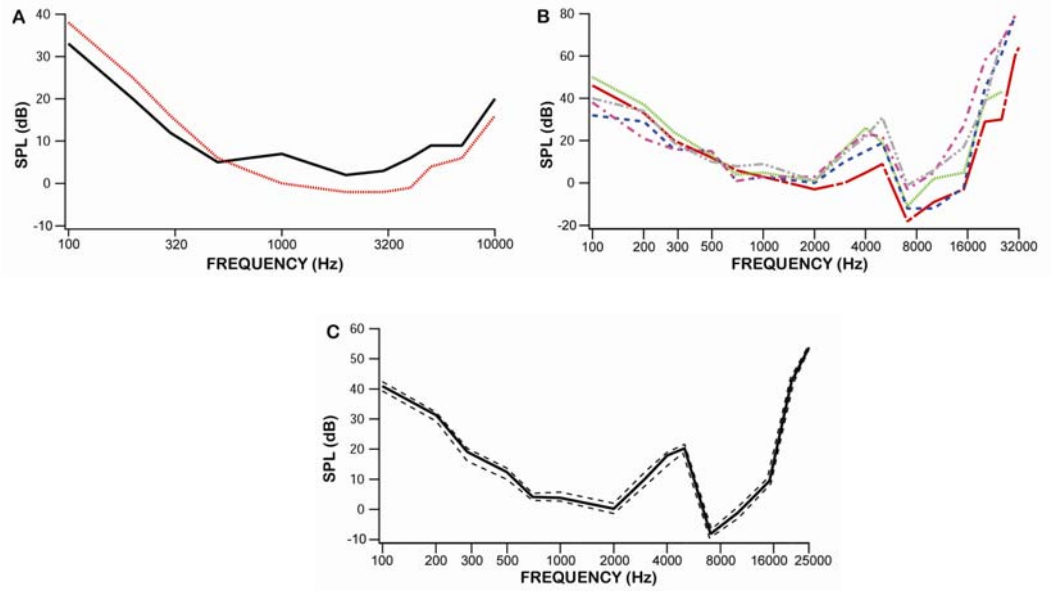

FIGURE 3.6 – Audiograms from Seiden 1957. **A**. Mean audiogram of Seiden's human subjects (———) compared with the ASA standard (▪▪▪▪▪▪). **B**. Individual *C. jacchus* audiograms (——— represents subject #1, ▪▪▪▪▪▪ represents subject #2, — — represents subject #3, — · — · — represents subject #5, and ▪ ▪ ▪ ▪ represents subject #6). **C**. Mean audiogram for all five subjects (———) with thresholds produced using ascending (– – – – above mean) and descending (– – – – below mean) series intervals.

been termed "the error of habituation" (Woodworth and Schlosberg 1954:197) and reflects the inclination for a subject to continue responding affirmative in a descending series and continue responding negative in an ascending series. Seiden considered these differences to be "small" (1957:39) and in fact the mean difference between the two series is just over 3 dB.

Also discernible from Figure 3.6C is the overall similarity in shape to the curves produced by the earlier studies. Seiden even went as far as to suggest that "there is a general hearing function for the sub-human primate independent of species…" possibly including lemurs and tarsiers (1957:39). However, there are slight differences in the marmoset audiogram and those produced by Elder, Wendt and Harris. For one, the mid-

range dip in sensitivity appears to peak around 5 kHz instead of closer to 4 kHz as had been previously proposed. Another difference is that Seiden's monkeys all show their greatest sensitivity at 7 kHz instead of 8 kHz. Seiden explained these differences as most likely an artifact of the frequencies that were tested in the previous studies. To more accurately isolate the dip and peak frequencies, explorations were made at 4.5 and 8.2 kHz. This led Seiden to conclude that the dip is not a sharp peak but a narrow range of 0.5 to 1 kHz of decreased sensitivity perhaps closer to 5 kHz than 4 kHz (1957:46). Likewise, the maximum is "not a point but a region extending from about 7 kHz to about 8.5 kHz, again with individual variations entering into the situation" (Seiden 1957:47). While these points are definitely worth noting it should also be pointed out that two of the marmosets (# 2 and #3) actually did show the dip at 4 kHz with a fairly strong slope down to 5 kHz while a third (#5) is essentially flat between these two frequencies (Figure 3.6B).

As for the high frequency limit of marmosets, the subjects had a range between 28 and 37 kHz when tested at the maximum intensity capable of being produced by the audio system (the exact thresholds were not given since is was impossible to calibrate the system at these frequencies). Seiden suggested that the upper limit of hearing in marmosets is probably somewhere between 35 and 40 kHz (1957:45) and further advocated the 35 kHz high frequency limit for all nonhuman primates (1957:48). However, examination of the data in Appendix 4 indicates that the traditional high frequency cut-off at 70 dB is actually just below 30 kHz when considering the mean for the group. It is also noteworthy to point out that the youngest subject in the study (#1)

does show a high frequency cut-off (at 70 dB) around 35 kHz. The effects of age on thresholds will be considered in more detail in section III of this chapter.

CLACK and HERMAN 1963

Starting in the early 1960's, a steady stream of studies producing audiograms began to be published starting with the research by Clack and Herman (1963). The primary goal of this study was to develop a psychophysical procedure for measuring auditory thresholds that is quickly learned by the subjects, easily automated, and produces rapid results. This allows for the determination of thresholds fast enough so that it is possible to measure shifting limens (TTS – temporary threshold shift) such as occurs during acoustic over-stimulation. Their method employed a shock avoidance operant technique and used six adult female *M. mulatta* as subjects. The monkeys sat in a minimum confinement restraint chair that was placed inside of a sound isolating booth and faced a loudspeaker, two lights (one white and one red), and a response lever. The animals were first trained to press a lever during the presentation of tone in order to avoid receiving a shock which was paired with the activation of the red light. Next, the white light was introduced into the sequence and was activated one second before the onset of the tone and stayed on until the tone, shock and red light were terminated. In addition, the red light and shock pairing was varied so that the animal received a shock alone for a false positive response but a shock and red light for a miss (false negative). Use of the white light was found to reduce the false positive rate. The third phase of training was used to eliminate the response to the fixed interval between the white light and onset of the tone. This was accomplished by switching to a random schedule of tone presentation

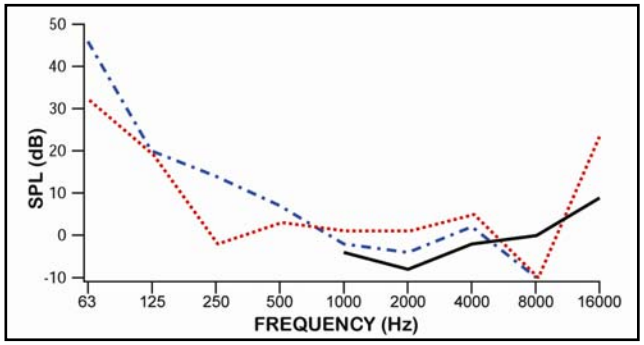

FIGURE 3.7 – *M. mulatta* audiogram from Clack and Herman 1963 plus macaque audiograms from Wendt 1934 and Harris 1943: ——— represents Clack and Herman, ▪▪▪ ▪▪▪ represents Wendt, and — ·— ·— represents Harris.

whereby the tone was presented in only 50 percent of the trials. The last phase of training consisted of changing the tone intensity using a staircase method (in 1 dB intervals) and switching to a variable ratio schedule (one to six successive misses had to occur) before delivering the shock after a miss. The animal was still informed of the miss by the red light. Using this method, it required between nine to 19 hours to produce an audiogram after which additional thresholds could be determined in minutes (depending on the intensity interval size). The macaques were tested on tones ranging from 1 to 16 kHz in one octave intervals.

The thresholds obtained in this study are presented in Appendix 5 and are illustrated in Figure 3.7. Although the audiogram shows the first peak of sensitivity at 2 kHz common to most of the previous curves, the second (and generally primary) peak is essentially missing (although there is a slight bump at 8 kHz). Furthermore, the threshold values (except 8 kHz) are somewhat lower than the values for macaques in the previous studies. The authors do not really address this except to state “the present group is sometimes more sometimes less than the comparative samples, indicating differences in

hearing acuity among animals rather than in the techniques used" (Clack and Herman 1963:180). Despite these peculiar results several subsequent studies used the "single-lever psychophysical adjustment technique" (or certain aspects of it) developed by Clack and Herman. One interesting application of this technique was to investigate TTS in their *M. mulatta* subjects caused by auditory fatigue following exposure to high intensity tones. Clack and Herman found that after a 15 minute exposure of narrow band noise at 100 dB intensity there was a 10 dB shift at 4 kHz, 30 dB shift at 2 kHz, and 0 dB shift at 1 kHz. These TTS's could last anywhere from 20 minutes to several hours. However, if the intensity was lowered to 95 dB there was no measurable shift in sensitivity.

SEMENOFF and YOUNG 1964

The first study of primate hearing sensitivity to use a classical conditioning procedure was that of Semenoff and Young (1964). Instead of training the subjects to elicit a conscious behavior in response to a tone (operant conditioning), the animals were trained to establish a conditioned reflex in the presence of an audible tone. The conditioned reflex was established by pairing an unconditioned stimulus (shock) that produced an unconditioned response (GSR - galvanic skin response) with a conditioned stimulus (sound). After a number of pairings, the conditioned stimulus was capable of producing a conditioned response (GSR) in the absence of the unconditioned stimulus. Semenoff and Young used this procedure to establish auditory thresholds in three adult pig-tailed macaques (*Macaca nemestrina*). Audiograms were also produced for three male graduate students although a key pressing response was substituted for the conditioned GSR technique. The subjects were tested inside of a large refrigerator that

was lined internally with acoustical tile and had an ambient noise level of 30 dB SPL. Tones were presented in 2 dB increments by means of headphones in an ascending method-of-limits technique. The frequencies tested were 0.13, 0.25, 0.5, 1, 2, 4, and 8 kHz. Thresholds were based on 10 separate measurements (using a psychogalvanoscope for the monkeys) at each frequency. Unfortunately, their threshold results are published in terms of root-mean-square voltage readings instead of SPL measurements which prevent them from being directly compared to other studies. Still, their conclusions in relation to the comparison with the humans tested are somewhat interesting since they conflict with the findings of most previous research.

Figure 3.8 shows the mean audiograms for both the humans and pig-tailed macaques. The individual threshold values and species means (in rms volts) are given in Appendix 6. The authors note that their study did not find a 4 kHz dip or that the monkeys were more sensitive than humans at 8 kHz (Semenoff and Young 1964:92). In fact, the monkeys appear to be inferior to the humans at all frequencies tested. They considered two possibilities to explain these findings in contrast to the results of Elder (1934), Wendt (1934), and Harris (1943). The first possibility is that there may have been

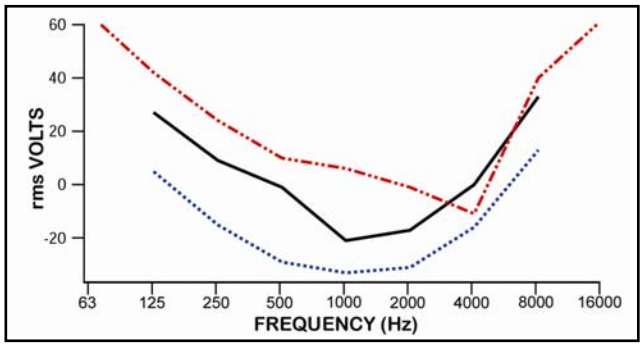

FIGURE 3.8 – GSR Audiograms from Semenoff and Young 1964: *M. nemestrina* mean (———), human mean (▪▪▪▪▪▪), and Wendt's monkey data (mean) without a corrective factor (— ▪▪ — ▪▪).

shortcomings with their methods: 1) a possible high-frequency roll-off in the headphones response; 2) the use of only ascending series tones in threshold determinations; 3) the criterion of 10 GSR reaction units to register an affirmative response may have been too high since it was found that GSR increased in amount with an increase in the intensity of the tone. For the second possibility, they suggested that the 4 kHz dip of the previous studies may just be an artifact that derives from the "apparent superiority" at 8 kHz (Semenoff and Young 1964:92). They went on to point out that when Wendt's original data is plotted without using a corrective factor, "the resulting audiogram closely corresponds to the one obtained in the present study" (Semenoff and Young 1964:93). This graph has also been included in Figure 3.8, though it should be kept in mind that the ordinal values represent two different units. While it is true that both monkey graphs display a single peak without a dip, the overall shapes are less than *closely corresponding* (e.g., the peaks are separated by 3 kHz). Furthermore, Semenoff and Young fail to address the study by Seiden (1957) which does not suffer from the main criticisms they direct at Wendt and Harris yet reached similar conclusions as these studies. One final point worth mentioning is that while the GSR approach produces audiograms in a short period of time and avoids certain problems associated with operant procedures, it has also been criticized on several points including the lack of controls (*e.g.*, unrelated stimulus modalities producing the conditioned reflex during testing) which confound its reliability (Green 1971:3).

FUJITA and ELLIOT 1965

The first of three publications on primate hearing in 1965 was that of Fujita and Elliot (1965) that examined three species of primates and compared three different procedures. The experimental subjects were all young adults and consisted of nine squirrel monkeys (*Saimiri sciureus*[16]), four rhesus macaques (*M. mulatta*), and three cynamolgus monkeys (*Macaca fascicularis*) although only the squirrel monkeys were tested in all three procedures. Tones were produced in "well calibrated" soundproof rooms for frequencies ranging from 0.625 through 32 kHz using one of four speakers depending on the frequency (Fujita and Elliot 1965:141). Thresholds were determined using a unique form of the method-of-limits that somewhat resembles the method-of-serial groups described above. Tone intensity was lowered in 10 dB steps until the subject failed to respond to two out-of-three presentations. The intensity was then increased by 5 dB and the procedure repeated. The threshold was then defined in the usual manner as the intensity lying between the last successful trial and the next lowest intensity tested.

The first procedure tested was an avoidance conditioning procedure using a double-grill cage similar to the apparatus employed by Seiden (1957). This test involved six squirrel monkeys that were trained to cross over a small barrier separating the two sides of the cage. To discourage spontaneous movements within the cage the animals were punished with shock during the training process. The trials were given at random time intervals ranging from 20 to 50 seconds and trials that were preceded by spontaneous movements were discarded. To ensure stable thresholds, the final values had to meet a criterion of five consecutive sessions where the thresholds did

[16] The study was performed before *S. scuireus* was split up into more than one species so the exact species used in this study is uncertain.

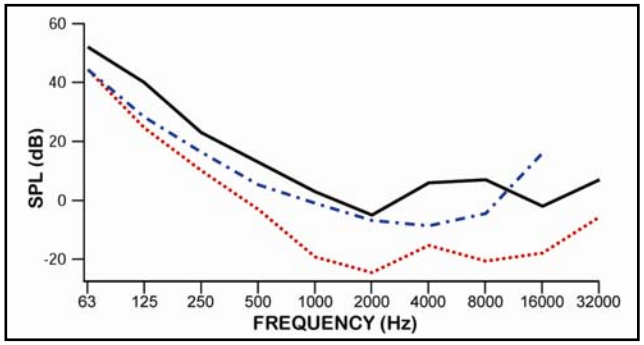

FIGURE 3.9 – Audiograms for squirrel monkeys, humans and cats from Fujita and Elliot 1965: ——— represents the mean for six monaural squirrel monkeys derived using a double-grill cage shock avoidance procedure, ▪▪▪▪▪▪ represents the mean for monaural cats using the same procedure, and — · — · — represents the human audiogram from Sivian and White 1933.

not vary by more than 5 dB. The mean thresholds of five squirrel monkeys (one was discarded because it was patently deviant at 2 kHz) are given in Appendix 7 and presented in Figure 3.9. At most frequencies, 80% of the subjects fell within ± 5 dB of the median monkey (all within ± 10 dB of the median) with an average range for all frequencies of less than 9 dB. The authors note there is no appreciable variation in inter-individual range as a function of frequency (Fujita and Elliot 1965:141). The shape of this audiogram resembles the familiar peak, dip, peak configuration but shows some distinctions from the previous species tested. For one, the first peak at 2 kHz appears to represent the most sensitive frequency tested (similar to Clack and Herman's findings) although the second peak at 16 kHz is only 3 dB higher. Another difference is that the dip demonstrates a rather wide range from 4 to 8 kHz supporting Seiden's contention that it is actually more of a range than a sharp point (Seiden 1957:47). Compared with humans (Figure 3.9), they find similar differences as did Wendt (1934) and Harris (1943) in that the monkeys are slightly inferior at lower frequencies (<1 kHz), markedly inferior at mid-

range frequencies (4 and 8 kHz), but increasingly superior starting somewhere between 8 and 16 kHz (Fujita and Elliot 1965:142). Also included in this figure are the results from their lab on monaural cats tested with the same procedure. Fujita and Elliot note that although the cats were more sensitive than squirrel monkeys and humans at all frequencies, the cats also display a 4 kHz dip which has been proposed as reflecting the resonant characteristics of a double-chamber middle ear cavity (Möller 1965; Lynch 1981). They suggest, however, that since monkeys do not have such a cavity arrangement that this argument loses some of its credence. To the contrary, many primates do have a multi-chambered middle ear cavity and attempting to correlate these structures with the response properties of the middle ear is one of the aims of this dissertation.

The second procedure involved a bar pressing response to an auditory signal with a food reward (sugar pellets) as the reinforcement for a correct positive, while a false negative (miss) resulted in no reward. The inter-trial interval varied from 30 to 60 seconds; a false positive resulted in an additional inter-trial delay of 30 to 80 seconds (time-out period). For this procedure two squirrel monkeys, two cynamolgus monkeys, and two rhesus monkeys were used (all binaural).The individual thresholds, species means, and ranges for the squirrel monkeys are presented in Appendix 7 and Figure 3.10A. The two individual audiograms are in fairly close agreement except at 1 and 2 kHz. The authors suggest that the high thresholds of monkey number 10 may be the result of the animal's death before the completion of testing (Fujita and Elliot 1965:143). Despite these two elevated levels, the average difference for all frequencies between the two animals is 8.5 dB. The other notable difference is that the first peak appears at 500 Hz for animal 10 versus 1 kHz for animal 3. The results for the *M. fascicularis* are

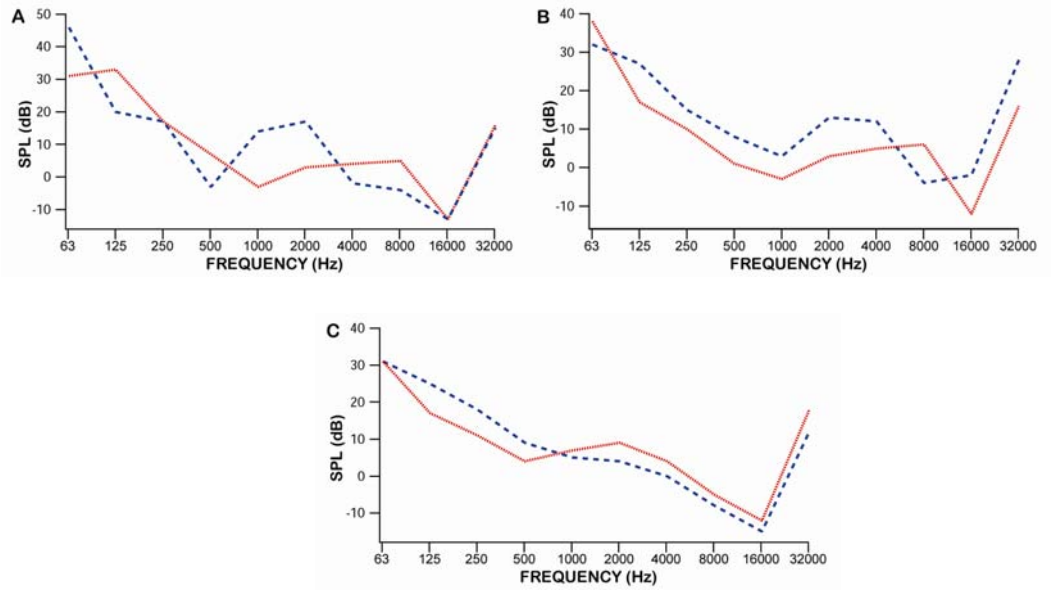

FIGURE 3.10 – Binaural monkey audiograms from Fujita and Elliot 1965 produced using positive reinforcement. **A**. Audiograms for *S. sciureus*: ▪▪▪▪▪▪ represents subject #3 and ▬ ▬ ▬ represents subject #10. **B**. Audiograms for *M. fascicularis*: : ▪▪▪▪▪▪ represents subject #1 and ▬ ▬ ▬ represents subject #2. **C**. Audiograms for *M. mulatta*: ▬ ▬ ▬ represents subject #5 and ▪▪▪▪▪▪ represents subject #6.

presented in Appendix 8 and Figure 3.10B. Again, the individual graphs are similar in shape and have an average difference for all frequencies of 7.9 dB. The major discrepancy in these two audiograms is that one subject (#1) peaks at 8 kHz while the other (#2) peaks at 16 kHz. The results for the rhesus macaques are given in Appendix 9 and Figure 3.10C illustrates the close agreement between the two animals in threshold values. In fact, the mean difference between thresholds is only 2.3 dB, the lowest of all the audiograms produced in this study using the positive reinforcement technique. One of the interesting aspects of these graphs is the shallowness of the dip which falls at 2 kHz for the mean audiogram.

The third procedure was similar to the second except that it involved negative reinforcement (shock) as the operant conditioning technique. Pressing the bar in response

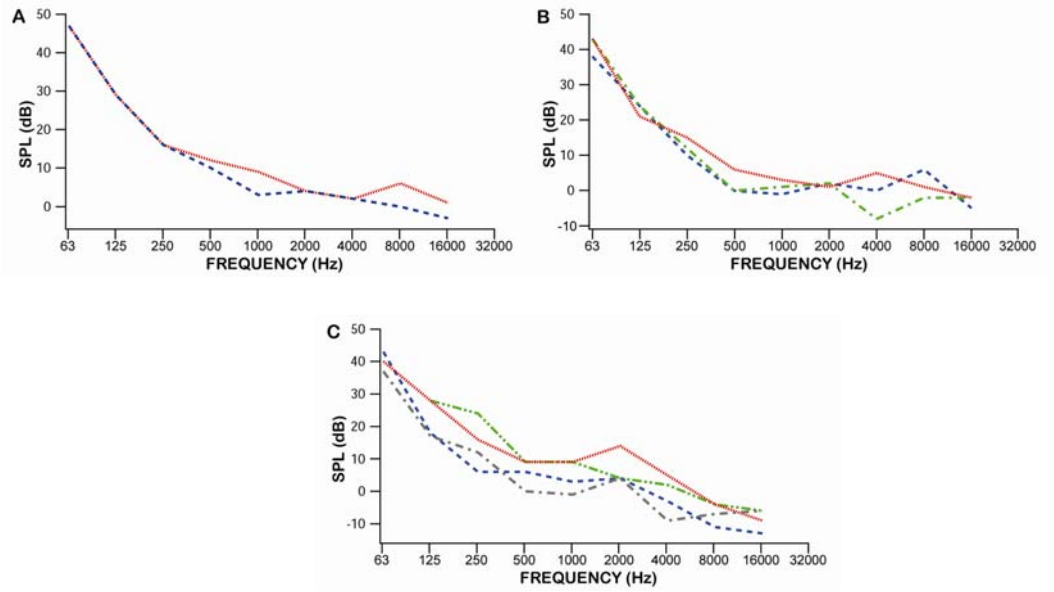

FIGURE 3.11 – Binaural monkey audiograms from Fujita and Elliot 1965 produced using negative reinforcement. **A**. Audiograms for *S. sciureus*: ▪▪▪▪▪▪ represents subject #3 and ▬ ▬ ▬ represents subject #18. **B**. Audiograms for *M. fascicularis*: : ▬ ▬ ▬ represents subject #1, ▬ ▪ ▬ ▪ ▬ represents subject #2, and ▪▪▪▪▪▪ represents subject #27. **C**. Audiograms for *M. mulatta*: ▬ ▪ ▪ ▬ ▪ ▪ represents subject # 5, ▬ ▬ ▬ represents subject #6, ▪▪▪▪▪▪ represents subject #7, and ▬ ▪ ▬ ▪ ▬ represents subject # 26.

to a tone prevented a shock, whereas a miss or inter-trial response resulted in a brief shock. The inter-trial intervals were the same as in the previous procedure. The animals used in these tests were two squirrel monkeys, three cynamolgus monkeys, and four rhesus monkeys (again all binaural). The threshold data for the squirrel monkeys are presented in Appendix 7 and Figure 3.11A. Below 500 Hz there is perfect agreement between the curves as well as at 2 and 4 kHz. However, at 2 kHz #18 shows a slight dip while the dip appears at 8 kHz for monkey #3. Still, these dips are slight and both animals are most sensitive at 16 kHz. The average difference between the graphs is 2 dB reflecting their unison at over 50% of the frequencies tested. The cynamolgus monkey data are presented in Appendix 8 and Figure3.11B. At 2 kHz and below the graphs are very similar whereas at 4 and 8 kHz the animals have a range of 13 and 8 dB,

respectively. The high range at 4 kHz results from the fact that this is the most sensitive frequency for #2 while it falls in the dip for #27. The range at 8 kHz is expanded because animal #1's dip occurs at this frequency. Despite this high variation, the average for all frequencies is a moderate 5.4 dB. The shock avoidance data for the rhesus monkeys are presented in Appendix 9 and Figure 3.11C. Unlike the previous avoidance audiograms, there is a fair amount of scatter in the low frequency thresholds as well as at the middle and high frequency ranges (mean range = 10.2 dB). Some of this variability may stem from the inclusion of more individuals. However, most of the animal's audiograms still reflect a similar shape. For example, three out of four monkeys show a small first peak around 1 kHz, a dip at 2 kHz, and maximum sensitivity at 16 kHz. Subject #5 is the odd-monkey-out which neither shows a first peak nor dip (probably correlated) in addition to showing a high threshold value at 250 dB.

Figure 3.12 compares the mean audiograms for each species produced using the different procedures. Despite the small number of individuals representing the three species and the fact that different individuals were sometimes involved in one procedure versus another, Fujita and Elliot consider there to be "fair agreement in the auditory characteristics of the species, regardless of the procedure used" (1965:143). They do note however, that the mid-frequency dip is more pronounced in the data obtained with reward reinforcement. This is well illustrated in the comparison involving *M. fascicularis* (Figure 3.12A). On the other hand, the specific procedure does not seem to have much impact on the dip in *M. mulatta* (Figure 3.12B). In fact, these audiograms are nearly identical at most frequencies regardless of procedure, with an average difference of only 2.3 dB across all frequencies. This difference would be even less if not for the 9 dB spread at 63

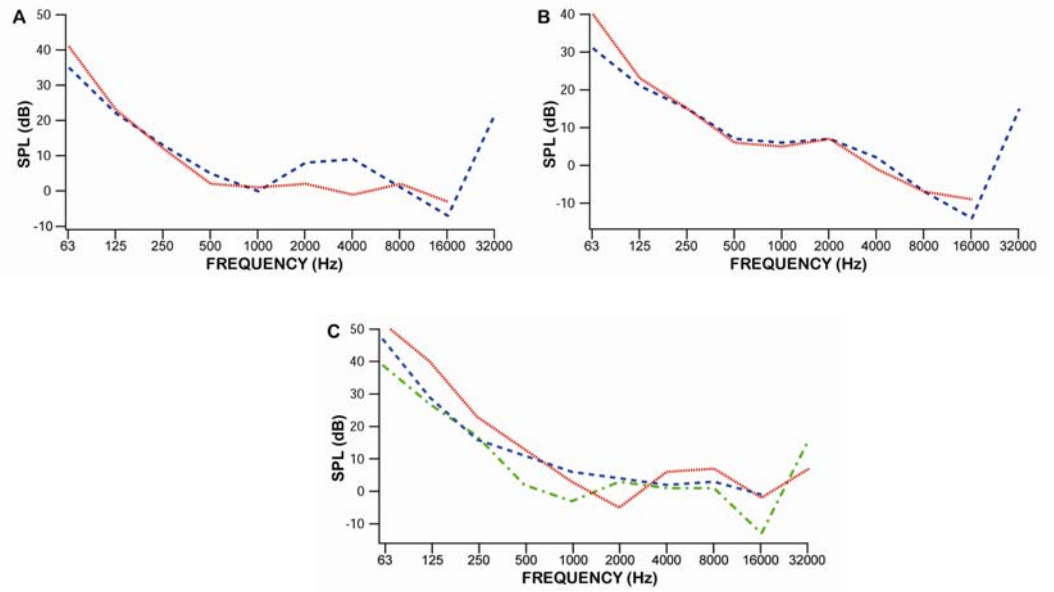

FIGURE 3.12 – Audiograms from Fujita and Elliot 1965 comparing different conditioning procedures. A. Mean audiograms for *M. fascicularis*: ▬ ▬ ▬ represents mean using positive reinforcement and ▪▪▪▪▪▪ represents mean using negative reinforcement. B. Mean audiograms for *M. mulatta*: same coding as in Figure 3.12A. C. Mean audiograms for *S. sciureus*: ▪▪▪▪▪▪ represents mean using double-grill cage shock avoidance, ▬ ▬ ▬ represents mean using negative reinforcement and ▬ ·▬ ·▬ represents positive reinforcement.

Hz. Similarly, the mean audiograms for *M. fascicularis* are only noticeably dissimilar at the mid-frequency dip. On average, there is a 3.6 dB difference between the reward and avoidance audiograms for this species. Considering just the bar pressing procedures for the squirrel monkey (Figure 3.12C), there is once again considerable harmony between the two curves. The prominent difference is the lack of prominent peaks in the negative reinforcement data (although 16 kHz is still the most sensitive frequency for both procedures). The average difference between the audiograms amounts to 4.7 dB. However, when the double-grill cage avoidance data are included the variation at most frequencies becomes greater (mean = 9.4 dB) and the general shape is somewhat shifted. Although the 16 kHz peak is still evident, the most sensitive frequency appears to occur

at 2 kHz as pointed out earlier. In addition, this graph has the mid-frequency dip more common to the positive reinforcement graphs than the shock avoidance data. Curiously, the authors consider this to be the preferred method because it is the quicker and more efficient procedure (Fujita and Elliot 1965:144).

BEHAR, CRONHOLM, and LOEB 1965

The next publication was that of Behar *et al*. (1965) and was initiated to explore the conflict in results between Semenoff and Young (1964) with those of previous investigators (Wendt 1934; Harris 1934; Clack and Herman 1963) as well as to probe the higher frequency capabilities of anthropoids. Behar *et al*. (1965) used four rhesus monkeys (three adult males and one adolescent female) and seven young adult human males (17-26) as subjects. The subjects were tested in a double-walled sound room that had an ambient noise level of 45 dB centered at 63 Hz. The following frequencies were tested: 0.05, 0.1, 0.125, 0.25, 0.5, 1, 2, 4, 6.3, 8, 10, 12.5, 16, 20, 25, and 31.5 kHz and the intensities were calibrated by taking multiple free-field measurements performed in the area of the subject's heads. The monkey thresholds were determined using the single-lever psychophysical adjustment technique of Clack and Herman (1963) with a few minor variations. False positives were punished by a mild shock while false negatives were always matched with a red light and paired with a strong shock 30% of the time. Tones were attenuated in 2 db intervals using the staircase method. The procedure was identical for the humans except no shock was administered. The final thresholds were based on six threshold determinations at each frequency for the macaques but only two determinations for the humans.

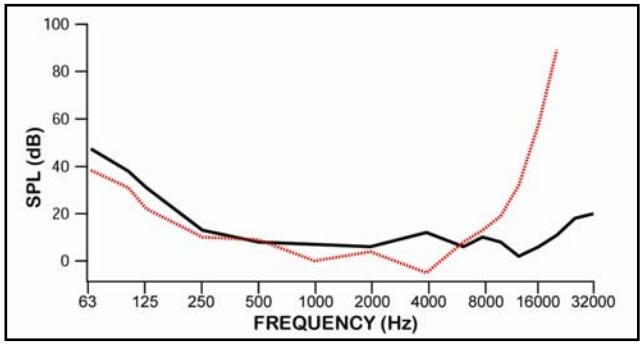

FIGURE 3.13 – Audiograms from Behar *et al*. 1965: ——— represents mean for *M. mulatta* and ▪▪▪▪▪▪ represents mean for humans.

The individual thresholds, ranges, and species means are given in Appendix 10. The individual standard deviations for all subjects were relatively small (.7 to 7.6 dB), reflective of the daily reproducibility of the procedures (Behar *et al*. 1965:427). The mean audiograms (Figure 3.13) show that the human thresholds were generally lower below 6.3 kHz (except at 500 Hz) but above this frequency the humans showed a strong roll-off compared to the much more gradual decrease in *M. mulatta*. This is in strong contrast to the results presented by Semenoff and Young (1964). The mean threshold difference for frequencies between 0.125 and 8 kHz is 3.9 dB in the study by Behar *et al*. (1965) compared with 18.9 dB in the study by Semenoff and Young (1964). Behar *et al*. (1965) present four factors that might explain these inconsistencies: 1) Different species of macaques were used in the two studies (*M. mulatta* versus *M. nemestrina*); 2) Semenoff and Young used a behavioral procedure to determine the human thresholds but the monkey thresholds were measured using the GSR procedure. Semenoff and Young did not show that the response criteria would give comparable percentages of responses for a given frequency and intensity under the two conditions (*i.e*., they did not test one procedure with both species); therefore, their response threshold of 10 GSR reaction units

may have in fact been too high as they proposed; 3) the reinforcement training was minimal but may have produced lower intensities if further conditioned; 4) the use of headphones may have diminished the high frequency responses. Any or all of these factors probably contributed to the excessively low values for the macaques in the study by Semenoff and Young.

Behar *et al*. (1965) concluded their report by expressing their surprise at the unexpectedly high sensitivity of the rhesus macaque to frequencies above the human upper limit. They felt that these results were valid considering the careful controls they employed to rule out the possibility of responses to sub-harmonic frequencies or other artifacts. With a threshold of only 20 dB SPL at 31.5 kHz and the fact that their data did not show a strong upward slope approaching this frequency, the upper limit of hearing in rhesus macaques is probably considerably higher (as shown by later studies).

FARRER and PRIM 1965

The third study in 1965 to generate information on primate hearing sensitivity was an Aeromedical Research Laboratory technical report by Farrer and Prim which sought to establish the upper limits of hearing in humans and chimpanzees. They examined five chimpanzees (*Pan troglodytes*) ranging in age from 4 to 6 years old and 90 humans - three at each age level from 5 to 34. The subjects were tested inside a double-walled acoustic chamber (beginning to become standard) with an ambient SPL of 40 dB. The tones were delivered with headphones (described as a ½ inch speaker mounted in a headset – similar to circumaural headphones) and ranged from 10 to 40 kHz. The chimpanzees were trained to press a button in response to tones. False positives were

penalized with shock 100% of the time but false negatives were punished with "aperiodic" shock reinforcement (described below) (Farrer and Prim 1965:5). The psychophysical technique was yet another variant of the traditional approach called the method-of-limits with a modified extinction condition. A failure to respond on the first ascending series resulted in shock reinforcement and that frequency was repeated. If the subject responded to the second presentation, the next higher frequency was presented (increasing in 500 Hz increments) with the chance of negative reinforcement. However, if there was failure to respond to the second presentation, the ascending series was terminated and all remaining tests for the day were without aversive reinforcement using a standard method-of-limits procedure. The inter-trial intervals were randomly varied from one to 15 seconds. The human subjects were tested in a similar manner except without shock and using the standard psychophysical method-of-limits.

The means and ranges of the high frequency limit at 80 dB for each age group are given in Appendix 11. The combined chimpanzee values were found to be significantly higher ($P < 0.01$) than those of the youngest human age group (5-9) as can be seen in Figure 3.14. The upper limit of hearing for the youngest age group of chimpanzees

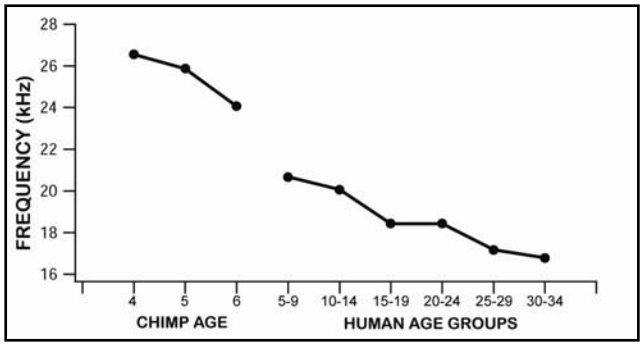

FIGURE 3.14 – High frequency limit as 80 dB SPL for different age groups of *P. troglodytes* and humans.

(4 years old) was approximately 26.5 kHz while the mean for individuals in all three age groups combined was closer to 24.5 kHz (the mean of each age group's mean was 25.9 kHz). It can also be seen that there is an apparent decline in high frequency limit in chimpanzees with increasing age although the low sample size prevents statistical evaluation. The human sample is large enough for statistical evaluation and it was found that there was a decrease in hearing sensitivity in ten year intervals (the 5-9 year old group was different from the 15-19 year old group and so on). The mean for the youngest human age group (5-9) was found to be 20.6 kHz and for the oldest age group (30-34) to be 16.9 kHz.

The authors point out that none of their chimpanzees could hear tones as high as 30 kHz at 80 dB SPL, in contrast to the 7 year old subjest (Moos) in Elder's 1935 study that had a high frequency limit of 33.5 kHz (unknown intensity). However Alpha, the three and a half year old female in Elder's study, had a high frequency limit (~26.5 kHz taken from Figure 2 in Elder 1935) that was nearly identical to the 4 year old mean (26.5) found in the present study. This would support Farrer and Prim's supposition that "these values represent individual variations, and the small samples employed tend to magnify these differences" (1965:10), although they did not advocate a limit as high as Elder suggested. On the other hand, they did agree with Elder's conclusion that chimpanzees can hear higher frequencies than children. Farrer and Prim also noted that their study produced 28 individual threshold values above 20 kHz at 80 dB which does not agree with the mean value of 88 dB in the study by Behar *et al*. (1965). They suggested that "the random orientation of the ear away from the sound source (speaker) in a free-field situation increases the probability of obtaining higher dB threshold values" (Farrer and

Prim 1965:10). An interesting point, but four factors diminish the magnitude of this discrepancy: 1) The Behar *et al*. value is based on only five individuals; 2) one of these individuals did have a value lower than 80 dB at 20 kHz (76 dB); 3) Farrer and Prim's mean value for the age groups (15-19 and 20-27) that corresponds approximately to the ages of the subjects in Behar *et al*.'s study (17-26) is 18.78 kHz. Interpolating this value up to 20 kHz would produce a SPL closer to 88 dB; and 4) the difference is relatively small (it is difficult to interpret how small since they do not state exactly what the average frequency for these thresholds was). Still, this point is worth mentioning since it is often assumed that use of headphones may elevate thresholds at lower frequencies (Packer 1983; Jackson *et al.* 1999), but it has seldom been suggested that the use of speakers may slightly elevate thresholds at higher frequencies (however see below).

STEBBINS, GREEN, and MILLER 1966

In 1966, Stebbins *et al*. determined auditory thresholds in three young male *M. fascicularis*[17], and one adult male *M. nemstrina* using a psychophysical method that had never been applied to primates before called the method of constant stimuli. The positive reinforcement conditioning technique also introduced some new approaches for determining thresholds. The animals were trained to press one of two telegraph keys (A) for food reinforcement in the presence of a tone. The monkeys were then conditioned to press a second key (B) which aperiodically caused a three second tone to sound during which time a press of key A resulted in food reward. Pressing key B during the presence of a tone had no effect and pressing key A during the absence of a tone resulted in a three second time-out. The average interval between presentations of the tone was about 15

[17] Originally designated as *Macaca irus* but now recognized as *Macaca fascicularis*.

seconds. After the subjects had been trained, their thresholds were roughly estimated by decreasing the intensity of a tone until no response on key A occurred. Next, five intensities above and below the threshold, in 10 dB intervals, were selected and presented to the animal in mixed order with each intensity being presented a total of 10 times. The absolute threshold was then calculated as that intensity which produced a response on key A 50% of the time. Testing was continued until on two successive sessions, the thresholds were not more than 5 dB apart. The mean of these last two values was taken as the final threshold value. Thresholds were calculated in this manner for the following frequencies: 0.06, 0.125, 0.25, 0.5, 1, 2, 4, 8, 10, 15, 20, 30, 40, and 45 kHz. The subjects were tested in a double-walled sound proof room and all tones were presented through headphones. SPL was measured by inserting a probe tube through the cushion of the headphone so that the end of the probe was located at the entrance of the ear canal. Despite this rigorous and novel approach to accurately determine intensity levels, the authors warn that there may be some error in the measurement of high frequency tones due to standing waves in the probe tube and ear canal (Stebbins *et al*. 1966:1647).

The species means and ranges for *M. fascicularis* and all individual thresholds are given in Appendix 12. The three audiograms of *M. fascicularis* (Figure 3.15) all show a strong consistency in shape at most frequencies and the mean range for all frequencies is 10.5 dB. The most sensitive frequency is 1 kHz, followed by the mid-frequency dip between 2 and 4 kHz, with a double secondary peak at 8 and 15 kHz (although 8 kHz averages 2 dB lower). These animals show a strong roll-off between 40 and 45 kHz and the authors report that a response could not be evoked at 50 kHz with an intensity of 95 dB SPL. The audiogram for *M. nemestrina* is also quite similar to these audiograms

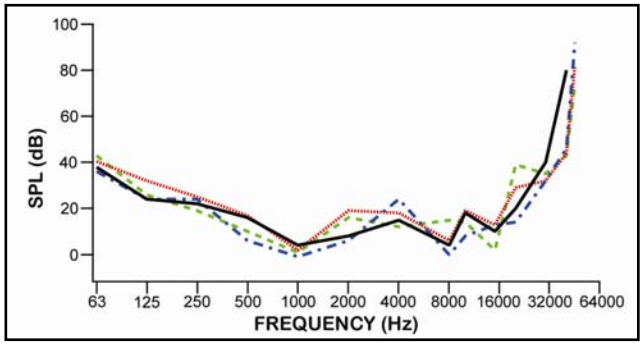

FIGURE 3.15 – Macaque audiograms from Stebbins *et al*. 1966: ——— represents subject #5 (*M. nemestrina*), — — — represents subject #2 (*M. fascicularis*), ▪▪▪▪▪▪ represents subject # 3 (*M. fascicularis*), and — ▪ — ▪ — represents subject #6 (*M. fascicularis*).

(Figure 3.15) and if one considers the frequencies between 0.06 and 30 kHz the mean range including all individuals is elevated just 0.5 dB to 11 dB. The main differences are the upper limit of high frequency sensitivity and that the peak at 8 kHz is equal to the first peak at 1 kHz (4 dB). In *M. nemestrina*, the threshold rises 40 db between 30 and 40 kHz and the researchers were unable to get a response at 45 dB even with a tone as loud as 100 dB SPL! However, this is also the oldest individual in the study so the authors warn against putting much meaning in this difference (Stebbins *et al*. 1966:1647). This study not only confirms many of the characteristics found by previous researchers in these and closely related species but it was also the first to conclusively establish the high frequency limit for any monkey other than the marmoset.

CLACK 1966

The aim of the study by Clack (1966) was to assess the effects of signal duration on auditory thresholds in humans and monkeys. Previous studies on various sensory modalities of humans have shown that for some limited time period the absolute

threshold is linearly related to signal duration due to the accumulation of energy over time and this relationship is referred to as the temporal integration function (Clack 1966:1140). However, since the majority of results and conclusions of this report are outside of the scope of this chapter they will not be discussed but instead the information summarized here relates to the determination of thresholds with tones presented with normal (≥ 1 second) duration.

The subjects were two female rhesus macaques (*M. mulatta*) of unstated age and seven women ranging in age from 19 to 34 years old. The conditioning procedure and psychophysical techniques were identical to those used in the previous study by Clack and Herman (1963) except that the human subjects did not receive shock for false positives and false negatives. The monkeys were tested both binaurally using a loudspeaker and monaurally (both ears) using headphones attached to the outside of a helmet that appears to be similar to the audio-helmet used in the studies by Dalton 1968 and Dalton *et al*. 1969 (see below). The frequencies tested using the speaker ranged from 1 to 16 kHz in octaves and from 0.125 to 16 kHz in octaves using the headphones. The humans were tested with left ears only using standard headphones (TDH-39 in an MX 41/AR cushion) on frequencies ranging from 0.500 to 8 kHz. The only mention of calibrating the transducers is for the monkey headphones. A microphone was placed in the approximate position of the pinna (the headphones were not on the subjects) and the surrounding opening was sealed off using modeling clay to simulate the animal's head. All testing was conducted in a sound attenuating booth (IAC 401).

All of the human and monkey thresholds are presented in Appendix 13. Figures 3.16A and 3.16B show the monaural and binaural audiograms for the macaques. Clack

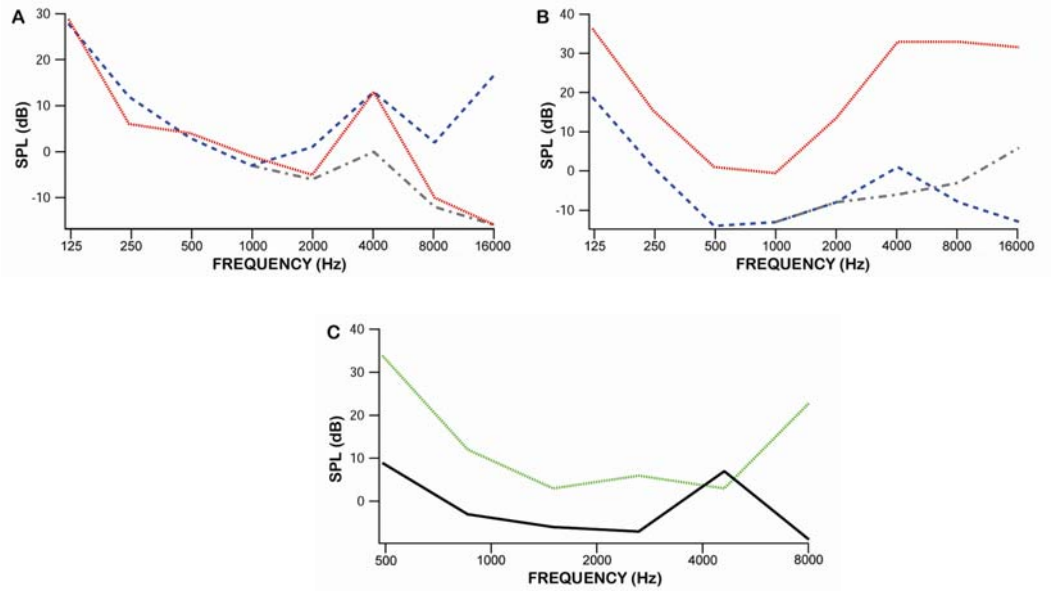

FIGURE 3.16 – *M. mulatta* and human audiograms from Clack 1966. **A**. Audiograms from macaque subject c2: ▪▪▪▪▪▪ represents mean of right ear thresholds, ▬ ▬ ▬ represents mean of left ear thresholds, and ▬ ▪ ▬ ▪ ▬ represents binaural thresholds. **B**. Audiograms from macaque subject c4: coding the same in Figure 3.16A. **C**. Mean audiograms for macaques (▬▬▬) and humans (▪▪▪▪▪▪).

concluded that subject C4 (Figure 3.16B) had high frequency loss in the right ear (a difference of 45 db at 16 kHz) although it appears that this animal may have had presbycusis (age-related hearing loss) over the entire frequency range with a mean difference for all frequencies of 25 dB between the right and left ear thresholds. Furthermore, subject C2 (Figure 3.16A) demonstrates a difference of 33 dB at 16 kHz although the author makes no specific reference to this possible indication of hearing loss. Clack did note however, that the binaural measurements tended to reflect the animal's more sensitive ear and that the monaural measurements show the 4 kHz notch although the magnitude of the notch was "relatively unstable" (1966:1144).

Figure 3.16C shows the mean audiograms of the human and macaque subjects (the data from the defective ear of monkey C4 were excluded). The human audiogram

appears to have a normal contour except the slight notch at 2 kHz. Likewise, the macaque audiogram illustrates the typical shape with a first peak between 1 and 2 kHz, a dip at 4 kHz, and a second peak at 8 kHz (although the individual data presented in Figures 3.16A and 3.16B suggests the best sensitivity may be at 16 kHz). The unusual aspect of the macaque audiogram is that the mean thresholds are considerably lower than the human thresholds at all frequencies below 4 kHz. All previous (and subsequent) studies comparing humans and macaques have found that humans generally have equal if not slightly better hearing sensitivity at these frequencies. Although Clack noted the apparent superiority of *M. mulatta* in this range, he did not comment on the inconsistency of his data to that of previous researchers (Wendt 1934; Harris 1943; Behar *et al*. 1965).

DALTON 1968

The study by Dalton (1968) was the second technical report to be produced by Aeromedical Research Laboratory at Holloman Airforce Base in conjunction with New Mexico State University. The main purpose of the study was to establish the degree of agreement between electrophysiological and behavioral techniques in determining auditory thresholds. The three primary goals were to ascertain the sensitivity of capuchin monkeys, to compare intra-species audiograms using three techniques (conditioned suppression, Galvanic Skin Response, and Evoked Cortical Response), and to evaluate these techniques as to sensitivity, reliability, rapidity, and complexity. The conditioned suppression paradigm was chosen as the technique to determine behavioral audiograms in part since the pairing of stimulus (sound) with shock serves as training for the GSR procedure. The subjects consisted of eight cebus monkeys (*Cebus capucinus*) and four

rhesus macaques (*M. mulatta*) arbitrarily distributed over the techniques (described below), however three of the cebus monkeys died before the completion of the study. The tones were produced using either a 12 inch extended range speaker or a specially constructed closed-system "audio-helmet" – essentially custom headphones that completely enclosed the pinnae with minimal physical distortion (Dalton *et al*. 1969:179). The speaker was positioned directly over the subject's heads in the midline. Unfortunately, it was not made clear which transducer was used with which technique and no mention was made of calibrating the measurement of intensity levels. The test stimuli were tones ranging from 0.5 to 8 kHz in octaves.

Conditioned suppression is an operant conditioning procedure which is characterized by the suppression of an operant behavior by pairing a neutral stimulus with a brief unavoidable shock (first established by Estes and Skinner 1941). One of the key features of this procedure is the independence of the auditory stimulus to the positive reinforcement (Dalton 1968:2). This technique was conducted in a double-walled sound attenuating chamber and the subjects were two rhesus macaques and four cebus monkeys. The apparatus for testing consisted of a "noise reduced" lever, lamp module, and a food hopper (Dalton 1968:10). A blue light in the lamp module would light every time the subject pressed the response key and served as secondary reinforcement to the response. A red light in the module served as a "go" signal to the subject and the food hopper delivered nutrient pellets into a food cup that was lit by a white lamp at the distribution of each pellet. The animals were trained to press the lever to receive food reinforcement. Gradually, the reinforcement schedule was reduced until a variable interval schedule was introduced. Throughout the schedule reductions, a steady state of responding was

maintained. No set number of responses was required but a "smooth" baseline of responses per minute was desired (Dalton 1968:13). Once a stable baseline was established, suppression training commenced and consisted of presenting a 20 second tone followed by a shock. As training progressed, the animal ceased to respond in the presence of an auditory signal. During testing, each session consisted of 12 stimulus trials, five control trails, and five baseline trials. During the control trials, the signal was completely attenuated and no shock occurred. The baseline trials were accomplished by measuring two consecutive trials of response baseline for comparison. Threshold was defined as the intensity of the stimulus which yielded a mean suppression ratio of 0.50 or below on three consecutive sessions. The suppression ratio was defined as the pre-stimulus response rate minus the during-stimulus response rate divided by the pre-stimulus response rate (Hoffman *et al*. 1963). The psychophysical method employed was the method of constant stimuli in 2 dB intervals although a variant of this method was used to establish the initial threshold estimate.

The basic principles of the GSR were previously described (Semenoff and Young 1964). For this procedure, four cebus monkeys and two rhesus macaques were tested in a Suttle audiometric chamber. No set number of trials was established since conditioning acquisition was found to vary greatly within subjects (Dalton 1968:18). Training was continued in each subject until the intra-subject variability was reduced to a minimum. The criterion used to establish a response was determined empirically for each subject based on individual baselines. Even in subjects with an active baseline the response was "quite clear" (Dalton 1968:19). Threshold was defined as that intensity that yielded three

positive responses out of a block of five trials. The ascending series of the method-of-limits was used after initial training at 60 dB SPL.

The evoked cortical response is an electrophysiological procedure that records the evoked potential to an auditory stimulus. Two cebus monkeys and two rhesus macaques were used as subjects and tested in a specially built electroencephalograph (EEG) chamber which was isolated within its own room. The subjects were implanted with stainless steel screw electrodes placed on the cortex along the midline in 12 mm intervals (one at vertex, one anterior to vertex, and seven posterior to vertex). These were then attached with stainless steel wires to an EEG and the resulting wave graphs analyzed by a data retrieval computer (DRC). The subjects were then tested using white noise to check the presence of a response and rule out artifacts (the response was only detected at the electrode placed on the vertex). The response was apparently "quite evident" on the DRC (Dalton 1968:22). A total of 50 responses were averaged for each 5 dB interval using a descending series of the method of limits. Thresholds at each frequency were defined as the point at which the evoked response was no longer observable from the EEG.

Only one subject produced usable threshold data using the conditioned suppression technique. Even though two rhesus monkeys produced audiograms, one (#518) suffered from chronic bilateral otitis media (initially diagnosed from the audiogram prior to otological and radiological confirmation). However, this pathology did not appear to affect the responses at 4 and 8 kHz. The thresholds for both individuals are given in Appendix 14 and the mean difference between the two individuals at 4 and 8 kHz was an insignificant 0.2 dB. The intra-subject variability was also found to be quite low producing mean values of 1.14 dB (#3014) and 0.88 dB (#518), illustrating the

consistency of the technique (even in the pathological subject). No final thresholds were able to be determined for the cebus monkeys using this procedure because stable baselines could not be established. In retrospect, it seems possible that the colored lights were not useful for conditioning the capuchin monkeys since it is now known that this species is not routinely trichromatic (Jacobs 1995).

The results for the GSR procedure are also given in Appendix 14 and in this case both species produced thresholds. Once again, the otits media in subject 518 is reflected in the thresholds at 2 kHz and below. However, above this frequency there is only a 5.5 dB mean difference between the thresholds for the macaques and the intra-subject variability was found to be less than 7.5 dB at any given frequency. Only the mean threshold values for the capuchins are presented in Appendix 14 and Figure 3.17A, although all four subjects met the threshold criterion. The intra-subject variability for the capuchins was less than 10 dB at any frequency while the mean inter-subject variability was 10.4 dB. These larger variability estimates may be due in part to the difficulty of determining a response as the intensity approached threshold, described by Dalton as a "twilight zone" (1968:50).

The macaque thresholds produced using the ECR procedure are given in Appendix 14 and although both subjects tested in this procedure appeared to have normal hearing, there is a wide range between the two individuals (Figure 3.17B) with a mean differences of 16 dB. Only one of the cebus monkeys lived to the end of the ECR testing so there is no way to evaluate inter-subject variability in this species. There was no intra-subject variably for either of the species; if a subject gave a positive response

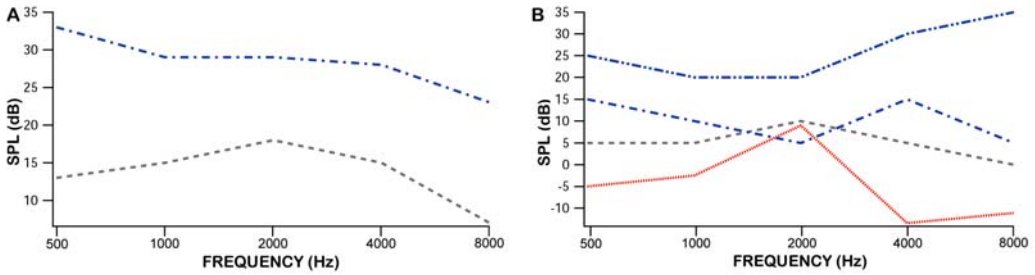

FIGURE 3.17 – Audiograms from Dalton 1968 comparing different techniques. **A**. *C. capucinus* audiograms produced using GSR (— — —) and ECR (— · — · —). **B**. *M. mulatta* audiograms produced using CS (▪▪▪▪▪▪ - #3014 only), GSR (— — —), and ECR (— · — · — represents subject #583 and — ·· — ·· represents subject #614).

once at a given intensity (based on averaging 50 evoked potential responses) the same exact value was produced over and over (Dalton 1968:42).

In the end, Dalton was unable to achieve all the goals he set out to accomplish due to numerous problems encountered during testing: the capuchins were not compatible with the conditioned suppression technique; three subjects died during the study; and one of the macaques involved in two of the procedures had a pathological hearing condition. Therefore, it was not possible to do a statistical analysis of the data. However, Dalton was able to reach some tentative conclusions regarding differences in the techniques. The conditioned suppression procedure appeared to be the most sensitive of the techniques based on the low thresholds produced for the macaque subjects (Figure 3.17B) and also resulted in the least amount of intra- and inter-subject variability. However, it was also the most time consuming of the three techniques and proved to cause many challenges to the experimenter such as differential deprivation (food) schedules for each of the subjects and an inability for automated programming (due to different requirements for each of the subjects). The GSR procedure on the other hand proved to be much quicker and easier but resulted in higher thresholds (up to 14 dB higher), the second highest inter-subject

variability, and the highest intra-subject variability. The ECR procedure was the quickest of the methods but appears to be the least sensitive of the three and resulted in the highest degree of inter-subject variability (Figures 3.17A and 3.17B). As a result, Dalton feels it would be unwise to speak of a "typical" (mean) threshold statement from the ECR data (1968:50). Based on these findings, Dalton ranked the techniques in the following order: 1) Conditioned suppression is the preferred method when accuracy of threshold determination is desired but time is not a factor; 2) ECR when time is a factor and intra-subject reliability is necessitated; 3) GSR when a rapid estimate of the threshold is desired with no major concern for overall reliability (1968:iii).

One additional point worth highlighting, not discussed by Dalton, is the degree of correspondence between the shapes of the audiograms produced by the different procedures. Figure 3.17B shows that despite the difference in threshold values between the conditioned suppression and GSR techniques there is considerable similarity in their shapes. Both show the highest values (respectively) at 2 kHz, the lowest values at the higher frequencies, and an upward trend in the slope at 1 kHz. However, the degree of separation between the two curves is variable and changes at each frequency. As for the ECR procedure there does seem to be some similarity in shape when compared with the GSR audiograms in cebus monkeys (Figure 3.17A), particularly at 1 kHz and above. On the other hand, the ECR curves for the rhesus macaques could hardly be more different from the audiograms produced by conditioned suppression and GSR procedures. Only with further testing with more subjects and frequencies explored will it be possible to verify a true relationship between the shapes of audiograms produced using the conditioned suppression and GSR procedures.

DALTON, TAYLOR, HENTON, and ALLEN 1969

The following year, Dalton and colleagues applied the conditioned suppression technique to establish thresholds in a larger sample of rhesus macaques (four adolescent *M. mulatta*). The frequency range was the same (0.5 to 8 kHz) and the tones were presented exclusively with the "audio-helmet" (Dalton *et al*. 1969:178). Again, there was no mention of calibrating the intensity levels. The training and testing were essentially the same as in the previous study except that a single testing session consisted of ten suppression trails (instead of 12), five control trials, and five baseline trials. As previously demonstrated, the range of intra-subject variability was found to be low (< 2 dB) and the thresholds were as reliably reproduced across sessions as they were within sessions (Dalton *et al*. 1969:179). The individual thresholds, ranges, and species means are given in Appendix 15.

Figure 3.18A shows the species mean as well as individuals audiograms for all subjects. The inter-subject range never exceeded 10 dB at any frequency and the mean for all frequencies was 8 dB. The only mention of how these results measure up to prior studies (Fujita and Elliot 1965; Stebbins *et al*. 1966) was to state that they are comparable to those previously established if only "a bit lower" (Dalton *et al*. 1969:180). However, they failed to mention the fact that their data did not show the mid-frequency dip that is evident in both the *M. mullata* data of Fujita and Elliot (1965) at 2 kHz (reward technique) or the 4 kHz dip in the macaque data (*M. fascicularis* and *M. nemestrina*) of Stebbins *et al*. (1963) (Figure 3.18B). The lack of this dip is probably what accounts for their data being "a bit lower" since the 500 Hz and 8 kHz points are very similar to the *M.*

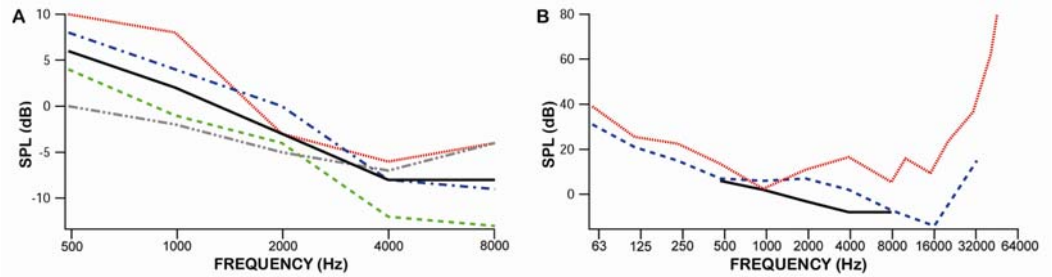

FIGURE 3.18 – *M. mulatta* audiograms from Dalton *et al*. 1969. **A**. Species mean (▬▬▬) and individual audiograms (▪▪▪▪▪▪ represents subject #508, ▬ ▪ ▬ ▪ ▬ represents subject #557, ▬ ▬ ▬ represents subject #566, and ▬ ▪ ▬ ▪ ▬ represents subject #608). **B**. *M. mulatta* mean audiogram (▬▬▬) compared with macaque mean (▪ ▪▪▪▪) from Stebbin *et al*. 1966 and *M. mulatta* mean positive reinforcement audiogram (▬ ▬ ▬) from Fujita and Elliot 1965.

mulatta data of Fujita and Elliot (1965). One possible explanation for this discrepancy is that the experimental "audio-helmet" used by Dalton *et al*. (1969) had a reduction in frequency response at 2 and 4 kHz that was not corrected for with proper calibration.

BRAGG and DREHER 1969

The study by Bragg and Dreher (1969) was another attempt to compare three different procedures for determining auditory sensitivity. In this case, the techniques employed were negative reinforcement (shock), conditioned suppression, and GSR. The test subjects were 14 adult capuchins monkeys (*C. capucinus*) with an approximately even split between sexes. It was noted that there were no behavioral differences between the sexes during training and testing. However, the capuchins were found to be "high-strung, temperamental, and difficult subjects to work with" (Bragg and Dreher 1969:276). As a result it was impossible to train the animals to participate in either the conditioned suppression or GSR procedures. In addition, it was found during the GSR training that "a rhythmic pattern of skin resistance changes persisted which masked any responses to the

stimuli" (Bragg and Dreher 1969:276). Therefore, the only technique that resulted in threshold determinations was shock avoidance.

The shock avoidance procedure was similar to that used in other studies with a few variations. The response apparatus was a stainless steel touch screen located directly in front of the subjects. During training a small light behind the response screen was activated with tone onset and extinguished when the tone was terminated by a correct response. Once shock training began the light was removed. False negatives were punished with a low voltage continuous shock while false negatives received a higher voltage brief shock. This differentiation of shock intensities and durations was found to facilitate training in all but three of the subjects (initially 17 animals were used). The animals were tested in a plexiglas restraint chair housed inside of a double-walled sound room which had an ambient noise level that ranged from 56 to 64 dB SPL. Gross threshold values were determined using a descending method-of-limits in 4 dB intervals and threshold was defined as the lowest intensity at which a subject gave at least three correct responses for four presentations. In other words, Bragg and Dreher used a 75 to 100 percent response criterion instead of the traditional 50 percent response point. Afterwards, a single ascending and descending series was used to insure that the threshold limit had been achieved. The final thresholds represented the mean of five threshold measures obtained on five different days. Five frequencies were tested (0.5, 1, 2, 3, 4 kHz) and were presented using earphones that were inserted into the external auditory meatus. However, the exact SPL at the eardrum was not measured so it is not feasible to compare these results directly with other studies. Nevertheless, the internal results are of interest and the shape of the audiograms should still be relevant.

Regrettably, the audiogram for only one subject was presented (that later suffered from marked hearing loss described below) although it was stated to be representative of the animals in the group (Bragg and Dreher 1969:275). Comments also were made as to the variability of the thresholds of the group. The intra-subject variability was found to be low, but there were apparently "wide" differences between individuals, although no exact values were given (Bragg and Dreher 1969:277). The inter-subject variability was statistically significant ($P < 0.001$) but the intra-subject variances did not differ significantly at any of the test frequencies. The authors suggested that "the placement of the earpiece inserts could have been a contributing factor in the threshold variations between animals" (Bragg and Dreher 1969:277).

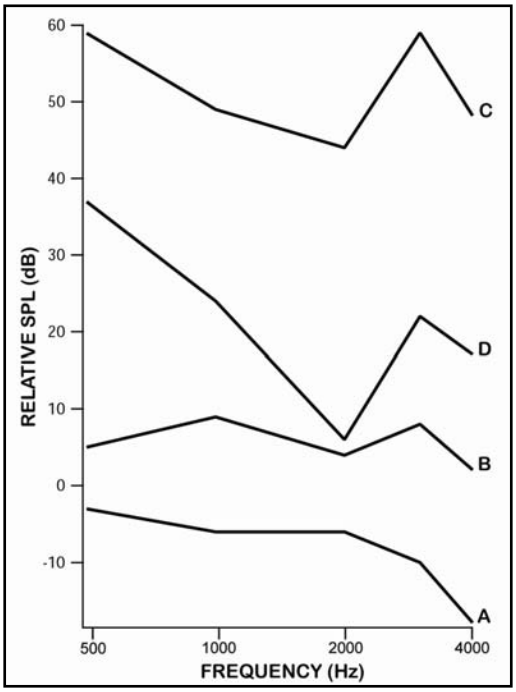

FIGURE 3.19 – *C. capucinus* audiograms for subject 7N8 from Bragg and Dreyer 1969. Curve A represents the normal audiogram produced using shock avoidance. Curve B is the audiogram produced after stapedectomy surgery. Curve C shows the elevated thresholds produced by an infection caused by the surgery and Curve D shows the thresholds after antibiotic treatment.

The audiogram for subject 7N8 (which appears to be the same subject used in the study by Dalton 1968) is presented in Figure 3.19 as the curve labeled A. It displays a slight elevation at 2 kHz but there is no distinct mid-frequency dip. The most sensitive frequency tested occurred at 4 kHz. After this audiogram was determined the animal was subjected to stapedectomy surgery which resulted in hearing loss at all frequencies with a mean loss of 14.2 dB (Figure 3.19, curve B). Forty-five days after the surgery, another hearing loss was detected (curve C) that was caused by an infection from the surgery and resulted in a 46.2 dB mean loss. Exploratory surgery revealed that the entire middle ear was occupied by edematous mucosa with passive congestion (Bragg and Dreher 1969:276). Six weeks after the second surgery and continued antibiotic treatment the hearing sensitivity returned near to the levels (30.6 dB mean increase) just after the stapedectomy (curve D). These curves are depicted to illustrate the effects of changes in middle ear structure on hearing sensitivity at different frequencies.

HEFFNER, RAVIZZA, and MASTERSON 1969

The first prosimian to be tested for hearing sensitivity was the bushbaby (*Galago senegalensis*) in a study by Heffner, Ravizza, and Masterson (1969a). The study was actually the fourth in a series examining the evolution of hearing in primitive mammals leading up to humans (Ravizza *et al*. 1969a, 1969b; Heffner *et al*. 1969b). Their subjects were two adult wild-born and experimentally naïve bushbabies. They used the increasingly popular conditioned suppression technique to establish thresholds. The animals were trained to lick a water spout to obtain a food reward. Once the lick rate became stable, a 10 second tone was introduced and at its offset a mild shock was

delivered to the subject's feet. After a few repetitions of the tone-shock pairing the subject would stop licking the water spout. During testing the threshold was determined using a mean suppression ratio of 0.50 as defined above (Dalton 1968). Controls trials were also included in every testing session without delivering a shock but all false negatives during a threshold trial included a shock. The psychophysical procedure used two methods: first a method-of-limits technique to estimate the threshold and then a final determination using the constant stimuli method, both with 5 dB intervals. The animals were tested in an oval cage placed in a burlap draped acoustical chamber. The test frequencies ranged from 0.250 to 64 kHz in one octave intervals and all tones were delivered with an extended range loudspeaker (0.03 to + 70 kHz). SPL's were calibrated by placing a microphone in the position of the animal's heads and measuring tones from the speaker at zero degree incidence (pointing directly at the speaker).

Appendix 16 presents the individual thresholds, ranges, and species means. The mean range for all frequencies is 5.1 dB. These values produce an audiogram (Figure 3.20A) that is somewhat different from the common peak-dip-peak pattern evident in most of the previous anthropoid graphs. There is a slight peak at 500 Hz and a dip at 1 kHz but this is driven by the inversion at these frequencies by one of the two subjects. The other subject shows more of a gradual decrease in threshold values down to 8 kHz at which point both individuals show little variation up to 64 kHz. The most sensitive frequency is at 8 kHz (4 dB SPL) but is only 2 dB lower than the value for 32 kHz (6 dB SPL) and 4 dB lower than the intermediate frequency at 16 kHz (8 dB). This results in a rather wide range of best sensitivity between 8 and 32 kHz (Heffner *et al*. 1969a:20). The threshold for 64 kHz was 57 dB SPL which with minor extrapolation implies a value over

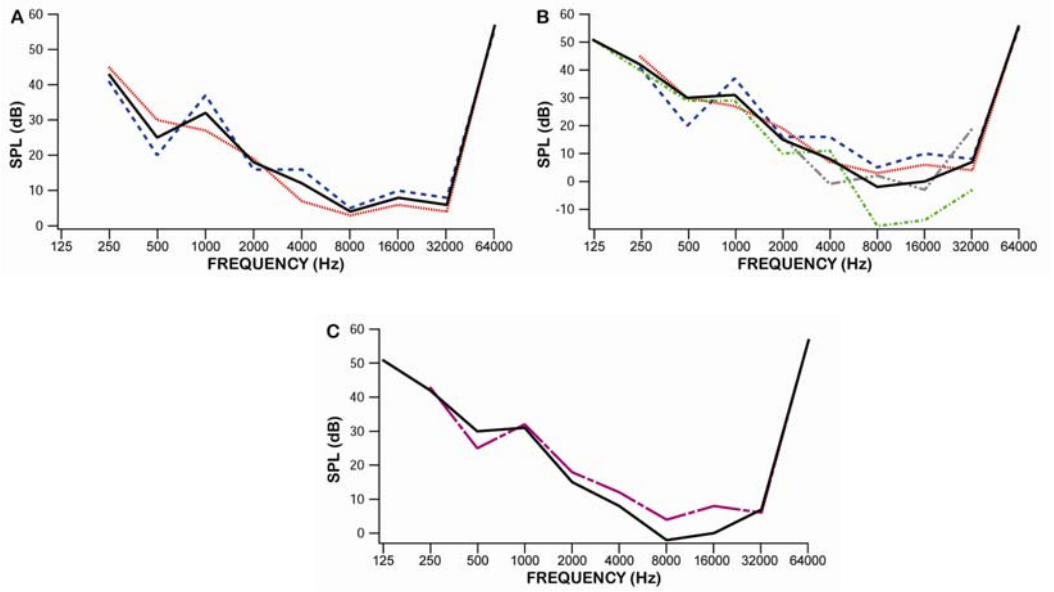

FIGURE 3.20 – *G. senegalensis* audiograms from Heffner *et al*. 1969. **A**. Species mean (——) and individual audiograms (– – – represents subject A and ▪▪▪▪▪▪ represents subject B) from original study. **B**. Audiograms for the two subjects from the original study (coded as for Figure 3.20A) and those for subjects C (— ·· — ··) and D (— · — ·) in addition to the resulting species mean (——). **C**. Comparison of the mean audiograms based on original two subjects (—— – —) and all four subjects (——).

65 kHz for the high frequency cutoff at 60 dB SPL. Heffner *et al*. took it several steps further to suggest that bushbabies can hear tones as high as 70 kHz at 80 dB SPL (1969a:20), although it appears from the audiogram that the intensity level would not have to be quite that high. Either way, this is at least 15 kHz higher than any monkey tested to date. The authors point out that although this seems to be a rather lofty high frequency limit, it is not unusual when compared with other mammals (*e.g*., opossum, hedgehog, and tree shrew). Conversely, they suggest that the lack of sensitivity to tones above 32 kHz (as in chimpanzees and humans) is a rare occurrence among extant mammals (Heffner *et al*. 1969a:21). Heffner and colleagues use the results from this study together with previously attained data on the opossum, hedgehog, and tree shrew to

propose several trends in the evolution of hearing leading up to humans (although as in the Seiden study, this represents a *scala naturae* conception of evolution): 1) high frequency sensitivity is a normal characteristic of non-hominoids; 2) overall and low frequency sensitivity improved markedly at least until the prosimian stages of man's (human's) lineage; and 3) the best frequency of animals in man's (human's) lineage probably remained in the 8 to 16 kHz range until after the prosimian stage was achieved. This may have been a lot of speculation after testing only one species of prosimain, but as subsequent studies on several other prosimians and monkeys have shown, many of their suggestions were probably not far off the mark. They proposed that attention should now (then) be turned to the identification of the anatomical changes accompanying this change in hearing capacity and the sources of selective pressure which caused them (Heffner *et al*. 1969a:21).

Although the initial study included only two animals, data on two additional subjects has been made available on the website from Heffner's Comparative Hearing Research Laboratory at the University of Toledo. These data are also included in Appendix 16.One of these subjects contains only partial data (animal C – 6 thresholds), while the other (D) did not produce a threshold at 64 kHz but was the only one of the group to generate a threshold at 125 Hz. When these data are added to the other two audiograms, the mean range for all frequencies is increased to 14.8 dB (Figure 3.20B). The largest deviation appears to be the extremely low value of -16 dB SPL at 8 kHz for animal D. Figure 3.20C shows that shape of the mean audiogram is only minimally altered compared to the mean audiogram produced using the first two specimens. The minor peak at 500 Hz now becomes essentially flat between 500 and 1000 Hz and the

frequencies above 16 kHz are unaffected. The primary difference is that the peak at 8 kHz becomes slightly more pronounced and is 6 db lower. Although subjects C and D may have been excluded from the original publication because of their more erratic thresholds, there seems to be no reason to exclude these subjects from the mean audiogram for the species.

HEFFNER and MASTERSON 1970

The next prosimians to be tested were members of the Lorisinae and consisted of two pottos (*Perodicticus potto*) and two slow lorises (*Nycticebus coucang*). One male and one female were represented for each species and all were judged to be young adults (Heffner and Masterson 1970:176). The training and testing procedures, testing apparatus and sound production equipment were exactly the same as in the previous study (Heffner *et al*. 1969) and will not be described. The individual thresholds, ranges, and species mean are given in Appendix 17 for all four subjects and presented in Figures 3.21A (loris) and 3.21B (potto).

The ranges for the slow loris thresholds are quite small at the lower frequencies but get as large at 18 dB at 8 kHz with a mean value for all frequencies of 7.4 dB. Heffner and Masterson state that it is a usual feature of audiograms to vary more at high frequencies than lower ones and this variation is due to individual differences in the conducting apparatus of the middle ear or in the elasticity of the basilar membrane (1970:179). Since the response properties of these structures are affected by aging, this may explain why the audiograms of older individuals often show reduced high frequency sensitivity. The shape of the loris audiogram shows many of the characteristics seen in

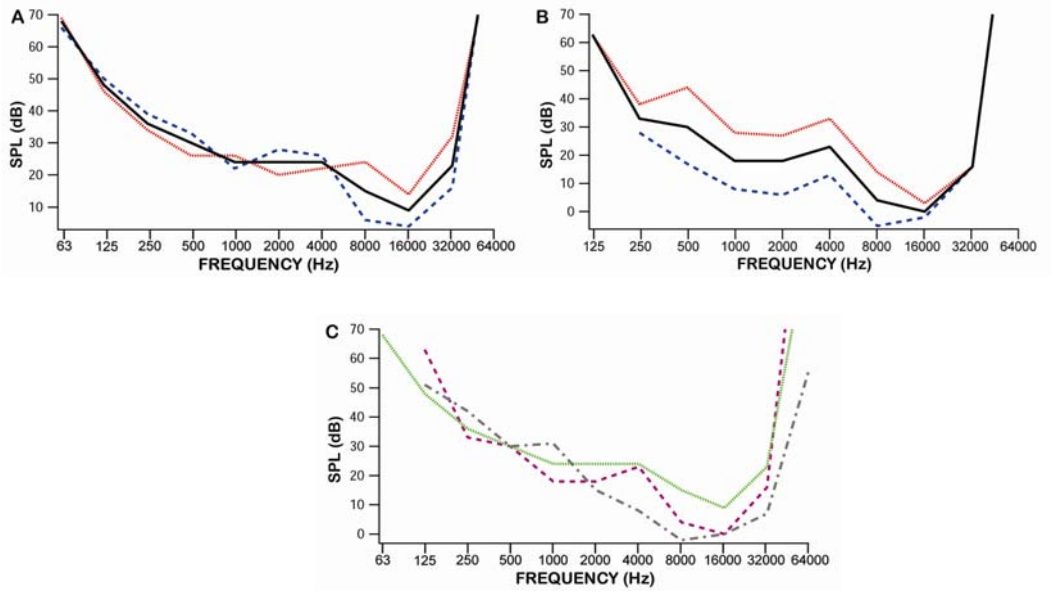

FIGURE 3.21 – Lorisoid audiograms from Heffner and Masterson 1970. **A**. Species mean (▬▬▬) and individual audiograms (▪▪▪▪▪▪ represents subject A and ▬ ▬ ▬ represents subject B) for *N. coucang*. **B**. Species mean (▬▬▬) and individual audiograms (▪▪▪▪▪▪ represents subject A and ▬ ▬ ▬ represents subject A) for *P. potto*. **C**. Comparison of species mean audiograms for *G. senegalensis* (▬ ▪ ▬ ▪ ▬), *N. coucang* (▪▪▪▪▪▪), and *P. potto* (▬ ▬ ▬).

the galago audiogram but not common to monkey hearing curves. In the mean audiogram there does not appear to be a mid-frequency dip but this may be an artifact of averaging. When considering the curves separately, there does appear to be small dip at 8 kHz in loris A and at 2 kHz in loris B. Still, the peak to the left of these dips is very minor in comparison to the primary peak which is centered at 16 kHz in both lorises (although loris B is only 2 db less sensitive at 8 kHz). On the low frequency side, the loris audiogram is approaching the low frequency cut-off with a value of 68 dB SPL at 63 Hz. On the other side of the graph, there is a strong roll-off above 32 kHz and the high frequency cutoff at 70 dB SPL is 48 kHz.

In general, the potto thresholds are much more variable than those of the lorises although there is not the same criss-crossing pattern visible in the latter. The threshold

ranges get as large as 27 dB at 500 Hz and show a mean range for all frequencies of 13.6 dB. Unlike the loris audiogram, the majority of the variation is found at the middle and lower frequencies, while the upper frequencies are almost perfectly consistent. Heffner and Masterson ruled out the possibility of measurement error to explain the different sensitivity of the two subjects since both had a low false positive rate and similar psychophysical functions (1970:179). Therefore they considered these audiograms to represent the true variation of hearing sensitivity in *P. potto*. Despite the high range of threshold values, the shapes of the curves show many similarities. In both subjects, there is a noticeable mid-frequency dip at 4 kHz, but again the low frequency peak is virtually nonexistent. It is difficult to evaluate the far low frequency side of the curve since only potto A produced a threshold at 125 Hz. The point of maximum sensitivity for potto A is at 16 kHz but at 8 kHz for potto B. Although potto B's threshold is 6 dB lower at the most sensitive frequency, the mean point of maximum sensitivity is still at 16 kHz due to the fact the potto B is only 3 dB less sensitive at 16 kHz compared with 8 kHz. Therefore, is seems fair to characterize the range of maximum sensitivity as lying between 8 and 16 kHz in pottos. The high frequency slope is also similar to the loris audiogram but the high frequency cutoff at 70 db SPL is 43 kHz.

Figure 3.21C presents the mean audiograms of galagos, lorises, and pottos. It can be seen that, in general, all three curves share many characteristics as previously described. The loris appears to be more sensitive than pottos at frequencies below 250 Hz (15 dB at 125 Hz) and at the high frequency cutoff (5 kHz), while the opposite appears to be true at most other frequencies (mean of 7 dB from 1 to 32 kHz). Galagos in comparison, seem to have low frequency sensitivity that is slightly less than that of pottos

or lorises at most frequencies but have superior high frequency sensitivity from 16 kHz to the cutoff point (the high frequency cutoff is18 kHz higher than the Lorisinae average). Galagos also appear to have the lowest threshold at best frequency but the difference with pottos is only 6 dB and it should be kept in mind that the galago average was lowered slightly by the inclusion of Galago D which had a threshold at 8 kHz that was 11 dB lower than that of any other galago individual. Therefore, the differences between galagos and pottos in this trait is probably not significant. However, the difference in thresholds between pottos and lorises at best frequency is 11 dB. In summary, lorises appear to have better sensitivity than pottos in the extreme low frequency range, pottos and galagos are more sensitive at the best frequency, and galagos have a considerably higher high frequency cutoff than either pottos or lorises. Heffner and Masterson previously demonstrated that there is an inverse correlation between high frequency cut-off and the functional distance between the outer ears due to the demand for accurate sound localization (Masterson *et al*. 1969). They suggested that this explains the superior high frequency sensitivity of galagos since they have a smaller ear separation than the Lorisinae, although the values they presented were only 2 mm different for the two groups. This is an interesting idea that deserves further consideration.

GOUREVITCH 1970

The book chapter by Gourevitch (1970) was an in-depth discussion of the methods used to obtain absolute thresholds and critical bands in monkeys and rats. Although little new data were presented, unpublished threshold data for two *M. nemestrina* were given and will be briefly discussed (no information was given as to

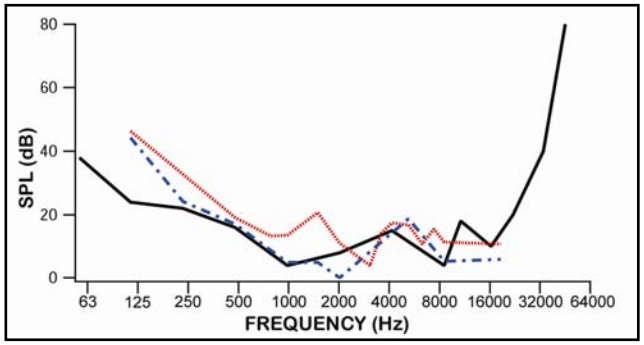

FIGURE 3.22 – Individual *M. nemestrina* audiograms (▪▪▪▪▪▪ represents subject A and ▬ ▬ ▬ represents subject B) from Gourevitch 1970 compared with *M. nemestrina* audiogram (▬▬▬) from Stebbins *et al*. 1966.

the age or sex of the subjects). The techniques employed were nearly identical to those used by Stebbins *et al*. (1966) with the exception that mild shock was occasionally used along with time-outs as punishment for responses made during inter-trial intervals. The thresholds, ranges, and species mean are given in Appendix 18. The average range for all frequencies is 6.4 dB, with the greatest variability occurring in the middle frequency range (7.7 dB). The audiograms for both individuals, along with the *M. nemestrina* audiogram from Stebbins *et al*. (1966) are presented in Figure 3.22. There is good agreement between these two studies at all frequencies except 125 Hz, where the Stebbins *et al*. (1966) audiogram is around 20 dB lower than that of Gourevitch (1970).

MITCHELL, GILLETTE, VERNON, and HERMAN 1970

In 1970, the only group of primates that had not been the subject of auditory testing was lemuroids (Mitchell *et al*. 1970:531). This problem was rectified by a series of studies by Mitchell and colleagues (Mitchell *et al*. 1970; Mitchell 1970, Mitchell *et al*. 1971; Gillette *et al*. 1973). The test subjects for the first study (Mitchell *et al*. 1970) were

six lemurs, consisting of males and females of each of three species (*Lemur catta*, *Eulemur fulvus*[18], and *Eulemur macaco*[19]). Three were judged to be adolescents (one *L. catta* and both *E. fulvus*) and the other three adults. The animals were trained and tested in small cages inside of a double-walled acoustic chamber lined with convoluted foam rubber and all tones were produced by an extended range speaker. The sound field was calibrated by moving a lemur-size paper-maché model with a microphone placed over it's "ear" to various positions favored by the subjects during testing and measuring intensity levels for each frequency (Mitchell *et al*. 1970:532). The average of all positions was taken as the calibration factor for that frequency. The frequencies investigated were: 0.1, 0.2, 0.5, 1, 2, 4, 8, 15, 25, and 40 kHz with a maximum intensity of 55 dB SPL.

The training procedure was a modification of the two lever method used by Stebbins *et al*. (1966). First the animals were trained to press a black bar for food reward. Next a tone was introduced and responses in the presence of the tone resulted in reward but responses in the absence of a tone (false positives) resulted in a 10 second lights out period. Once a response criterion was met, a second white bar was introduced. A single press of the white bar triggered a 10 second tone and responses on the black bar during tone presentation were considered hits (true positives) and were rewarded with food. The number of presses of the white bar necessary to start a tone was increased using a variable ratio schedule up to 10 presses in order to minimize temporal responding. The training criterion was 90% hits and less than 10% false positives, but the lights-out period proved ineffective at meeting the false positive standard. Therefore, a mild 0.5 second shock was added to the lights-out punishment to control for false positive responses.

[18] At the time of the study *Eulemur fulvus* was designated *Lemur fulvus*.

[19] At the time of the study *Eulemur macaco* was designated *Lemur macaco.*

Although this addition did bring down the false positive rate it also increased the miss rate. Consequently, an empirical balance between food deprivation and shock had to be maintained eventually resulting in achieving the training criterion. The psychophysical technique was the method of constant stimuli using intervals of 2, 3, and 5 dB according to the animal's performance. The threshold testing was considered complete when values for three days were within 6 dB of each other and showed no further reduction in intensity. The threshold estimates using the 50% correct standard were never more than 3 dB from the "raw data" (Mitchell *et al*. 1970:533).

The individual thresholds, ranges, and species means are reported in Appendix 19. Inspection of the thresholds for ring-tailed lemurs (*L. catta*) and Figure 3.23A show that up to 8 kHz both subjects show relatively good agreement but above this frequency the two curves diverge considerably. Considering all frequencies, the mean range is 14.8 dB with a maximum range of 49 dB at 15 kHz. Mitchell *et al*. proposed two factors which may explain the extremely high thresholds of lemur 2023 (1970:533). First, based on weight and dentition this subject appears to be an old animal. Second, shortly after acquisition, 2023 developed an infection on the left side of his face which may have caused damage to the auditory system. When the thresholds at 15 and 25 kHz are removed for this individual (it did not respond to 40 kHz at 55dB SPL), the mean range drops to 5.1 dB with a maximum single value of 14 dB at 4 kHz. Otherwise, the audiograms can be characterized as having a moderate roll-off at frequencies below 1 kHz (with minimal individual variation), a first peak of sensitivity between 1 and 2 kHz, and a modest notch at 4 kHz, although this dip is only evident in lemur 3183. Based

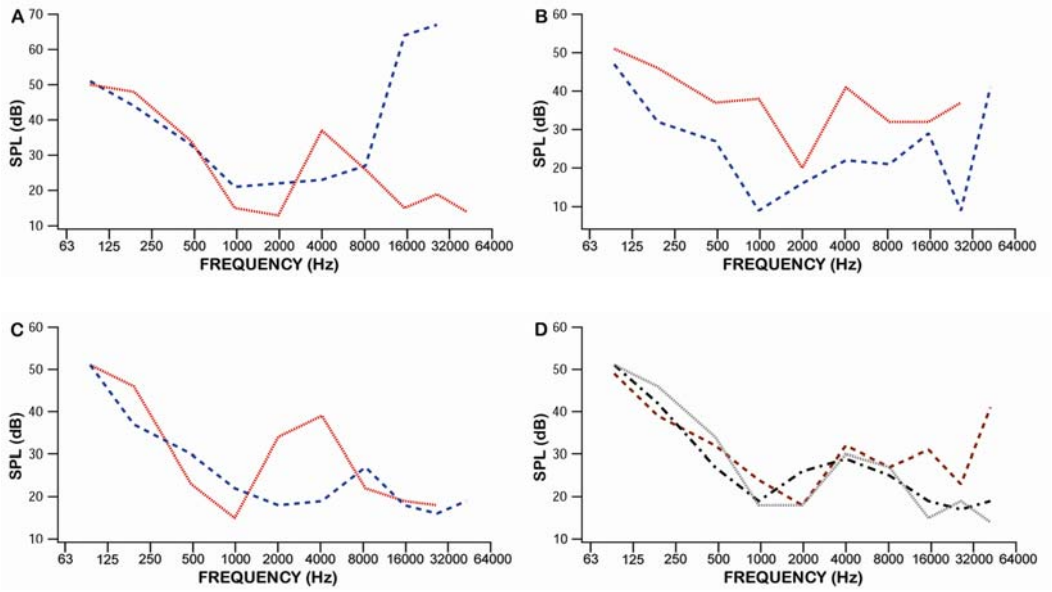

FIGURE 3.23 – Lemuroid audiograms from Mitchell *et al*. 1970. **A**. Individual audiograms for *L. catta* (▪▪▪▪▪▪ represents subject #3183 and — — — represents subject #2023). **B**. Individual audiograms for *E. fulvus* (▪▪▪▪▪▪ represents subject #3442 and — — — represents subject #3368). **C**. Individual audiograms for *E. macaco* (▪▪▪▪▪▪ represents subject #2548 and — — — represents subject #2549). **D**. Comparison of species mean audiograms for *L. catta* (▪▪▪▪▪▪), *E. fulvus* (— — —), and *E. macaco* (— ▪ — ▪ —). The *L. catta* audiogram includes data for only # 3183 above 8 kHz.

solely on 3183, ring-tailed lemurs appear to have good high frequency hearing from 15 kHz up to 40 kHz, the highest frequency tested.

The data for brown lemurs (*E. fulvus*) show a somewhat different pattern than the ones for *L. catta* (Figure 3.23B). The mean range for all frequencies is 13.6 dB but no particular frequency range seems to be solely responsible. Instead, it appears as though the audiogram for lemur 3442 is shifted slightly toward lower frequencies. Both brown lemurs show the first peak in the low-to-middle frequencies, followed by a dip, and a second peak at higher frequencies although this last trait is expressed most greatly in lemur 3368. However, the first peak is at 2 kHz for 3442 and 1 kHz for 3368, the dip is at 4 kHz for 3442 and 15 kHz for 3368, and the second peak is actually a flat region

between 8 and 15 kHz for 3442 while it forms a sharp peak at 25 kHz for 3368. Interestingly, both subjects show a fairly strong roll-off above their respective second peaks and lemur 3368 produced an intensity level of 41 dB SPL at 40 kHz (3442 did not respond to 40 kHz at 55 dB SPL). In general, black lemurs (*E. macaco*) show many of the patterns illustrated by ring-tailed lemurs (Figure 3.23C). The mean range for all frequencies is 7.4 dB and this is primarily accounted for by the variability at 2 and 4 kHz since there is relatively good agreement at the lower and higher frequencies. For example, the first peak occurs at 1 kHz for 2548 but has a broader range from 1 to 4 kHz for 2549, and the dip is at 4 kHz for 2548 but at 8 kHz for 2549. Both individuals show good sensitivity from 15 up to 40 kHz with no discernable roll-off, similar the result for *L. catta*.

Figure 3.23D depicts the mean audiograms for all three species (the curve for *L. catta* includes only the data for 3183 for frequencies above 8 kHz). All three audiograms share the following characteristics: At 1 kHz and below the thresholds for all species are within 7 dB of each other with a mean range of 5.5 dB; The first peak falls between 1 and 2 kHz; the dip occurs at 4 kHz. However, at the higher frequencies there is a clear break between *E. fulvus* on the one hand and *L. catta* and *E. macaco* on the other. Mitchell *et al*. noted this by stating that at 25 kHz two of the animals exhibited the start of their high frequency cutoff but the remaining animals demonstrated sensitivity that was within 3 dB of their most sensitive frequency and at 40 kHz two of the subjects (one *L. catta* and one *E. macaco*) were within 1 dB of their most sensitive threshold (1970:534). It is peculiar that they did not point out that the two that were approaching their high frequency cutoff were both brown lemurs. Furthermore, in a subsequent publication they stated that “no

differences in acuity were found among the three species" (Mitchell *et al*. 1971:710). However, the mean thresholds at 40 kHz are 14, 19, and 41 dB SPL for *L. catta*, *E. Macaco*, and *E. fulvus* respectively, a difference of 27 and 22 dB! It is also worth pointing out that the brown lemurs represented two of the three adolescents in the group, so their inferior high frequency sensitivity can not be attributed to age. Recently, an article by Heffner (2004-see below) presented some unpublished data on brown lemurs which had a high frequency cutoff at 60 dB SPL for brown lemurs at 43 kHz compared to a value of 58 kHz for ring-tailed lemurs. This supports the idea that *E. fulvus* is significantly less sensitive than *L. catta* at the upper end of its hearing range.

Mitchell *et al*. compared the results from this study (as one mean audiogram) with data on lorises, pottos, galagos, chimpanzees, and marmosets (all referenced above) and came to the conclusion that prosimians seem to have less overall sensitivity in the lower and middle frequencies than anthropoids but better sensitivity to higher frequencies (1970:534). Their final comment concerned the difficulty of working with the two-lever procedure for lemurs, recommending that it should not be used with this group. They illustrated the time-consuming nature of this technique with these animals by citing the example that it required from 1680 to 8850 trials to sample a 20 dB range around an estimated threshold value. The next report in this series sought to remedy this problem.

MITCHELL 1970, MITHCHELL, VERNON, AND HERMAN 1971

The next investigation in the study of lemur hearing was an unpublished Master's Thesis by Mitchell (1970) and a subsequent publication the following year (Mitchell *et al*. 1971). In this study, Mitchell focused exclusively on ring-tailed lemurs (*L. catta*) and

employed a slight modification of the single-lever shock avoidance method of Clack and Herman (1963). The testing consisted of two types of trials, tone and blank trials, that were accompanied by a white light above the response lever. A lever press during the presentation of a tone avoided the shock (paired with a red light) but a miss always resulted in shock (Clack and Herman used intermittent reinforcement for false negatives). Blank trials consisted of the white light only and false positives during this period resulted in shock (although of shorter duration than for a miss). The shock levels in the present study (0.4 to 0.8 ma) were generally at lower levels than in the previous study (0.5 to 1.6 ma). It was felt that excessive punishing for false positives (intra- and inter-trial) could result in elevated threshold estimates (Mitchell *et al*. 1971:710). The tone and blank trials each had a 0.5 probability of occurring with a variable interval (8 to 15 seconds) between trials. Another difference with the previous study was that the staircase method of intensity attenuation was used instead of the method of constant stimuli even though the authors acknowledged the work of Stebbins (1970) that suggested that auditory thresholds are insensitive to the psychophysical method. The final thresholds were determined using 2 dB attenuation intervals. The test frequencies were the same as in the previous study except for the inclusion of 32 kHz. The final difference between studies was that the speaker placement was changed from directly overhead to directly in front of the subject. The other aspects of the testing and threshold determination (*e.g*., threshold criterion, sound production equipment, calibration, etc.) were the same as in the previous study. Initially, eight subjects started the training but two of them never reached the 90% criterion for avoidance response training and a third produced partial results but continued to exhibit high false positive rates throughout testing. The five remaining

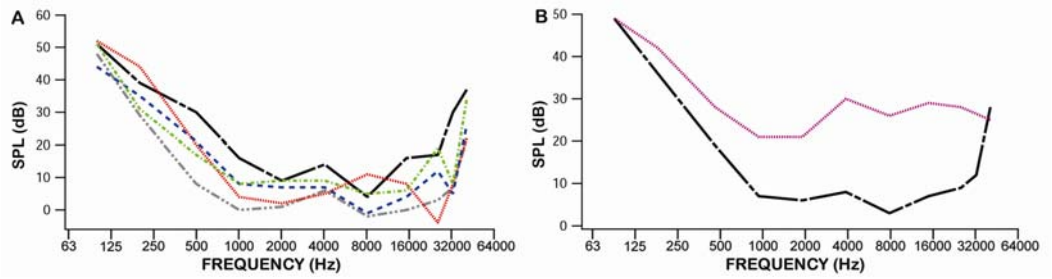

FIGURE 3.24 – *L. catta* audiograms from Mitchell 1970, Mitchell *et al*. 1971. **A**. Individual audiograms (— . . — . . represents subject #674, ——— — ——— represents subject #2023, ▪▪▪▪▪▪ represents subject #2024, — . — . — represents subject #2311, — — — represents subject #4059). **B**. Comparison of audiograms for subject #2023 from Mitchell *et al*. 1970 (▪▪▪▪▪▪) and current study (——— — ———).

subjects were four adult males and one adolescent female. Curiously, lemur 2023, the anomalous subject from the previous study was also included.

Individual thresholds, ranges, and species means are given in Appendix 20 and the resulting individual audiograms presented in Figure 3.24A. The mean range for all frequencies was 15.5 dB. Inspection of Figure 3.24A shows that lemur 2023 produced higher elevations than most other subjects at nearly all frequencies tested. If this animal's values are removed from the mean range calculation the value drops to 10.5 dB. Also evident from this figure is that lemur 674 expands the ranges considerably, especially at lower frequencies. Although this animal was not removed from the study because it achieved the 90% avoidance criterion, throughout training and testing lemur 674 produced much higher than average false positive rates (42%) requiring adjustment of at least two procedures (elimination of the white light and threshold criterion at 40 kHz). The deviation for this lemur from the mean (lower thresholds) is exactly in the direction one would expect from a high rate of false positives. If the values for 674 are removed

from the mean range calculation (in addition to 2023) the values drops even further to 8.5 dB, nearly half the original estimate.

The most obvious observation from these data is that at most frequencies the lemurs are more sensitive than suggested by the previous study (Figure 3.24B). A Mann-Whitney U test revealed that there was a significant difference in threshold values for all frequencies except 0.1 and 40 kHz at a 0.05 level of significance (0.5 to 15 kHz with a 0.01 level of significance). Therefore, it was concluded that the previous study produced elevated threshold levels for all frequencies except at the extreme low and high end of the range (Mitchell 1970:30; Mitchell *et al*. 1971:710). However, this does not render the findings of the previous research useless. The results should still be internally consistent (comparing the different lemur species) and in any case, the apparent difference between brown lemurs and the other two species was at frequencies that were unaltered in the present study.

Mitchell examined three factors that may have produced the elevated thresholds in the previous study: 1) speaker placement, 2) practice effects, and 3) methods. Although the speaker was placed in different positions in the two studies, it seems unlikely that this would account for the differences. Mitchell compared the sound field variations that were used to calibrate the SPL's in each study and found there to be only one frequency (15 kHz) that could have resulted in slight differences between the studies. This possibility was further discounted because the high range of variation found at this frequency was produced by one "deviant" point (microphone measurement) in the previous study and 11 other measurements were within the range of those in the present study (Mitchell 1970:30). Mitchell also considered the effect of speaker position on the

"pinna shadow" but rejected this explanation because it should have had the strongest influence on the highest frequencies, which was not the case. Considering the amount of practice required to train the animals in the previous study (at the exact frequencies that were most affected), practice effect was also not considered as a plausible explanation.

The most likely explanation for the differences between the two studies was the conditioning procedure. It was proposed that the forfeit of food rewards in the previous study did not allow adequate control of the miss rate, plus all false positives (intra- and inter-trial) were punished with shock, producing elevated thresholds (Mitchell 1970:32; Mitchell *et al*. 1971:711). Although previous studies (Fujita and Elliot 1965; Heffner *et al*. 1969b) have not found significant differences between shock avoidance and positive reward techniques, Mitchell points out that these studies did not punish false positives with shock, and therefore did not have the same difficulties mentioned above (Mitchell 1970:33).

The final remarks in both reports concern comparing lemurs, and prosimans in general, with other mammals. They suggested that prosimians (tree shrews[20], lemurs, galagos, lorises, and pottos) appear to be more sensitive at lower frequencies than primitive mammals (hedgehog and opossum) but less sensitive than other primates (rhesus macaques, cynamolgus monkeys, squirrel monkeys, and humans). Based on the finding that anthropoids are significantly more sensitive than prosimians at lower frequencies (250, 500, and 1000 Hz) they proposed that not only is good low frequency hearing not a primitive mammalian trait (Masterson *et al*. 1969) but that it is not a primitive primate characteristic either. Mitchell also suggests that there is a progressive

[20] At the time of the study tree shrews were considered to be prosimians but are now placed in their own order.

loss of high frequency hearing going from prosimians, to monkeys, to humans (1970:37). Within prosimians, there does not appear to be much difference in high frequency sensitivity, but lemurs may be more sensitive at frequencies below 2 kHz and show a broader range of sensitivity from 1 to 32 kHz compared with lorisoids (Mitchell 1970:34; Mitchell *et al*. 1971:711).

GILLETTE, BROWN, HERMAN, VERNON, and VERNON 1973

The final study in the series (although Mitchell was not included in this publication) examined the high-frequency range of ring-tailed lemurs. The frequencies examined ranged from 8 k to 75 kHz and the tones were tested at higher intensities than in the previous studies. The subjects included three lemurs from the previous study (2023, 2311, 4059) in addition to a young adult female. The training procedures, threshold testing techniques, and criteria were the same as used in the previous study (Mithchell *et al*. 1971). The only significant difference was in the method used to calibrate the SPL's. The accurate measurement of intensity levels presents many difficulties at high frequencies (>25 kHz) due to the small wavelengths and minor differences in position that can produce intensity differences as high as 30 dB (Vernon *et al*. 1966). Therefore, a new method was employed in this study which utilized "hot spots" or areas of maximum intensity, as the estimate of the "true" intensity value (Gillette *et al*. 1973:367). The authors discovered two hot spots of equal intensity, teardrop in shape, that were located on the transducer axis approximately two and ten inches inside the cage. Since two of the subjects consistently "sampled" from these regions and a third

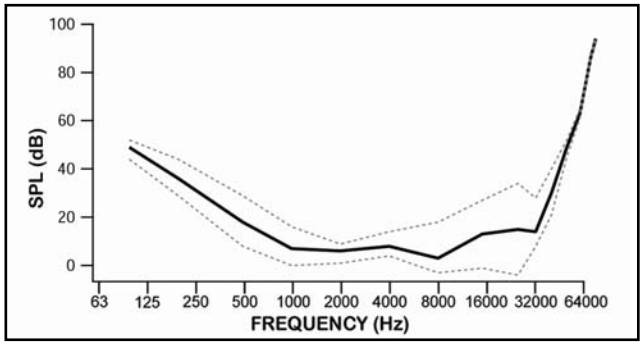

FIGURE 3.25 – Mean audiogram (▬▬▬) and individual ranges (– – –) for *L. catta* from Gillette *et al*. 1973.

animal in an area just adjacent, they were felt to best represent a conservative measure of the true intensity (Gillette *et al*. 1973:367).

The overlapping mid-range values (8 to 40 kHz) were averaged for the two studies and in only one case were there egregious differences between the threshold values (lemur 2023 showed a 25 dB difference at 15 kHz). The mean threshold values are given in Appendix 21 and the audiogram with approximate ranges is presented in Figure3.25. As this figure illustrates, the high frequency cutoff at 60 dB SPL is at 58 kHz and the 70 db SPL cut-off is around 63 kHz. The only effect of averaging the mid-frequency thresholds was that the values for 15 and 25 kHz are now 6 dB higher, resulting in a more prominent peak at 8 kHz. The ring-tailed lemur still shows good sensitivity ranging from 1 kHz (7 dB SPL) up to 32 kHz (14 dB SPL) with only a minor dip at 4 kHz. The slope on the low frequency side is relatively shallow and linear interpolation suggests a low frequency cutoff at 60 dB SPL of 67 Hz. The authors included this data into the comparison of primate hearing and proposed that there may be a trade-off between relatively good low versus relatively good high frequency sensitivity. They concluded that anthropoids have thresholds that are between 8 to 15 dB lower from

100 Hz to 3 kHz but do not display the same degree of high frequency sensitivity as prosimians (Gillette *et al*. 1973:368-369). However, it should be pointed out that the macaques tested by Stebbins *et al*. (1966) do show high-frequency sensitivity that is similar to that of the lorisoids yet retain the good low-frequency sensitivity found in other anthropoids. Therefore, being relatively more sensitive to either high- or low-frequencies does not appear to be an all or nothing situation. Gillette *et al*. (1973:369) restated the theory by Masterson *et al*. (1969) that good high frequency hearing is necessary for animals with small heads (and closely spaced ears) for accurate sound localization but that this trait was lost in anthropoids because their wider spaced ears provide larger disparities in time of arrival of sound waves to the two ears, thereby restoring sound localization ability. The authors then posed the question: How do New and Old World monkeys, and apes compare with prosimians in regard to the spacing between the ears? Although the appropriate comparison to test this hypothesis has not yet been attempted (then or now), as acknowledged by the authors, the fact that the macaques mentioned above most definitely have wider-spaced ears than either pottos or lories suggests that the relationship between high frequency sensitivity and ear spacing may not be as simple as previously assumed.

The final endeavor of this series on lemur hearing was to try and gain some insight as to other factors that may be selecting for heightened high-frequency sensitivity in this group. To do this, they recorded three "recognizably different" calls (although these did not include distress or alarm calls), and examined them using a spectrum analyzer. They found that the majority of sound energy was centered between 10 to 15 kHz with overtone components occasionally ranging as high as 30 kHz. Therefore, they

concluded that extreme high-frequency sensitivity was not needed for hearing these calls. However, it is interesting to note that the calls measured by Gillette *et al*. (1973), in addition to a much more extensive list compiled by Macedonia (1993), have primary frequency components that fall very close to the best range of hearing in this species.

GREEN 1971, 1975

The dissertation (1971) and subsequent publication by Green (1975) sought to compare the effects of aversive (negative reinforcement using shock) and appetitive (positive reinforcement using food) techniques on auditory sensitivity. The subjects were squirrel monkeys (*Saimiri sciureus*[21]) and the goal was to use the same experimental subjects in both procedures. Initially, the aversive experiments started with seven monkeys (an eighth was reserved for non-threshold testing procedures). However, three died during the course of experimentation and a fourth produced only preliminary and incomplete data due to problems with performance. The four remaining monkeys were also used in the appetitive experiment but subject 5 died during testing and subjects 1 and 2 did not meet the training criteria for appetitive threshold testing. Consequently, only subject 4 produced results for the appetitive procedure (and both techniques). All individuals were male and subjects 1 and 2 were adults, subject 4 was a juvenile and subject 5 was an adolescent during testing. The conditioning procedure for the aversive experiment was adapted from the reaction-time procedure of Stebbins (1966). The animals were trained to press and hold down a bar after the activation of a cue light until a tone occurred 0.5 to 4.5 seconds later. The release of the bar within one second of tone

[21] Similar comment as before for squirrel monkeys tested before *S. scuireus* was split into multiple species – the exact species is uncertain.

onset was counted as a true positive (hit) and avoided shock. Bar release after one second of tone initiation, bar release before tone onset, or not pressing the bar within two seconds of cue light activation resulted in shock. Responses during the 15 second inter-trial interval resulted in no reinforcement. Conditioning for the appetitive procedure was similar to the aversive procedure with a few exceptions. Releasing the response bar within one second of tone onset resulted in a food reward. The standard inter-trial interval (following a hit) was shortened to four seconds but bar release before tone onset or holding down the bar for more than one second resulted in an inter-trial interval of 15 seconds (essentially a time-out). Delayed bar press to the cue light and inter-trial responses had no consequences.

Thresholds were determined for both procedures using the method of constant stimuli and final thresholds represented the mean of the final three sessions that did not differ by more than 5 dB. Although the traditional 50% response point was used to interpolate the threshold values it was noted that a change of response from 100% detectability to no response spanned an intensity range of 15 to 30 dB. The test frequencies ranged from 0.125 to 32 kHz in octaves in addition to 40 and 46 kHz and were delivered using circumaural headphones. The headphones were calibrated by passing a condenser microphone through the headphone coupler and positioning it at the entrance of the external auditory canal. During calibration it was discovered that the ratio of sound energy of harmonics to the fundamental was relatively high at extremely low frequencies resulting in the exclusion of 60 Hz as a test frequency. Although it was also greater than 0.01 for 125 Hz (Green 1975a:105), the nature of the harmonic content was apparently considered acceptable since it was used in threshold testing. Testing was

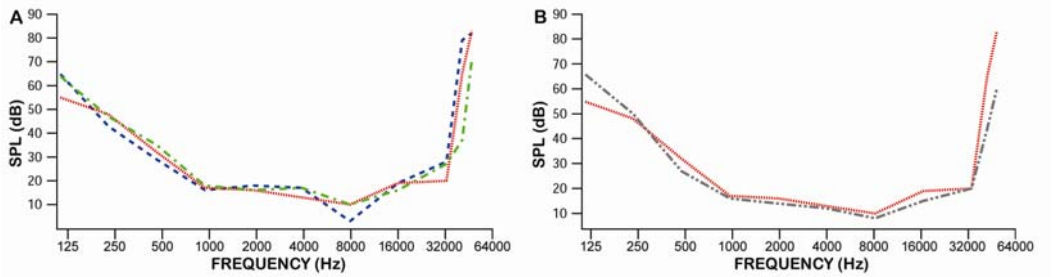

FIGURE 3.26 – *S. sciureus* audiograms from Green 1971 and 1975. **A**. Individual audiograms produced using aversive conditioning procedure (▬ ▬ ▬ represents subject #1, ▪▪▪▪▪▪ represents subject #4, and ▬ ▪ ▬ ▪ ▬ represents subject #5). **B**. Comparison of aversive (▪▪▪▪▪▪) and appetitive (▬ ▪ ▪ ▬ ▪ ▪) audiograms for subject #4.

conducted in a double walled acoustic chamber with ambient noise levels ranging from 40 to 60 dB SPL.

All individual thresholds for both procedures and the ranges and species means for the aversive procedure (excluding animal 2) are given in Appendix 22. Figure 3.26A plots the thresholds for the aversive procedure and it can be seen that there is close agreement between all subjects with a mean range for all frequencies of 8.9 dB. Although this is not an unusually high amount of variability, the threshold for subject 5 at 40 kHz is considerably lower than the value for the other two individuals. Excluding 40 kHz from the computation lowers the mean range to 5.6 dB. Figure 3.26B shows the single audiogram produced using the appetitive procedure along with the aversive audiogram for the same individual (4). Comparing the audiograms from the two different procedures, the values are quite similar in the 0.25 to 32 kHz region (Green 1971:79) with a mean difference of 2.1 dB. Green postulates that the "slight discrepancy" at 125 Hz may be attributed to masking effects of low frequency sounds and similarly, the differences at 46 kHz to problems related to measuring SPL at higher frequencies (Green 1971:79). Green does not address that fact that these thresholds were obtained in the

same chamber, using the same equipment and individual which would seem to minimize some of the problems he puts forth as explaining these differences. Including all frequencies the mean difference between the thresholds is 6.5 dB. Although not mentioned by Green, the appetitive audiogram is generally slightly below the aversive audiogram (except at 125 and 250 Hz), averaging 4.2 dB lower. Still, Green states that "in general, the results indicated that absolute threshold was invariant with the two procedures" (1971:86) and further that "sensory data are not influenced by the type of reinforcer used to maintain behavior during testing" (1975:261).

Green compared his data with monkey audiograms produced in previous studies and commented that the primary difference is in the absence of a distinct mid-frequency notch in his data (the negative reinforcement curve for *S. sciureus* produced by Fujita and Elliot 1965 also lacked the notch) (1971:53; 1975:262). However, since the positive reinforcement audiogram of the squirrel monkey by Fujita and Elliot did show a mid-frequency dip he rules out a true species difference for this feature (Green 1971:53), despite the fact that his positive reinforcement (appetitive) audiogram also lacked a significant notch. There is no comparison to the squirrel monkey data of Beecher 1974 (below) since the data in the Green study was collected before Beecher's publication. Green also noted that the threshold at the frequency of best sensitivity was a little higher than in previous reports but suggests this may be due to the stringent threshold criteria used in his study (1971:53). The only other shock avoidance study that attempted to determine the upper frequency limit of hearing was that of Seiden (1957) for *C. jacchus.* Green stated that although their appears to be over a 10 kHz difference in the upper limit (35 kHz for *C. jacchus* and 46 kHz for *S. sciureus*), it is likely that a difference of this

magnitude can be attributed to either dissimilarities in individual subjects (age) or experimental conditions (headphones vs. speakers) (1971:54). The first suggestion is ruled out by the fact that the only individual in Seiden's study that actually produced a threshold at 35 kHz was the youngest in the group (all others had a high frequency cut-off closer to 30 kHz). The possibility of a difference related to transducer type remains open to question. Nonetheless, Green proposes that high-frequency hearing is essentially the same in New and Old World monkeys (cutoff between 40 and 45 kHz) and is higher than that of the apes (Green 1975:261).

PUGH, HORWITZ, ANDERSON, and SINGLETON 1973

The purpose of the paper by Pugh *et al*. (1973) was to demonstrate a new method of measuring cochlear potentials in primates using a long term implant that preserves normal middle-ear physiology. Cochlear potentials are measurements of the electrical activity produced in the inner ear as a result of auditory stimulation. Although cochlear potentials do not mirror the sensitivity estimates obtained using behavioral methods (audiograms) they have provided valuable information on the function of the peripheral transducing mechanism in primates (Wever *et al*. 1958). However, this study determined behavioral thresholds for four pig-tailed macaques (*M. nemestrina*) for the purpose of demonstrating the pre- and post-operative effects of the surgical procedure required to implant the cochlear potential electrode. Two incidental functional observations were made and will also be reported.

The conditioning procedure used in generating the audiograms was the reaction-time procedure with a few variations. Briefly, the monkeys were trained to hold down a

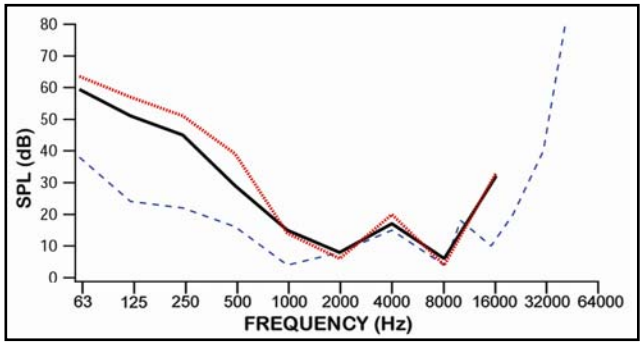

FIGURE 3.27 – Audiograms for *M. nemestrina* from Pugh *et al*. 1973: ▬▬▬ represents preoperative audiogram and ▪▪▪▪▪▪ represents postoperative audiogram for the same subject. The *M. nemestrina* audiogram (▬ ▬ ▬) from Stebbins *et al*. 1966 is also included for comparison.

key after the illumination of a red light signaling the start of a trail and then release the key at the sound of a tone resulting in food reward. False negatives (misses) were not punished and false positives resulted in a six second time-out (which also deactivated the red light). The psychophysical method was the staircase procedure and the intra-subject variability was reported to be less the 3 dB on a day to day basis (Pugh *et al*. 1973:353). The tones were presented with supra-aural headphones and the frequencies ranged from 0.06 to 16 kHz in octave steps.

The audiogram for only one monkey was presented and the threshold values are presented in Figure 3.27 and Appendix 23. This animal shows many of the features common to monkey audiograms: a first peak in sensitivity at 2 kHz, the mid-frequency dip at 4 kHz, and a second, slightly lower (2 dB) peak at 8 kHz. However, compared with the pig-tailed macaque measured by Stebbins *et al*. (1966) (Figure 3.27), this individual shows the first peak one octave higher (2 kHz instead of 1 kHz) and a higher threshold at 60 Hz, suggesting poorer low-frequency sensitivity. It is interesting to note that the slopes on the low-frequency side are similar (11.3 dB per octave versus 8.8 dB per octave from

0.06 to 1 kHz) suggesting that the downward shift in the first peak of sensitivity was correlated with a downward shift in the frequency low cut-off. The only other difference is that the subject in this study does not show the double-peak at the higher frequencies evident in the Stebbins *et al*. audiogram (which also appears associated with better high-frequency hearing). The agreement in the mid-frequency range is extremely good.

Also presented in Figure 3.27 is the audiogram for this monkey determined one month after the surgery to implant the cochlear potential electrode. The authors ascribed the loss of sensitivity, primarily in the lower frequencies, to fluid accumulation in the middle ear. The mean loss in sensitivity at frequencies below 1 kHz is 6.5 dB. This serves to illustrate the effects of middle ear volume on hearing sensitivity at lower frequencies. In another monkey, whose audiogram was not presented, it was noted that an inadvertent cementing of the incus during surgery resulted in a hearing loss that averaged 30 dB for all frequencies.

STEBBINS 1973

The article by Stebbins (1973) is essentially an updated review of the work to come out of his lab and incorporates data from several previously untested species. The species for which information is presented are all members of the Cercopithecinae and include: *Macaca arctoides*, *M. fascicularis*, *M. mulatta*, *M. nemestrina*, *Cercopithecus aethiops*, *Erythrocebus patas*, and *Papio papio*. The majority of subjects were juvenile and subadult males. The methods used to obtain audiograms (reaction-time procedure, headphone transducer, staircase method, etc.) are identical to those described for Pugh *et al*. (1973) and will not be discussed. The only difference is that frequencies were tested

from 63 Hz up to 45 kHz. In addition to determining auditory thresholds for pure tones, frequency difference and intensity differences thresholds (limens) were also determined for two macaque species and *P. papio*. Frequency and intensity difference thresholds are measures of the smallest interval an animal can detect in either tone frequency or intensity. Essentially the same procedure is used for determining both types of thresholds. The basic method will be described for obtaining frequency difference thresholds. All testing is conducted in the same sound attenuating chambers used to determine auditory thresholds. First, a pure tone is presented and the monkey is required to make contact with a metal disc located in front of the chair in which it is restrained. Following contact with the disc, a second tone is presented of a different frequency (or same frequency for catch trials) which alternates with the first tone for 2 1/2 seconds. The monkey's behavior is reinforced with food for correctly discriminating the frequency difference by breaking contact with the disc. A correct response serves to reduce the interval between the two frequencies and a miss serves to increase the interval between the tones (staircase tracking method). Thresholds are determined in this manner for a variety of frequencies and intensities.

Figure 3.28 is a composite audiogram for all seven species for which auditory threshold data had been gathered (Appendix 24). Stebbins presented this mean audiogram for Cercopithecinae because "the differences between species are no greater than the intra-species differences" (1973:358). However, it is stated that these generalizations are tentative since the number of species tested is relatively small. Three main features of the graph are highlighted: 1) the frequency range extends from below 60

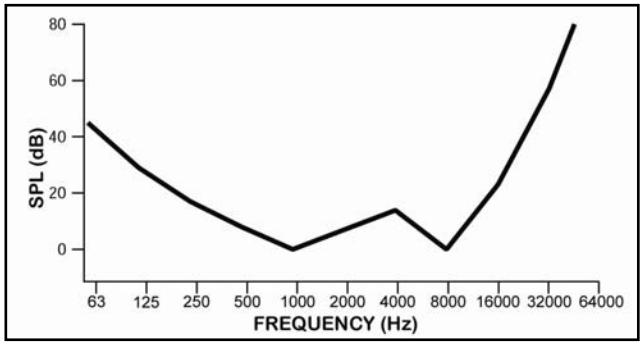

FIGURE 3.28 – Mean Cercopithecinae audiogram from Stebbins 1973.

Hz to 40-45 kHz; 2) maximum sensitivity is generally found at 1 and 8 kHz; and 3) a reduction in sensitivity (dip) usually occurs around 4 kHz. While these are not revolutionary new findings, Stebbins suggested that this puts Old World monkeys evolutionarily between prosimians and apes. As several of the previous reports have documented prosimians as a *group* (my emphasis) have better high frequency sensitivity but are less sensitive than anthropoids to frequencies below 8 kHz. Old World monkeys on the other hand have similar low-frequency sensitivity to apes but are more sensitive to higher frequencies (chimpanzee's upper limit is close to 30 kHz and human's is around 20 kHz). This appears to be one of the first studies to suggest a distinction within anthropoids and comes as the result of probing the upper frequency limit in monkeys.

As for frequency difference limens, Old World monkeys (based on macaques and baboons) can distinguish frequencies separated by around 5 Hz for 250 Hz to 1 kHz tones (at 60 dB SPL), a 50 Hz separation at 8 kHz, and a 500 Hz separation at 20 kHz. Humans, in comparison, can discriminate frequency differences as small as 2 Hz at 500 Hz and 20 Hz at 8 kHz. Conversely, intensity difference thresholds are relatively constant at different frequencies (with a slight increase at higher frequencies) but increase with

increasing intensity. For example, monkeys can differentiate intensity changes of 2 dB at 60 dB SPL, 1 dB at 50 dB SPL, and as small as 0.01 dB at 5 dB SPL. Humans appear to be only slightly more sensitive to changes in intensity and can distinguish an interval of 1 dB at 60 dB SPL. Although no information is available for prosimians, it would be interesting to investigate if they illustrate a different pattern than anthropoids as they do in auditory sensitivity to pure tones thresholds.

BEECHER 1974

In 1974, Beecher published two papers that presented threshold data on owl monkeys (*Aotus trivirgatus*[22]) and squirrel monkeys (*Saimiri sciureus*[23]). The article on owl monkeys will be described first (Beecher 1974a). Two male wild-born owl monkeys were the experimental subjects and were tested in a wire cage placed inside of double-walled sound insulated chamber that was lined with cotton batting to reduce sound reflections. Inside the cage were a response lever in the left-front corner and a liquid food dispenser in the back wall. A drinking tube projected to within 5 cm of the front wall and the subjects could reach this by putting their heads through an 8 cm^2 opening located in the center of the front wall. One of three speakers (for different frequency ranges) was located 0.36 m from the subject, 55° to the left at head level when he was positioned at the drinking tube. This arrangement fixed the animals head in a relatively consistent position during tone presentations. The conditioning technique was a version of the two-response method (Moody, Beecher, and Stebbins 1973). The monkeys were trained to lick the water tube to produce a tone (which initiated a trial after a variable inter-trial

[22] At the time of the study all owl monkeys were designated *Aotus trivirgatus* but now several species are recognized so the exact species is not known.
[23] Same comment as before for squirrel monkeys – unknown species.

interval averaging 30 seconds). If the subject left the tube and pressed the response lever within 3 seconds of tone onset, a food reward was delivered and the response was counted as a detection. Lever responses during the inter-trial interval were discouraged with a 10 second time-out. One-third of all trials were "catch trials" during which no tone was produced. A lever press during a catch trial was a "false alarm" (false positive) and if the false alarm rate exceeded 10 percent during a testing session, data for that session were rejected (Beecher 1974b:197). The psychophysical technique was a staircase (tracking) procedure that used 3 dB intervals and a minimum of 15 reversals of direction had to occur to meet the criterion of a threshold estimate. For most frequencies, the procedure was repeated in a second session and in all cases the estimates were within 3 dB of each other. The SPLs were calibrated by placing a microphone in the position of the animals head during tone presentations and these calibrations were carried out throughout testing (< 2 dB variation in all cases). The test frequencies were: 0.125, 0.25, 0.5, 1, 2, 4, 8, 10, 16, 20, 32, 40, and 45 kHz.

The individual thresholds, species means, and ranges for the owl monkeys are given in Appendix 25. The individual audiograms (Figure 3.29A) show close agreement between the threshold values of the two subjects. The largest difference at any frequency was 5 dB (at 32 kHz) and the mean difference for all frequencies was a mere 1.9 dB. The second study published by Beecher (1974b) used two male squirrel monkeys as test subjects. The animals were tested in the same laboratory under identical conditions as previously described for the owl monkeys (see above).The mean thresholds for both subjects are given in Appendix 3.25 and the audiogram presented in Figure 3.29B. Although the individual audiograms were not presented, Beecher states that the

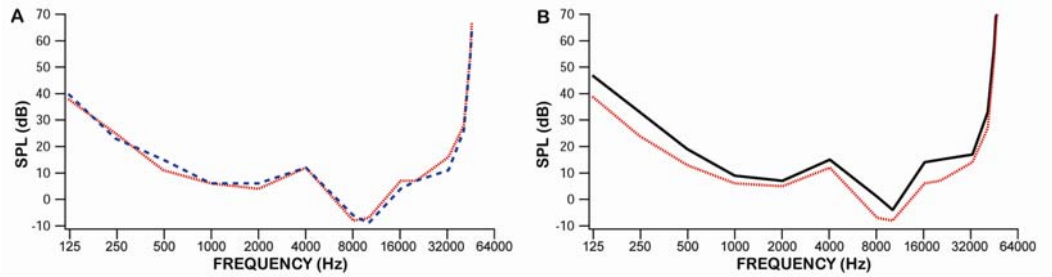

FIGURE 3.29 – Audiograms from Beecher 1974a and 1974b. **A**. Individual audiograms for *A. trivirgatus* (▪▪▪▪▪▪ represents #1 and ▬ ▬ ▬ represents #2). **B**. Comparison of species mean audiograms for *S. sciureus* (▬▬▬) and *A. trivirgatus* (▪▪▪▪▪▪).

maximum difference at any frequency was 6 dB with a mean for all frequencies of 3.9 dB (1974b:197). Although the low frequency limit was not explored, the slope on the low frequency side (≤ 1 kHz) is fairly shallow (10 dB per octave) suggesting a low frequency cut-off at 70 dB SPL. The first peak occurs at 2 kHz and the mid-frequency "notch" at 4 kHz (Beecher 1974b:197). The region of maximum sensitivity appears to occur at 10 kHz (-4 dB SPL) although Beecher stated it was in the 8 to 10 kHz region (presumably one animal peaked at 8 kHz and the other at 10 kHz). Above this frequency, the shape was described as "complex", illustrating a flat region between 16 and 32 kHz but becoming very steep above 40 kHz (Beecher 1974b:197). The high frequency cut-off at 60 dB SPL is 44 kHz and at 70 dB SPL is around 46 kHz (extrapolated).

The shapes of the mean audiograms for squirrel and owl monkeys are nearly identical (Figure 3.29B): a gradual slope on the low frequency side; the 4 kHz dip; maximum sensitivity between 8 and 10 kHz; and a high frequency cutoff at 70 dB SPL at approximately 46 kHz. The only minor difference in shape is that there is less of a flat region between 16 and 32 kHz in the owl monkey audiogram, primarily due to the lower threshold at 16 kHz (8 dB difference). However, owl monkeys were 2 to 9 dB more

sensitive at each frequency tested with a mean difference of 5.3 dB. Beecher (1974b) states that since the false alarm rate for both species averaged about 5%, the 5.3 dB difference represents a true species difference. Comparison of Figure 3.29A with Figure 3.29B, in addition to evaluating the mean threshold differences within species (*Saimiri* = 3.9 dB, *Aotus* 1.9 dB) suggests that the intra-specific variation is less than the inter-specific variation (in this case) despite the point for point matching in audiogram contours of the two species.

Beecher compared his squirrel monkey data with the *Saimiri* data produced by Fujita and Elliot (1965) and found there to be "a clear resemblance" up to 4 kHz although their curve is generally 5 to 10 dB lower (1974b:197). However, Fujita and Elliot found the most sensitive frequency to be at 16 kHz while Beecher's data suggests a peak in sensitivity somewhere between 8 and 10 kHz. Beecher presented no explanation for these differences. Beecher also compared his *Saimiri* data with the macaque data produced by Stebbins *et al*. (1966). He noted that although the macaques are slightly more sensitive at lower frequencies, they both displayed the mid-frequency dip at 4 kHz and had nearly identical high-frequency cutoff points. The major difference is in the high-frequency region between 20 and 40 kHz. Beecher posited that this discrepancy could either reflect a real species difference or simply be the result of presenting the tones with two different types of transducers. He went on to suggest that differences related to transducer type may in part be due to the effects of the head and pinnae which are greatest at higher frequencies (Beecher 1974b:197). The final comparative point that Beecher makes is that the audiograms for squirrel monkeys and macaques produced by Fujita and Elliot (1965) were also highly similar (like Beecher's and Stebbins *et al*.'s) but that their macaque

function differed from that of Stebbins' in the same way that their squirrel monkey audiogram differed from that of Beecher (*i.e.*, it generally showed lower thresholds). Beecher asserts these discrepancies are evidently related to methodological differences. Beecher suggested that it is fair to speak of a general "monkey audibility function" without specifying a particular species based on the similarity of the squirrel monkey and macaque audiograms (Beecher 1974b:197). While it is true that a basic pattern was emerging for the shape of most primate audiograms and the particular ones he selected for comparison shared many characteristics, it ignored some of the more subtle details not shared by species he did not reference (*e.g.*, *C. jacchus* high-frequency cutoff of < 35 kHz and the various frequencies of the peak of maximum sensitivity in different species including Stebbins *et al*.'s macaques).

Beecher (1974a) used these data to address the general question of whether the hearing sensitivity of nocturnal primates shows any specialization for activity cycle. He did this by summarizing three measures of auditory function in eight primate species, four nocturnal and four diurnal. The measures of auditory function were based on the criteria of Masterson *et al*. 1969: high-frequency cutoff at 70 dB SPL; threshold at 1 kHz (an index of low-frequency sensitivity; and lowest threshold (an index of best sensitivity). Beecher concluded that "none of these parameters is (are) systematically related to the nocturnal/diurnal classification. Examination of these closely related species thus reveals that there is no *necessary* (his emphasis) relationship between nocturnality and auditory sensitivity. In particular, the nocturnal primates are not necessarily more sensitive to high frequencies nor more sensitive to sound in general, than are the diurnal primates" (1974a:901). This hasty dismissal of a possible relationship between hearing sensitivity

and activity cycle may be a bit premature. For one, it seems strange that he would expect there to be a difference in high frequency sensitivity (last sentence in quotation) based on his findings in these two studies (*Aotus* and *Saimri*'s values for high-frequency cutoff were exactly the same). Furthermore, this comparison does not take body size or phylogenetic history into account. A recent analysis by Coleman and Ross (2004) found that when examining the region of best sensitivity (lowest threshold), combining anthropoids and prosimians may obscure patterns that are more evident when the groups are considered individually. As for his list of diurnal primates, tree shrews were one of the species listed but are no longer considered a member of the primate order and it is possible that *Lemur catta* is at a state of behavioral disequilibrium if only recently (in geologic time) becoming diurnal. The last point is that there does appear to be a difference in low-frequency sensitivity between *Aotus* and *Saimiri* (this comparison although limited to only two species controls for body size and phylogeny). The average difference between thresholds from 0.125 to 1 kHz is 6.5 dB (higher than the total audiogram difference). An increase of 6 dB is considered to represent a doubling of perceived intensity so this *could* be a biologically meaningful difference. In fact, the long call of *Aotus* has a fundamental frequency of 300 Hz (Moynihan 1964; Wright 1985) falling right in the middle of their low-frequency range. The issue of whether activity cycle has a significant influence on hearing acuity clearly deserves further investigation.

PFINGST, HIENZ, and MILLER 1975

The research objective of Pfinst *et al*. (1975a, 1975b) was to use the reaction-time (RT) procedure to estimate and evaluate auditory thresholds in humans and rhesus

macaques and compare these results with those obtained in the same subjects (human only) using different psychophysical procedures and stimulus presentation-calibration techniques. In addition, the results using the RT procedure were compared to other human and macaque subjects from previous studies which utilized both similar and dissimilar techniques. The human subjects were a 27 year old male, a 27 year old female, and a 35 year old male with a slight high frequency hearing loss (two other humans with impaired hearing were tested but their results were not published in this report). The monkeys were two *M. mulatta* males, one 3-4 years of age and the other 4-5 years of age.

The details of the RT procedure were nearly identical to those used by Green (1975) in appetitive testing except the time-out for false positives was seven seconds and the inter-trial interval was one second. Catch trials were also incorporated to estimate the guessing rate. Thresholds were calculated as the halfway point between the false positive rate (0 – 20%) and the 100% correct point (*i.e.*, between 50 – 70%). One human subject was also tested with a method known as a forced choice (FC) procedure. In the FC procedure the subject pressed a key at the onset of a cue light. After 0.5 seconds of the key press, an observation period consisting of either a one second tone or one second period of silence was initiated. The end of the observation period was signaled by extinguishing the cue light. Release of the key started a one second inter-trial interval after which the same sequence was repeated. The tone was randomly assigned to only one of the two observation periods and after the second period the subject was required to indicate in which period the tone had occurred. The threshold was determined as the 75% correct point. In both procedures, tones were presented monaurally using the method of constant stimuli in 2 dB steps and circumaural headphones with probe calibration.

Using probe calibration, SPL's are measured using a probe tube connected to a microphone which is inserted into the headphone ear cushion and is aligned vertically approximately 1.5 cm from the concha wall in human subjects and approximately 2.25 cm from the concha wall in monkey subjects (Pfingst *et al*. 1975:422). Testing was conducted in a double walled sound attenuating chamber and consisted of tones ranging from 0.125 to 45 kHz.

All of the human subjects also had thresholds tested using standard clinical procedures. Clinical procedures present tones with no cues as to when a tone will sound and using only the ascending method of limits procedure. Responses are scored whenever the subject states they heard the tone and thresholds are defined as the intensity at which there were two out of four responses. The tones were presented monaurally with supraaural headphones that were calibrated using a 6-cm^3 coupler. This type of calibration measures SPLs with a microphone directly in a coupler that rests against the ear cushions. Testing was performed in a sound attenuating suite at the University of Washington Otolaryngology Clinic and consisted of tones ranging from 0.25 to 8 kHz.

Appendix 26 presents the ranges and species means where applicable and all individual thresholds. Figure 3.30A shows the audiograms for one of the human subjects measured using all three psychophysical procedures (note that these results were obtained with the subject wearing the same supraaural headphones with 6-cm^3 coupler calibration). The RT procedure produced thresholds that generally fell between those of the clinical and FC procedures. For this subject, the RT values were on average 3.7 dB lower than the clinical values and the mean for all human subjects was 2.7 dB. The difference between the RT procedure and the FC procedure averaged 5 dB. The authors noted that the

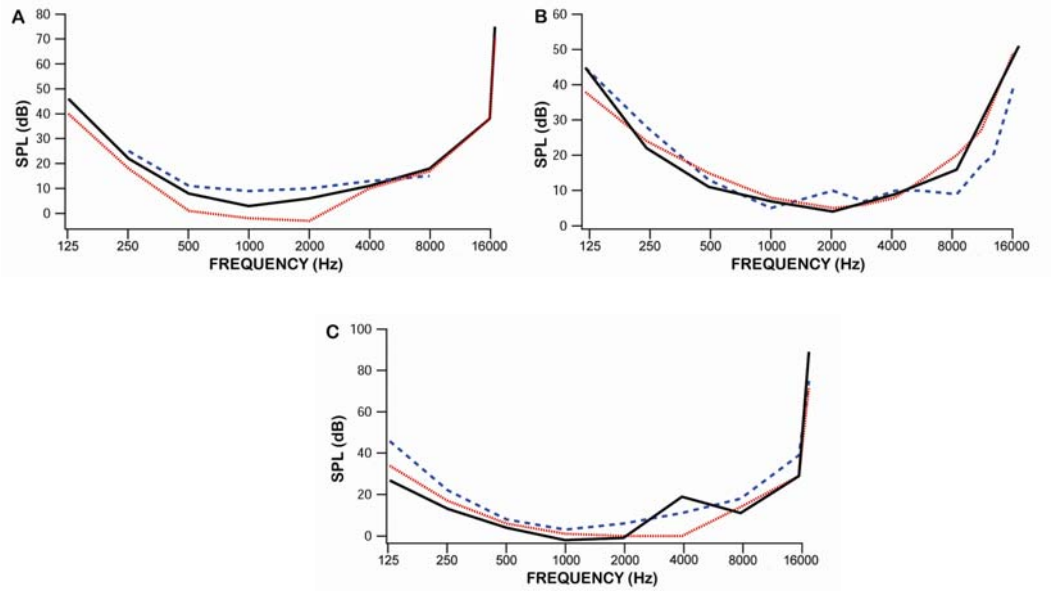

FIGURE 3.30 – Audiograms from Pfingst *et a*l. 1975. **A**. Audiograms for human subject H-1 comparing reaction-time (———), forced choice (▪▪▪▪▪▪▪), and clinical (— — —) psychophysical procedures. **B**. Comparison of human mean audiogram (———) produced using the reaction-time procedure with those from Sivian and White 1933 (▪▪▪▪▪▪) and Dadson and King 1952 (— — —). **C**. Audiograms for human subject H-1 comparing three different transducer-calibration combinations. Curve A (— — —) used supraaural headphones with 6-cm^3 calibration, curve B (▪▪▪▪▪▪▪) used supraaural headphones with probe calibration, and curve C (———) used circumaural headphones with probe calibration.

perithreshold graphs used to interpolate the 50% correct point were much steeper and produced smoother results in one-sixth the number of trials for the RT procedure compared with the FC procedure. A steeper slope results in less change in SPL with changes in percentage correct and consequently the specific criteria used to define threshold (*e.g*., 50 versus 70%) will result in only small differences in the intensity estimate. Pfingst *et al*. attributed the higher clinical thresholds to the fact that only an ascending series of intensities was used which typically yields higher threshold values and to the better observing conditions of the RT procedure (*i.e*., use of a cue light to "set" the subject) (1975:434). As far back as Elder, it was noted that to prepare the subject for a

trial and maintain attention to the stimulus over long periods of time a "ready" signal must be given (1934:165). He was under the opinion that "an experimental situation which does not offer the subject the opportunity to work under the most favorable conditions gives results not truly representative of sensory capacity" (Elder 1934:165). Pfingst *et al*. ascribe the higher thresholds of the RT procedure compared to the FC procedure to the high response criterion of the RT procedure in order to reduce false positive responses (1975:434). In the FC procedure no response criterion is required. The RT procedure also produced very stable thresholds: this subject was measured twice, nine months apart, and the values were within 2 dB at all frequencies except 6 kHz which was 6 dB different.

Figure 3.30B shows the mean audiogram for all three human subjects produced with the RT procedure and the human audiograms of Sivian and White (1933) and Dadson and King (1952), two of the more commonly cited reports. There is close agreement between these audiograms with a mean difference for all comparable frequencies (0.125 through 8 kHz) of 5.6 dB. Thus, the authors felt that the RT procedure was measuring what is commonly accepted as the "threshold of hearing" in subjects with normal hearing (Pfingst *et al*. 1975:435). Figure 3.30C shows the audiograms of one human subject produced using the RT procedure but utilizing three different transducer-calibration combinations. Curve A used supraaural headphones with 6-cm^3 calibration, curve B used supraaural headphones with probe calibration, and curve C used circumaural headphones with probe calibration (used for the majority of thresholds presented here). These curves illustrate the considerable variation that can be introduced just from calibration procedures (compare curves A and B) and headphone type (compare

curves B and C). It is interesting that only curve C shows a mid-frequency dip (not generally considered common to human audiograms), although the authors noted that this same subject showed a slight notch at 4 kHz when measured six months earlier using configuration A (Pfingst *et al*. 1975:436). The researchers stated that they would have preferred to use supra-aural headphones with probe calibration (B) for their monkey measurements since this is a popular combination and calibration was stable and easy to replicate. However, the cushion was found to depress the tragus and block the ear canal in some of the monkey subjects (Pfingst *et al*. 1975:435). Therefore, the circumaural headphones with probe calibration were used. Despite the potential variation that can be introduced as these results suggest, it should be pointed out that there was still close conformity in the three human audiograms from different studies (Figure 3.30B) in spite of the fact that they did not use exactly the same transducer-calibration procedures.

Figure 3.31A presents the individual thresholds of both monkey subjects. Repeated measures of the mid-range frequencies over several months produced intra-subject thresholds that were within 4 dB of the final values and the subjects varied by about the same amount (< 4 dB) at these frequencies (Pfingst *et al*. 1975). The greatest variability occurs at the upper and lower ends of the audiogram (particularly the 22 dB inter-subject range at 46 kHz) resulting in a mean range for all frequencies of 6.3 dB. Also included in this figure is the macaque audiogram from Stebbins *et al*. (1966) which was produced with similar methods to those used in this study. It differed in that it used binaural simulation, supra-arual headphones, a different method for calibrating the probe tube, a somewhat different behavioral method, and used different species. Considering the close correspondence between the audiograms at most frequencies, the authors

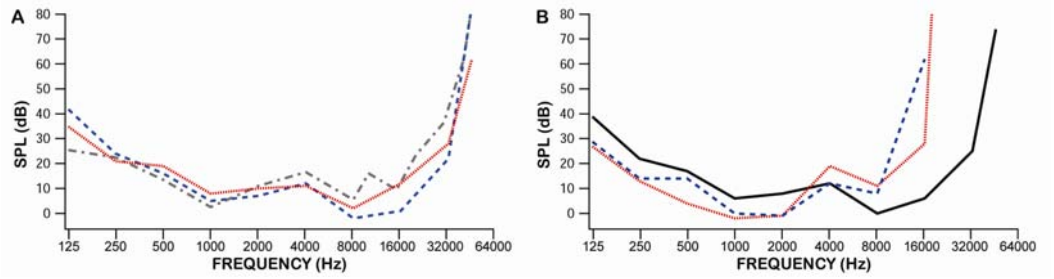

FIGURE 3.31 – **A**. Audiograms of *M. mulatta* subjects M-1 (▬ ▬ ▬) and M-2 (▪▪▪▪▪▪) with macaque mean (▬ . ▬ . ▬) from Stebbins *et al*. 1966. **B**. Comparison of *M. mulatta* mean (▬▬▬) with human subjects H-1 (▪▪▪▪▪▪) and H-5 (▬ ▬ ▬).

concluded that the differences between the two procedures are relatively unimportant although they do not rule out the possibility that differences due to one variable are canceled out by those due to one or more other variables (Pfingst *et al*. 1975:434). Compared to other studies that measured thresholds in a free-field situation (*e.g*., Clack and Herman 1963; Fujita and Elliot 1965) the rhesus monkey audiograms in this study were generally higher which is consistent with data from human experiments where free-field audiograms are typically lower than those obtained using a closed (headphone) system (Pfingst *et al*. 1975:434).

The final comparison from this study to be discussed was between the monkey and human subjects (Figure 3.31B), where both the calibration and behavioral procedure were held constant. Their results demonstrated that the monkey curves were slightly higher than the human's at lower frequencies but lower than the human curves at higher frequencies. Pfingst *et al*. note that these findings parallel those of Behar *et al*. (1965) who compared humans and rhesus macaques using the same free-field calibration and behavioral procedures for both species (1975:435). More details about the monkey audiograms will be discussed in the next segment.

PFINGST, LAYCOCK, FLAMMINO, and LONSBURY-MARTIN 1978

Three years after the initial publication by Pfingst *et al*. (1975), the first author reported on a much larger sample of *M. mulatta*. This study measured absolute thresholds in 13 rhesus macaques and this remains the largest number of individuals successfully tested for a single species in one study. The methods were identical to those used in the first study and the range of frequencies tested was the same. However, numerous intermediate frequencies were also investigated including 0.707, 1.414, 2.828, 5.656, 10, 11.312, 22.624, and 40 kHz.

The individual data were not presented, although the species means and standard deviations were given and are presented in Appendix 27 and Figure 3.32. The mean standard deviation for all frequencies was around 5 dB, with the highest variation at higher frequencies (± 6.6 dB), intermediate levels of variation at lower frequencies (± 5.3 dB) and the least variation in the middle range (± 3.8 dB). The mean audiogram displays the characteristic W-shaped contour with the first peak at 1.414 kHz, the dip at 4 kHz, and the second peak at 11.312 kHz. The most sensitive frequency is at 11.312 kHz but this is only 1 dB less than the peak at 1.414 dB. Both peaks actually show a fairly broad range of good sensitivity (1 to 2 kHz for the first peak and 8 to 16 kHz for the second peak) with the thresholds being separated by no more than 3 dB. Interpolation reveals that the high-frequency cut-off is around 41 kHz at 60 dB SPL (43 kHz at 70 dB SPL). The slope on the low-frequency side is fairly shallow and the lowest frequency tested, 125 Hz with an intensity of 39 dB SPL, does not approach the low-frequency cut-off.

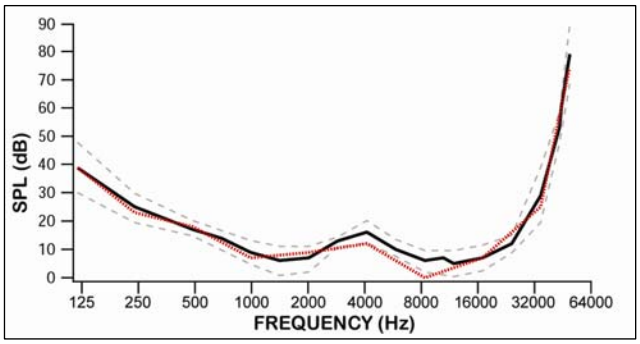

FIGURE 3.32 – Mean *M. mulatta* audiogram (———) and individual ranges (— — —) based on 13 individuals from Pfingst *et al*. 1978 compared with previous audiogram from Pfingst *et al*. 1975 based on 2 individuals (▪▪▪▪▪▪).

The mean *M. mulatta* audiogram from Pfingst *et al*. (1975) is also presented in Figure 3.32 and several observations can be made from this comparison. First, there is considerably good agreement between the two mean audiograms, despite the fact that the Pfingst *et al*. (1975) audiogram was produced with only two individuals. The mean difference for all frequencies was 2.7 dB with the highest variability occurring at the mid-range frequencies (3.5 dB). It also appears that by testing more frequencies, the points of best sensitivity are shifted slightly, although the peaks from the Pfingst *et al*. (1975) audiogram still fall within the regions of best sensitivity. This agrees with the notion put forth by Seiden (1957) that the points of maximum sensitivity are actually "regions" and that some apparent distinctions between different species may be the product of the limited number of frequencies tested. Still, the upper and lower portions of the audiograms are nearly indistinguishable.

LONSBURY-MARTIN and MARTIN 1981

The study by Lonsbury-Martin and Martin (1981) measured hearing threshold shifts and recovery time on behavioral auditory thresholds and compared these to similar changes in the response properties of single brain stem neurons when exposed to short-lasting, moderately intense sound in eight adult rhesus macaques (one female and seven males). The magnitude of threshold shift and time to recovery were found to be a function of the frequency of the stimulus. The behavioral thresholds showed a 3 to 8 dB loss that lasted from 3 to 7 minutes at lower frequencies and up to a 14 dB loss lasting 15 minutes at middle and high-range frequencies. The magnitude and duration of the neuronal activity were much greater and longer lasting than those of corresponding behavioral threshold measures (Lonsbury-Martin and Martin 1981:563). The baseline audiograms were measured using a reaction-time procedure that contained 10% catch trials. Tone intensity was varied in 2 dB intervals (near threshold) using the method of constant stimuli and final thresholds were determined as the halfway point between the false positive rate and 100% correct point. Tones were presented monaurally using headphones (Beyer DT-48 with circumarual ear cushions) at frequencies ranging from 354 Hz to 32 kHz in half-octave intervals. Intensity levels were calibrated by placing a microphone in the ear cushion just lateral to the tragus and testing was conducted in double-walled sound attenuating chamber.

The species means and ranges in standard deviations are given in Appendix 28 and presented in Figure 3.33. The mean standard deviation for all frequencies was 5.5 dB and the greatest variability was at the highest frequencies (± 5.7 dB) although the middle (± 5.5 dB) and lower frequencies (± 4.9) were only slightly less variable. The shape of

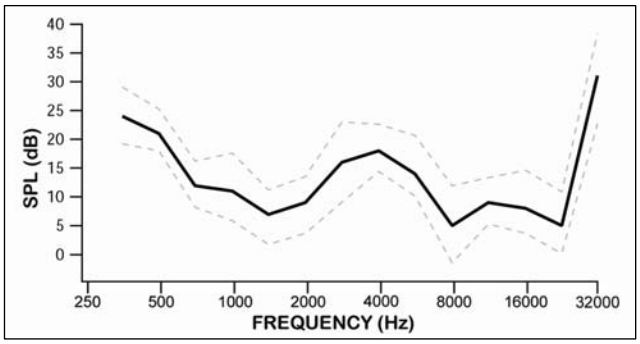

FIGURE 3.33 – Mean *M. mulatta* audiogram (———) and range in standard deviations (— — —) from Lonsbury-Martin and Martin (1981).

the audiogram is typical at most frequencies although the high-frequency side displays a double peak at 8 and 22.5 kHz (similar to Stebbins *et al*. 1966) with an intensity level of 5 dB SPL. The low threshold at 22.5 kHz is actually the highest frequency at which a rhesus macaque has demonstrated a peak.

HIENZ, TURKKAN, and HARRIS 1982

The research by Hienz *et al*. (1982) was part of a long-term study on the effects of noise on auditory sensitivity and noise-induced changes in hemodynamic, hormonal, and immune systems in baboons. In addition, the authors were interested in generating audiograms for baboons since the early study by Wendt (1934) produced data that was not in close agreement with the audiograms of other Old World monkeys and the work of Stebbins (1973) did not present individual thresholds for the baboons in his study (Hienz *et al*. 1982:71). The subjects in this study were four adult yellow baboons (*Papio cynocephalus*) and the method employed was the reaction-time procedure used by previous investigators (Stebbins 1966, 1973; Pfingst *et al*. 1975). However, unlike all the previous researchers that employed this procedure, Hienz *et al*. presented the test

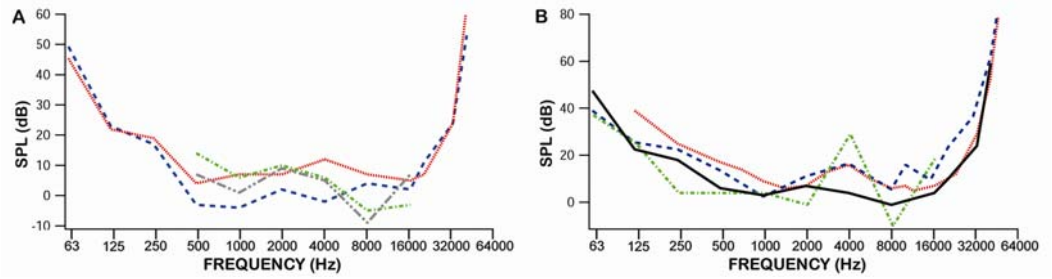

FIGURE 3.34 – **A**. P. *cynocephalus* individual audiograms from Heinz *et al*. 1982 (▬ ▬ ▬ represents subject AL, ▬ ▪ ▬ ▪ ▬ represents subject LE, ▪▪▪▪▪▪ represents subject MA, ▬ ▪ ▬ ▪ ▬ represents subject MO). **B**. *P. cynocephalus* species mean audiogram (▬▬▬) compared with macaque audiograms from Stebbins *et al*. 1966 (▬ ▬ ▬) and Pfingst *et al*. 1978 (▪▪▪▪▪▪) and *P. anubis* audiogram from Wendt 1934 (▬ ▪ ▬ ▪ ▬).

frequencies using a wide range speaker suspended 20 cm directly over the subjects head. All testing was conducted in a double-walled sound attenuating chamber and intensities were calibrated by using microphones located at ear level with 0° incidence to the speaker. The frequencies tested were 0.062, 0.125, 0.50, 1, 2, 4, 8, 16, 20, 32, and 40 kHz. Tone intensities were attenuated using the method of constant stimuli. All threshold estimates were corrected for false positives by defining threshold as the halfway point between the false positive rate and 100% (*i.e*., between 50 and 70%). Complete audiograms were obtained for two of the subjects, while the other two subjects were only tested at the mid-range frequencies.

Figure 3.34A presents the individual and species mean audiograms and all thresholds and ranges are given in Appendix 29. The majority of the variability is found in the mid-range frequencies with a maximum range of 17 dB and a mean for all frequencies of 8.1 dB. However, many of the individual audiograms reflect the same shape characteristics, just at different intensities. For example, three out-of-four show their first peak at 1 kHz and the mid-frequency dip at 2 kHz while two out of four have

their maximum peak at 8 kHz. Monkey MA on the other hand shows the first peak at 500 Hz, the dip at 4 kHz, and the second peak at 16 kHz. Still, except for 4 kHz, the values from 500 Hz to 20 kHz are all within 3 dB of each other. The two individuals tested at all frequencies (AL and MA) are approaching the high-frequency cut-off with a mean threshold of 59 dB SPL at 40 kHz. Extrapolation on the low-frequency side suggests a low cut-off at 60 dB SPL around 45 Hz.

Hienz *et al*. compared these data with the rhesus macaque data from Pfingst *et al* (1978) and the macaque data from Stebbins *et al*. (1966) since both of these studies employed the same psychophysical procedures and tested over similar frequency ranges as in the present study (Figure 3.34B). Also included in this graph is the baboon audiogram from Wendt (1934). The authors comment that their baboon audiogram parallels the macaque audiograms over the entire frequency range but averages about 5 dB lower than the mean of the other two audiograms. Hienz *et al*. speculate that the lower intensity values may be due to the fact their study used free-field acoustic stimuli while the other two studies used headphones although they do not rule out a slight species (or genus) difference (1982:74). Comparing the *P. anubis* audiogram of Wendt to that of the other species, the olive baboon is almost indistinguishable from the yellow baboon and Stebbins *et al*.'s macaques at the lowest frequencies tested and the slope on the high-frequency side also resembles that of the other species. The largest differences appear to be in the amplitude of the mid-frequency dip and the second peak. Still, the overall fit is surprisingly good for a study that used a completely different method, did not have proper sound field calibration, and was conducted almost 50 years before the Hienz *et al*. (1982) study.

BENNETT, DAVIS, and MILLER 1983

This study represents the second published report investigating presbycusis (age related hearing loss) in non-human primates, although it was actually an extension of an unpublished master's thesis by Weisenburger (1979). Unlike most studies that have documented presbycusis in humans, it utilized both longitudinal and cross-sectional threshold data to maximize age-related changes in hearing loss. To achieve this goal, Bennett *et al*. (1983) determined audiograms for several animals in three different age groups at three separate times (at approximately one year intervals). The subjects were seven rhesus macaques (*M. mulatta*): the "old" group consisted of three 31 year old females; the "middle-aged" group consisted of two 24 year old males; and the "young" group consisted of two 9 year old females (Bennett *et al*. 1983:603).

The testing procedures utilized a mixture of old and new approaches. After the illumination of a signal light, a subject initiated a trial by putting its head into a wire chamber and pushing its nose through a hole in one end of the chamber, interrupting a photocell beam. In two-thirds of the trials, this caused a two second tone to sound after a variable interval of up to six seconds. The other one-third of trials were catch trials and all trials were followed by a 12 second inter-trial interval. A correct response was recorded when the animal withdrew its head from the chamber during a tone trial or maintained its position during a no tone trial. Both responses resulted in a food reward (essentially the double reward system of Elder 1934). False positive and false negative responses resulted in food forfeit (no reward) and if the false positive rate exceeded 15% the data were discarded. Thresholds were determined using the tracking procedure with 2 dB intervals around the threshold (10 db increments were used to establish gross

threshold estimates). Two independent tests were used to estimate the final threshold (for that year) unless the thresholds differed by more than 6 dB, in which case the entire procedure was repeated. All testing took place in a sound attenuating booth that had an average ambient noise level of 23 dB. Seven frequencies were tested ranging from 0.125 to 32 kHz, with the lower frequencies (125 and 500 Hz) being delivered using 8.9 cm speakers placed 5 cm lateral to the head chamber. All other frequencies (2, 4, 16, 22.6, and 32 kHz) were presented using headphone speakers (TDH-49). However, since these "speakers" were placed on the sides of the head chamber (about 2 cm lateral to the subject's ears) the authors stated that this situation was a free-field environment (Bennett *et al*. 1983:606). In truth, considering the small size of the speakers and their close position to the subject's ears, the situation was probably somewhat intermediate between free- and closed-field environments. Right and left ears were tested independently, although the setup probably prevented complete isolation of the ear being tested from the other ear. The intensity levels were calibrated by placing a probe microphone 1 cm lateral to a "dummy" monkey head placed within the head chamber (Bennett *et al*. 1983:603).

Figure 3.35A shows the mean audiograms for each age group with the data averaged for both ears and for each replication. All three age groups illustrate relatively similar contours with the maximum point of sensitivity occurring at 4 kHz. However, the mid-frequency dip (at 2 kHz) is only patently evident in the audiograms of the middle-aged and old individuals and there is an almost perfectly consistent decrease in all thresholds with increasing age. Additionally, none of the old subjects responded to the 32 kHz tones and one of the individuals in this group never responded at 22.6 kHz. Appendix 30 presents the left ear thresholds for all three replications of all individuals.

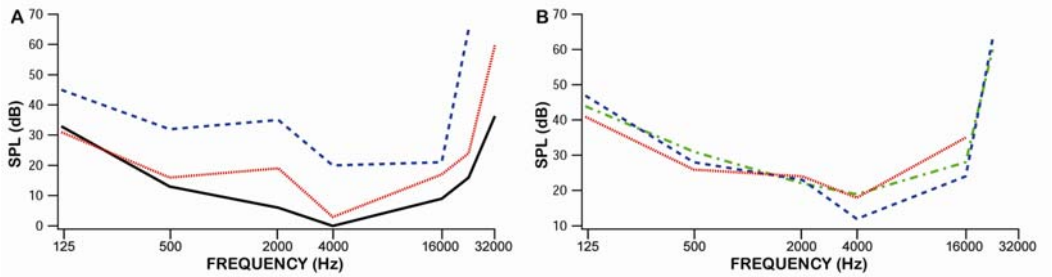

FIGURE 3.35 – *M. mulatta* audiograms from Bennett *et al*. 1983. **A**. Comparison of mean audiograms of old (– – –), middle-aged (·····) and young subjects (———). **B**. Left ear audiograms for old age group subject A-1 illustrating loss of high frequency sensitivity between replication 2 (– – –) and 3 (·····). The increase in sensitivity at some frequencies between replication 1 (– · – · –) and 2 was attributed to practice affects.

Although the threshold data on right ears were not presented, it was stated that the small differences between ears were non-significant (Bennett *et al*. 1983:604). The mean range of thresholds among individuals in an age group was greatest for the old group (13 dB), intermediate for the young group (8.2 dB), and least for the middle-aged group (4.3 dB). The old group also showed the greatest range between replications (7.4 dB), but in this case the middle-aged group was intermediate (6.2 dB), and the young group showed the least replication variability (5.2 dB). It should be pointed out that in some instances the second replication was actually lower than the first replication and this was attributed to practice effects (Bennett *et al*. 1983:604).

At higher frequencies there was a consistent loss of sensitivity in successive replications for both the middle-aged and old groups (Bennett *et al*. 1983: 605). This is well illustrated in Figure 3.35B which shows the left ear thresholds for monkey A1. At 22.6 kHz this animal completely stopped responding by the third replication and showed an 11 dB loss at 16 kHz between replications two and three. Similarly, monkey A2 showed a 14.2 dB loss at 16 kHz and never responded at 22.6 or 32 kHz and monkey A3

had an 11 dB loss at 16 kHz and a 20 dB loss at 22.6 kHz. Although not as dramatic (no complete non-responses), the middle-aged group demonstrated losses at large as 17 dB (at 22.6 kHz for monkey B2). Conversely, the young group produced values that were relatively stable across replications and actually decreased in threshold intensities from replication one to replication three at five out-of-seven frequencies.

Bennett *et al*. suggest that these shifts in threshold may be due to the same mechanisms that have been put forth for presbecusis in humans (1983:606). The hearing loss at high frequencies may be related to the destruction of hair cells and eighth nerve fibers in the basal turn of the cochlea (Bennett *et al*. 1983:607). The loss at all frequencies, although not as large at low and middle-range frequencies as at high frequencies, could be due to changes in the blood supply and stria vascularis to the cochlea as Schuknecht (1974) proposed for humans. In their closing statement, the authors recommend that the age of the subjects must be taken into consideration, particularly in comparative and evolutionary studies of hearing (Bennett *et al*. 1983:607).

BROWN and WASER 1984

The study by Brown and Waser (1984) was part of an extensive investigation into the hearing sensitivity, localization abilities, and vocalizations of Old World monkeys. In this study the hearing and vocal communication of the blue monkey (*Cercopithecus mitis*) as well as field measurements of natural habit acoustics were analyzed. Only the results pertaining to the blue monkey's hearing will be discussed. Two juvenile monkeys, one male and one female, served as subjects as well as four young adult humans (19-35 years old). The conditioning procedure used was the popular time-reaction procedure

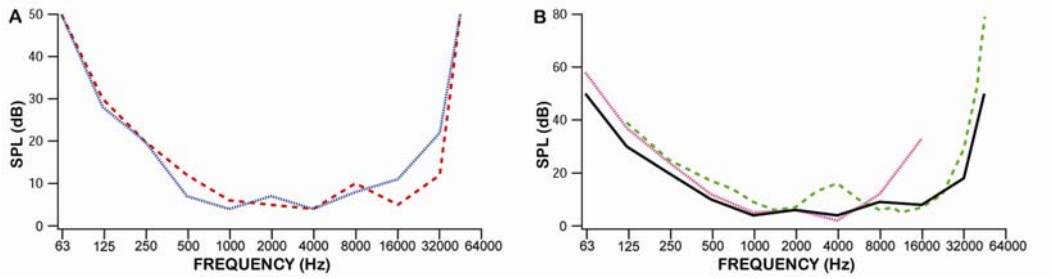

FIGURE 3.36 – **A**. Individual audiograms for *C. mitis* from Brown and Waser 1984 (▬ ▬ represents subject M1 and ▪▪▪▪▪▪ represents subject M2). **B**. *C. mitis* (▬▬▬) and human (▪▪▪▪▪▪) species mean audiograms from Brown and Waser compared with *M. mulatta* mean audiogram (▬ ▬ ▬) from Pfingst *et al*. 1978.

with few notable exceptions. The researchers employed both the method of constant stimuli and the staircase method to determine thresholds. They reported that the two methods yielded indistinguishable results although the majority of the thresholds were collected using the staircase procedure (Brown and Waser 1984:69). Similar to Seiden (1957), they found only small differences (< 3 dB) between the threshold estimates determined with one series compared to the other (descending versus ascending). Testing was carried out in a semi-anechoic room and tones were produced using either a loudspeaker or piezoelectric-transducers located 1 m from the subject. The auditory stimuli were calibrated and consisted of tones ranging from 0.063 to 32 kHz in octaves and 45 kHz.

The individual thresholds, ranges, and species means for both the blue monkey and human subjects are given in Appendix 31. The two monkeys had remarkably similar threshold values with a mean range for all frequencies of 2.6 dB and a maximum value of 10 dB at 32 kHz. Figure 3.36A presents the individual and species mean audiograms and it can be seen that the monkeys had extremely good hearing from 1 to 16 kHz with the lowest threshold at 4 kHz. The mean audiogram (Figure 3.37B) shows a double-dip at 2

and 8 kHz, but both are relatively slight. In fact, there is only a 5 dB difference between any of the thresholds in this range (1 to 16 kHz). Compared to the humans in the study, blue monkeys were more sensitive to frequencies below 1 kHz, very similar from 1 kHz to 4 kHz, and much more sensitive at all higher frequencies. There was no overlap between humans and blue monkeys in the thresholds for individuals below 500 Hz or above 8 kHz. This is in contrast to other studies comparing monkeys to humans where the humans usually appear slightly more sensitive at lower frequencies (*e.g*., Behar *et al*. 1965; Pfingst *et al*. 1975). Brown and Waser also compared these data with the rhesus macaque data from Pfingst *et al*. (1975) which used the same conditioning procedure (Figure 3.36B). This led them to propose that *C. mitis* possesses better low frequency hearing than *M. mulatta* and similar ground-dwelling monkeys (Brown and Waser 1984:72). However, they acknowledged that their human subjects appear to have heightened low frequencies thresholds, perhaps elevated as much as 15 dB, compared to the values for humans in Sivian and White's study (1933). The authors attributed this to the ambient noise levels of their test chamber which was as high as 51 dB SPL at 63 Hz and could have caused the masking of tones trying to be perceived by the test subjects. Therefore, the true threshold values for blue monkeys are probably lower than reported (Brown and Waser 1984:73). To evaluate this possibility, they compared their results to the two previous studies that included both monkey and human subjects (Behar *et al*. 1965; Pfingst *et al*. 1975) and used the humans as a "biological reference level" (Brown and Waser 1984:73). Using this standard, the blue monkeys still appeared to possess superior low frequency sensitivity to that of the rhesus macaque. It should also be noted

that while the Pfingst *et al*. study used headphones to deliver the tones, the study by Behar *et al*. used speakers.

Brown and Waser propose that the heightened low-frequency sensitivity of the blue monkey is one part of the communication system that aides in long distance vocal propagation. Their measurements of ambient noise levels in the environments occupied by blue monkeys showed the presence of a "frequency window" between 100 and 1000 Hz with a minimum intensity at 630 Hz (Brown and Waser 1984:69-70). One of the sounds that *does* occupy this frequency range is the low-frequency "boom" call of *C. mitis* which concentrates almost all of the acoustic energy at 125 Hz (Marler 1973). It has also been observed to be extremely loud for such a low-frequency call (Waser and Waser 1977). Brown and Waser propose that even slight increases in auditory sensitivity, such as 10 dB in this range, could lead to a four-fold increase in the audible range of a call (1984:74). The authors take all of the findings to suggest that the superior low-frequency sensitivity, the use of a loud and low-frequency long call, and reduced ambient noise work in concert to promote long distance signaling.

BROWN 1986

The next study in this series sought to investigate how well the auditory system detects vocal signals under ecologically relevant conditions. The specific goals were to measure the auditory sensitivity in several species and the ability to detect representative vocalizations in quiet and simulated rain forest noise. The test subjects were blue monkeys (*C. mitis*), grey-cheeked mangabeys (*Lophocebus albigena*[24]), and humans. The

[24] At the time of the study this species was in the genus *Cercocebus* but is now designated as *Lophocebus albigena*.

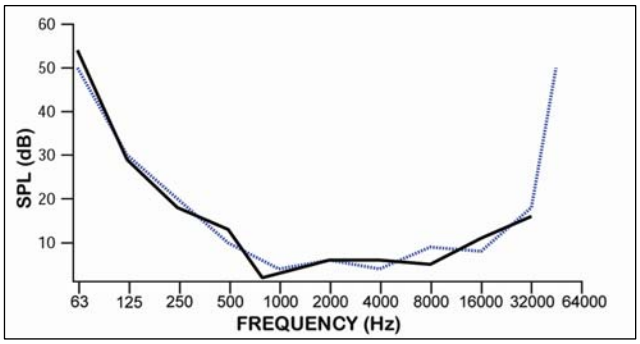

FIGURE 3.37 – *L. albigena* mean audiogram (———) from Brown 1986 compared with *C. mitis* mean audiogram (▪▪▪▪▪▪) from Brown and Waser 1984.

humans and blue monkeys were the same individuals used in the previous report (Brown and Waser 1984) and the mangabeys were represented by one adult male and one adult female. Since the hearing had already been tested in the humans and blue monkeys, auditory thresholds were only determined for the grey-cheeked mangabeys. The testing procedures, auditory equipment and facilities were exactly the same as those used for the previous subjects (Brown and Waser 1984). The test frequencies were nearly identical and ranged from 63 Hz to 32 kHz but did not test 45 kHz.

The species mean thresholds are given in Appendix 32 and presented in Figure 3.37 along with the species mean audiogram of the blue monkey (the audiograms of individuals were not published). This figure illustrates that both species have virtually identical hearing (Brown 1986:151) with only a 2.3 dB difference at frequencies up to 32 kHz. The interspecific variability was actually less the intraspecific variability for blue monkeys (2.6 dB – see above). The primary differences were that mangabeys were about 4 dB less sensitive at the 63 Hz, 2 dB more sensitive at the best frequency (800 Hz in *C. albigena* and 1 kHz in *C. mitis*), and 5 dB more sensitive at 8 kHz. As was the case with *C. mitis*, Brown stated that at 1 kHz and lower the thresholds are likely underestimated

due to the higher than desirable ambient noise in the test chamber (1986:150). In comparison to the human subjects tested in the previous research (Brown and Waser 1984), grey-cheeked mangabeys show the same patterns found with blue monkeys (better low- and high-frequency hearing, but no distinct differences at mid-range frequencies). These findings led Brown to hypothesize "that many arboreal species with specializations for low-frequency sound production" (*e.g.*, extra-laryngeal vocal sacs) "are likely to have complimentary specializations for the reception of these minimally attenuated low-frequency signals" (1986:151). Furthermore, he suggested that many forest dwelling primates, such as blue monkeys and grey-cheeked mangabeys, may have hypertrophied middle ear chambers to aid in low-frequency reception, although studies on the anatomy of the auditory systems of the primates are (were and still are) currently lacking (Brown 1986:151). One of the important conclusions from these two studies is that this was the first research to suggest that there appears to be differences in the low frequency sensitivity of certain monkeys compared with apes and that these differences are related to ecological specializations.

Although the other components of this study will not be covered in detail, the relevant findings will be briefly summarized. Sixteen representative vocalizations for all three species such as the word baseball (humans), the boom call (*C. mitis*), and the chorused grunt (*L. albigena*) were tested for audibility in masking noise. It was found that the monkey calls were about 10 dB more audible than were the human speech sounds. In addition, the monkeys were 3.4 dB more sensitive to calls from conspecifics than to calls of sympatric species in the presence of forest noise but no difference was found when testing was conducted in the absence of masking sounds. This led to the conclusion that

differences in the audibility of vocalizations of related species are due primarily to acoustical differences between signals, yet more subtle receptive specializations may also be involved (Brown 1986:146). Taking this information along with the results on hearing in both monkey species it seems that selection has "acted on both the receptive and productive mechanisms to promote vocal communication in adverse environmental conditions" (Brown 1986:146).

SMITH, MOODY, STEBBINS, and NORAT 1987

The study by Smith *et al*. (1987) sought to examine the function of the outer hair cells (OHCs) of the cochlea in determining frequency selectivity in patas monkeys (*Erythrocebus patas*). Patas monkeys were chosen as test subjects because they show a unique reactivity to ototoxic aminoglycoside antibiotics (specifically hydrostreptomycin-sulfate (DHSM)) that produce selective loss of OHCs while leaving inner hair cells intact. This selective loss of OHCs was used to help isolate their function in auditory processing. Audiograms and psychophysical tuning curves were obtained both pre- and post-treatment, but only the information on audiograms will be reviewed.

The study used four juvenile male patas monkeys as test subjects although audiogram data on only two subjects were presented. The monkeys were tested using the reaction-time procedure and thresholds were determined by the tracking procedure in 10 dB increments. Testing continued until 8 out of 10 consecutive sessions produced thresholds that were within 10 dB of each other and the average of these 8 thresholds was taken as the final value. The test stimuli were steady and pulsed tones ranging from 63 Hz to 40 kHz. The steady tones were 2.5 seconds in duration and were used to evaluate

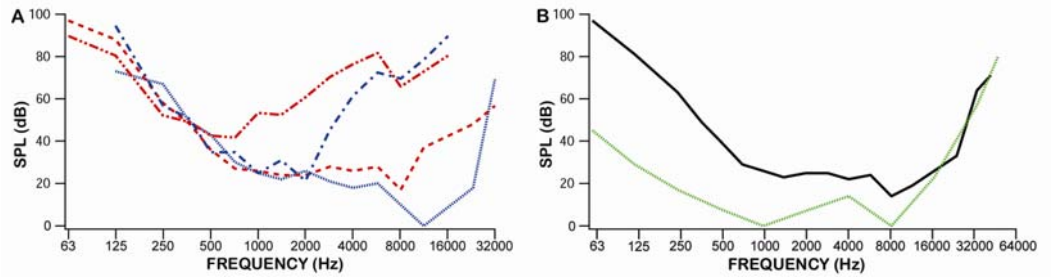

FIGURE 3.38 – **A**. Individual audiograms of *E. patas* from Smith *et al*. 1987 illustrating the effect of loss of cochlear outer hair cells on thresholds at middle and higher frequencies (▪▪▪▪▪▪ represents pre-treatment and ▬ ▪ ▬ ▪ ▬ represents post-treatment thresholds for subject M-155; ▬ ▬ ▬ represents pre-treatment and ▬ ▪▪ ▬ ▪▪ represents post-treatment thresholds for subject M-157). **B**. Pre-treatment species mean audiogram for *E. patas* (▬▬▬) compared with Cercopithecinae audiogram (▪▪▪▪▪▪) from Stebbins 1973.

the normality of the ear prior to treatment. The pulsed tones consisted of 10-25 millisecond pulses separated by 235 milliseconds, resulting in a total test duration of 2.6 seconds. The absolute threshold audiograms presented in the text were produced using the pulsed tones. All tones were presented using headphones (TDH-49) with supraaural cushions (MX-41/AR cushions) and were calibrated using a condenser microphone with a 6 cm^3 coupler. The testing was conducted in a double-walled sound attenuating chamber.

The pre- and post-treatment thresholds for both subjects are given in Appendix 33 and presented in Figure 3.38A. The pre-treatment audiograms show relatively similar contours with a slight peak around 1.5 kHz, a moderate dip in the mid-range frequencies (2 kHz for M-155 and between 2.9 and 5.7 kHz for M-157), and a primary peak at higher frequencies (8 kHz for M-157 and 11.2 kHz for M-155). The mean range for all frequencies was 10.1 dB but the audiogram for M-157 demonstrates markedly elevated thresholds at the higher frequencies with a mean range between subjects above 8 kHz of

27 dB. The post-treatment audiograms are also fairly similar to each other in shape with a mean range of 13.7 dB. However, these two audiograms differ primarily in the mid-range frequencies with a mean range of 20.3 dB between 1 and 8 kHz. Compared to the pre-treatment audiograms, the post-treatment audiograms show a significant loss of sensitivity at the middle and high-range frequencies. The difference between the means for both groups averages 38.1 dB from 1 to 16 kHz. Despite the significant roll-off at middle and high-frequencies for the post-treatment audiograms they still retain their respective relationships to each other (*i.e.*, M-155 generally lower than M-157 with a criss-cross towards the higher frequency range. Another observation of note is that they still retain a small notch at 5.7 kHz and a slight peak at 8 kHz. Smith *et al*. take these data to support the notion that the physiological filtering function of the ear is a product of two interrelated processes (1987:136). The first process reflects the passive mechanical properties of the basilar membrane and the dynamics of the surrounding fluids that act as a low-pass, broadly tuned filter. The second process reflects the active function of the OHCs and operates near the high-frequency cut-off of the first process to increase sensitivity and frequency selectivity. While the results from their study provide strong evidence in support of the role of the OHCs, it still remains an open question as to what mechanisms are responsible for specific contours of the audiogram that are still evident even in the absence of normal OHC function.

Figure 3.38B shows the mean pre-treatment audiogram of the patas monkeys along with the composite Cercopithecinae audiogram from Stebbins (1973). Both sets of data employed similar conditioning procedures and used headphones. The audiograms are quite similar at 16 kHz and above (mean range from 16 to 40 kHz = 3 dB) but the

patas monkey audiogram becomes increasing less sensitive as frequency decreases. The mean range for all frequencies is 23.4 dB but the range for frequencies from 63 to 500 Hz averages 45.5 dB and becomes as large as 52 dB at 63 and 125 Hz. Although Smith *et al*. (1987) did not compare their data with that of other researchers, these differences are substantial enough to warrant consideration. One possible explanation for these discrepancies is that they represent a true species distinction. However, the Stebbins audiogram included patas monkeys and it should be recalled that it was stated that the inter-species variability was no greater than the intra-species variation (1973:358). Another possibility relates to the calibration procedures that were used in the Smith *et al*. (1987) study. Pfingst *et al*. (1975) demonstrated that calibration procedures can have a significant effect on thresholds, particularly at low-frequencies. The use of a 6-cm^3 coupler, which was designed for use with human subjects, can underestimate low-frequency SPL's and produce artificially low thresholds when applied to an outer ear with less volume than that typical of humans (see below - Owren *et al*. 1988; Smith and Olszyk 1997), as is the case with most monkeys. However, this is exactly opposite the trend observed, so it is unlikely that these differences are explained by the calibration techniques. One final explanation is the fact that the published patas monkey audiograms were produced using pulsed tones instead of steady tones as in the Stebbins (1973) study (and all other studies producing audiograms). Since it is known that signals of shorter duration result in higher thresholds (due to temporal integration) this may represent a possible explanation for the unusually high patas monkey thresholds of the Smith *et al*. (1987) study. Still, the reason why this would have a disproportionate effect on low and middle-range frequencies remains unclear.

OWREN, HOPP, SINNOTT, and PETERSON 1988

Somewhat similar to the studies by Brown and Waser, the article by Owren *et al*. (1988) was part of a larger study examining basic hearing functions in Old World primates. In this report, absolute auditory thresholds were measured in three vervet monkeys (*Chlorocebus aethiops*[25]), five de Brazza's monkeys (*Cercopithecus neglectus*), and five Japanese macaques (*Macaca fuscata*). All the monkeys were juveniles or sub-adults except two vervets and one de Brazza's monkey that were young adults. In addition, 4 humans were tested ranging in age from 20 to 33. A reaction-time procedure was used to test the subjects that included 15% catch trials. Data were discarded for trials in which the catch trial rate exceeded 15%. The psychophysical method used to determine thresholds was the method of constant stimuli and final thresholds were calculated as the mean of the five lowest thresholds from a group of 15 consecutive sessions that produced values that were within 10 dB of each other. Test tones ranged from 63 Hz to 45 kHz in half-octave intervals (in addition to 34.9, 38, 40, 42, and 43 kHz) and were presented binaurally using headphones (TDH-49P). Intensity levels were initially calibrated using a 6 cm^3 coupler for both humans and monkeys but large discrepancies (5-15 dB between 63 Hz and 2 kHz) were detected when the monkey calibrations were performed using a condenser microphone placed at the entrance to the external auditory canal (there was no difference in the human calibrations using the two calibration procedures). This resulted in the authors suggesting that the 6 cm^3 coupler is inappropriate for the calibration of low-frequency signals presented to monkeys since it was designed to approximate the volume of the human ear enclosed by a

[25] At the time of the study this species was designated *Cercopithecus aethiops*.

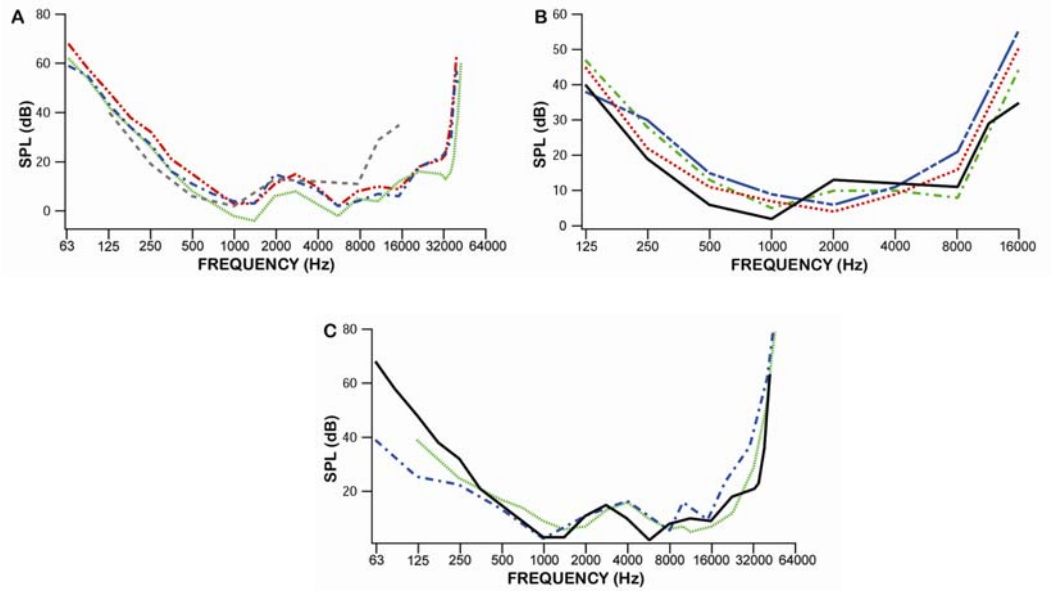

FIGURE 3.39 – **A**. Species mean audiograms from Owren *et al*. 1988 for humans (— — —), *C. aethiops* (▪▪▪▪▪▪), *C. neglectus* (— ▪ — ▪ —), and *M. fuscata* (— ▪▪ — ▪▪). **B**. Human mean audiogram from Owren et al. 1988 (———) compared with human audiograms from Sivian and White 1933 (——— — —), Dadson and King 1952 (— ▪ — ▪ —), and Pfingst *et al*. 1978 (▪▪▪▪▪▪). **C**. M. fuscata mean audiogram from Owren *et al*. 1988 (———) compared with macaque audiograms from Pfingst *et al*. 1978 (▪▪▪▪▪▪) and Stebbins *et al*. 1966 (— ▪ — ▪ —).

headphone cushion (1988:100). Therefore, all monkey calibrations were performed using a condenser microphone - one for frequencies ranging from 63 Hz to 2 kHz and another for all tones above 2 kHz. Testing was conducted in a single-walled sound attenuating chamber.

The species means and ranges are given in Appendix 34 and the mean audiograms are presented in Figure 3.39A. At 250, 353, and 500 Hz, the humans were found to have significantly better hearing than the monkeys, although the monkeys did not differ from each other. Two of the humans (the 33 year old and one suspected of a high frequency loss) were found to be consistently less sensitive than the other two at frequencies between 5.6 and 16 kHz. Regardless of whether the two with inferior high-frequency

sensitivity were included or not, above 8 kHz, the monkeys showed much better sensitivity than the humans. Among the monkeys, the vervets had significantly better hearing at 2 kHz and were also the only species to respond to tones at 45 kHz. In addition, only one de Brazza's monkey and one Japanese macaque responded to stimuli at 43 kHz, suggesting that the vervets had better mid-range sensitivity and high-frequency sensitivity at 22.6 kHz and above. Owren *et al*. (1988) compared their human data with that of other studies (Sivian and White 1933; Dadson and King 1952; Pfingst *et al*. 1975) and found the only notable differences to be at 16 kHz (Figure 3.39B). This difference was attributed to the fact that their human audiogram used in this comparsion was based on only the 2 humans that had the best high-frequency hearing, apparently biasing the results (Owren *et al*. 1988:102).

Owren *et al*. (1988) also compared their *M. fuscata* data with that of other macaques (*M. nemestrina* and *M. fascicularis* mean - Stebbins *et al*. 1966 and *M. mulatta* - Pfingst *et a*l. 1978) obtained in studies using headphones and similar conditioning procedures (Figure 3.39C). They noted that their macaques were more than 10 dB less sensitive at 125 and 250 dB than that of the other species. They proposed that this difference may be due to the fact that they tested their monkeys in a single-walled chamber, whereas the other two studies used double-walled chambers (1988:102). They tested this idea by normalizing their data, along with that of Pfingst *et al*. (1975) and Brown and Waser (1984), with respect to the humans that were also tested in the same studies. These relative thresholds suggested that there was very little difference between Japanese and rhesus macaques: at 250 Hz the difference is 3.7 dB (the previous difference was 6.5 dB) and at 125 Hz *M. fuscata* now appears about 3 dB more sensitive

than *M. mulatta* (the previous difference was 8.6 dB in the opposite direction). Thus, Owren *et al*. attribute the differences at 125 and 250 Hz to the sound attenuating characteristics of their single-walled booth (1988:103).

Despite the persuasive argument presented by Owren and colleagues, several facts suggest that the explanation may not be quite so straightforward. For one, if their test chamber contained excessive ambient noise that masked the audibility of signals at lower frequencies then this bias should also be evident in their human data. However, inspection of Figure 3.39B shows that their humans are actually more sensitive than the humans from the Pfingst *et al*. (1975) study with an average difference of about 4.5 dB from 125 Hz to 1 kHz. It is also worth noting that at 125 Hz the Stebbins *et al*. (1966) audiogram is actually more divergent from the *M. mulatta* audiogram (~11.5 dB), than is *M. mulatta* from *M. fuscata* (~8.6 dB), yet both Stebbins *et al*. (1966) and Pfingst *et al*. (1975) used double-walled chambers. Furthermore, the normalizing procedure is based on the assumption that the humans in the respective studies had approximately equal hearing. However, only three humans were used to derive the audiogram in the Pfingst *et al*. (1975) study and Owren *et al*. (1988) used a maximum of four humans (it is unclear whether this comparison included the two humans with high frequency loss). Therefore, it is possible that the human averages (even relatively) are not "approximately equal". The final point worth considering is that each of these studies investigated different species. Considering the rigorous calibration procedures employed by the authors in each study it seems feasible that these differences may represent true species distinctions.

Prior to their investigation, it was suspected that the de Brazza's monkey might exhibit enhanced low-frequency sensitivity similar to that of blue monkeys since both are

forest dwelling guenons that produce loud, low-pitched boom calls (Owren *et al*. 1988:100). However, the de Brazza's monkeys were no more sensitive at lower frequencies than were the vervets (although both were somewhat more sensitive than the macaques). This led the authors to propose that the hearing difference between blue monkeys and de Brazza's monkeys may reflect habitat-specific evolutionary pressures that caused the divergence in the use and perception of a possibly homologous (boom) call (Owren *et al*. 1988:104). In support of this argument was the finding by Waser and Brown (1986) that the riverine forest occupied by de Brazza's monkeys did not display the "sound window" at low-frequencies as did the rain forest habitat of blue monkeys and that de Brazza's monkeys do not appear to use their boom call for long distance communication (Gautier-Hion and Gautier 1978). Owren *et al*. (1988:104) also used the evidence marshaled by Waser and Brown (1986) to suggest that the enhanced mid-range sensitivity of the vervets may be correlated with their use of a diverse repertoire of middle-frequency, short-range sounds since their savanna habitat places a constraint on long distance signaling and that the ambient characteristics favor calls in this range. The authors also commented that the finding that vervets demonstrated the best high-frequency sensitivity of the species they investigated and have the smallest head size lends support to the theory by Masterson *et al*. (1969) that the upper end of the frequency range for a species is inversely related to inter-aural distance (Owren *et al*. 1988:104).

KOJIMA 1990

Kojima (1990) measured absolute auditory thresholds, frequency and intensity difference thresholds, and the resonance of the external auditory meatus in chimpanzees

and humans in order to evaluate whether great apes (chimpanzees) have hearing characteristics more similar to monkeys or humans. To determine absolute thresholds, a reaction-time procedure was used and thresholds were presented using the method of constant stimuli (the selected intensities were in 10 dB steps from -10 to 90 dB SPL). Threshold was defined as the intensity associated with a reaction time of 0.8 seconds. Tones were presented monaurally using headphones (TDH-39 with MX-41/AR ear cushions) and were calibrated using a 6 cm^3 coupler. All testing was conducted in a double-walled sound attenuating chamber. The test frequencies ranged from 125 Hz to 32 kHz in octave steps plus 24 kHz for the chimpanzees and from 125 Hz to 16 kHz for the humans. The subjects were two female chimpanzees (5 and 7 years old) and one male human (42 years old). To determine the frequency and intensity difference thresholds, the same acoustic apparatus and chamber were used as in the absolute thresholds experiment and the subjects were the same except the 7 year old chimpanzee was replaced by a 4 year old female. A similar reaction-time procedure was employed and the thresholds were determined in a manner very similar to that used by Stebbins (1973-see above). For measurements of frequency difference thresholds, comparison tones (ranging from 500 Hz to 4 kHz at 70 dB SPL) were varied from 5 to 80 Hz for the chimpanzees and from 2.5 to 40 Hz for the human. For measurement of intensity thresholds, the intensities ranged from 50 to 90 dB SPL (for a 1 kHz tone) and comparison intensities varied from 1 to 8 dB for the chimpanzees and from 0.25 to 4 dB for the human. The resonance of the external auditory meatus was measured in one cadaveric chimpanzee and three humans by presenting tones up to 10 kHz at 80 dB SPL and measuring the intensities with a

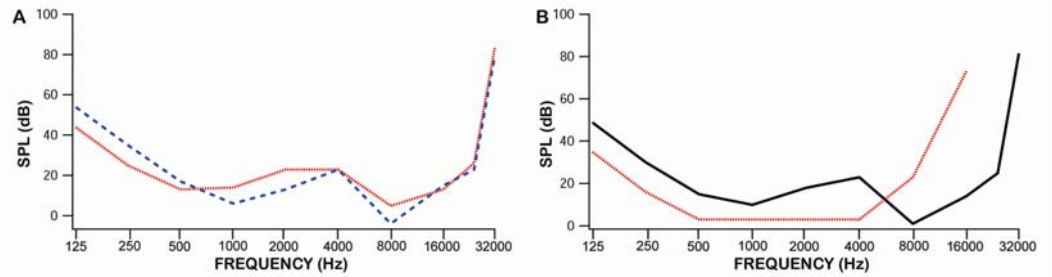

FIGURE 3.40 – **A**. Individual P. troglodytes audiograms for Popo (▬ ▬ ▬) and Pen (▪▪ ▪▪▪▪) from Kojima 1990. **B**. *P. troglodytes* species mean audiogram (▬▬▬) compared with human subject (▪▪▪▪▪▪) from study.

microphone placed in the meatus (a reference microphone was placed at the tip of the nose).

The absolute auditory thresholds for all three subjects, and the ranges and species mean for chimpanzees are given in Appendix 35. The chimpanzee audiograms are presented in Figure 3.40A and it can be seen that both individuals have relatively similar thresholds at most frequencies. The mean range for all frequencies was 6 dB and the greatest variability was at the lower frequencies (8 dB). They illustrate the classic non-human anthropoid W-shaped contour with peaks at 1 and 8 kHz (8 kHz was the most sensitive frequency) and the mid-frequency dip between 2 and 4 kHz. Thus, Kojima concluded that chimpanzees are more similar to Old and New World monkeys than humans (1990:64). However, Kojima also noted that the study by Brown and Waser (1984) did not follow the general Old World monkey pattern (W-shape) and proposed that procedural differences (*i.e.*, the use of speakers by Brown and Waser (1984)) may be responsible for the absence of a mid-frequency dip. Figure 3.40B shows the human and mean chimpanzee audiograms. It can be seen that below about 6 kHz humans are more sensitive whereas above this frequency chimpanzees are more sensitive. Kojima proposed

that the enhanced sensitivity in the low- and mid-range frequencies may be a specialization for the perception of human speech sounds and that the lack of sensitivity in chimpanzees at these ranges explains their difficulty in discriminating vowel sounds with formats at 300 Hz [i] and [u] and 2 kHz [i] and [e] (1990:65-66). The unchanging thresholds for humans from 500 Hz to 4 kHz may be related to the rather wide intensity intervals of the psychophysical technique employed and could be indicative of somewhat gross threshold estimates in this study.

With respect to frequency difference thresholds, the chimpanzees could differentiate tones that were separated by about 10-15 Hz for frequencies between 500 Hz and 2 kHz but it took tones separated by 35-40 Hz when the frequency reached 4 kHz. The humans showed a similar trend in that it was more difficult to discriminate between tones at higher frequencies but still illustrated threshold values that were 1.5-5.6 times smaller than those of chimpanzees. The intensity difference thresholds for the chimps at 1 kHz were 1.4-1.5 dB at 70-80 dB SPL although thresholds were elevated at lower and higher intensities. Differences between humans and chimpanzees were relatively small at 70-80 dB SPL but humans averaged 1.25 dB less at all intensities tested. Again, Kojima suggested that these differences may influence the perception of speech sounds (1990:69).

The resonance of the external auditory meatus was found to be similar between chimpanzees and humans with a peak of around 20 dB SPL at 2.5 kHz. Since this frequency falls in the mid-frequency dip of chimpanzees, it was stated that the "external ear does not contribute to auditory sensitivity in chimpanzees" (Kojima 1990:66). Rather, it was proposed that the resonance of the outer ear may actually contribute to the lack

(loss) of sensitivity in the mid-range frequencies since the loud calls of chimps are amplified by the outer ear (Kojima 1990:66-67). In contrast, the lower intensity vocalizations of humans apparently do not result in hearing loss at mid-range frequencies. Kojima ends by offering the suggestion that "the evolution of human hearing may accordingly have some relation to the evolution of human speech" (1990:67).

SMITH and OLSZYK 1997

Smith and Olszyk (1997) measured thresholds in four juvenile male Japanese macaques (*M. fuscata*) using insert earphones. Insert earphones were chosen in an attempt to limit sources of error due to variability in head size, headphone fit, daily headphone placement, and animal movement during testing. In addition, these earphones used form-fitted foam eartips that permitted better intra-aural attenuation compared with typical headphones (Smith and Olszyk 1997:324). The earphones were calibrated by inserting each one into an artificial ear canal (based on diameter and length measurements from a *M. fuscata* cadaveric head) and measuring SPL's at the tympanic membrane end of the canal. Testing was conducting inside of single-walled sound attenuating chambers that were placed inside of a large double-walled sound attenuating chamber. Thirteen frequencies were tested ranging from 0.73 up to 30.5 kHz, the upper range of the transducers. The reaction-time procedure was used incorporating a 20% catch trial rate. Thresholds were determined using a tracking procedure and the traditional 50% detection criterion.

Appendix 36 gives the right and left ear thresholds for each individual and the individual and species means. It was noted that the contours were similar in both ears and

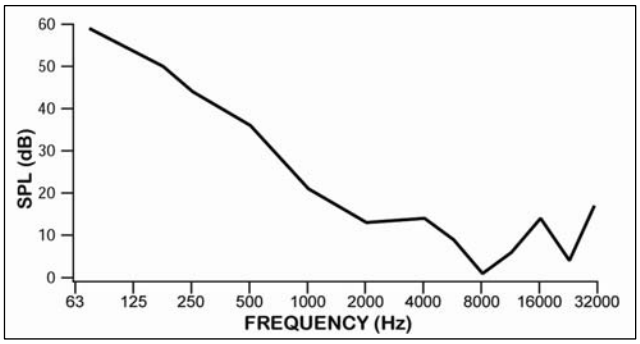

FIGURE 3.41 – *M. fuscata* species mean audiogram from Smith and Olszyk 1997.

across all subjects (Smith and Olszyk 1997: 326). The mean range for all frequencies (based on individual means) was 5.5 dB, although the range at lower frequencies was as large at 17 db at 500 Hz (Smith and Olszyk 1997: 326). Still, the authors note that the standard deviations for measures repeated within a session were less than half of those obtained in their previous investigations using supraaural and circumaural- type headphones (Smith and Olszyk 1997: 328). Figure 3.41 shows the mean audiogram for all subjects and illustrates a fairly typical contour with a minor dip at 4 k and maximum sensitivity at 8 kHz. However, somewhat similar to the Stebbins *et al*. (1966) macaque audiograms, there is a second dip and peak above the primary peak. Smith and Olszyk compared their data with those from five previous studies on other macaque species that used similar conditioning techniques and closed-field transducers (Stebbins *et al*. 1966; Stebbins 1973; Pfingst *et al*. 1975, 1978; Lonsbury-Martin and Martin 1981) and found that there is generally good agreement at mid-range and high-frequencies. However, at lower frequencies the mean thresholds from their subjects fell consistently above the range of the other macaque species. They admitted that it was unclear whether these discrepancies were due to real species differences (since the data from other studies did

not include data on *M. fuscata*) or differences in calibration and transducer techniques (Smith and Olszyk 1997:327). An attempt to tease apart these possibilities will be considered further in section III of this chapter.

JACKSON, HEFFNER, and HEFFNER 1999

The study by Jackson *et al*. (1999) was the most recent investigation of primate hearing to come out of the Heffner laboratory. The test subjects were three male Japanese macaques (two were 13 years old and the other was 17) and seven humans ranging in age from 20 to 44 years of age (three males and four females). The monkeys were tested using a conditioned suppression procedure with water reward similar to that used in previous conditioned suppression studies (Heffner *et al*. 1969; Heffner and Masterson 1970). The humans simply held down a button and released it whenever they heard a tone. The response rate (hit rate) was corrected for false alarms by subtracting the hit rate by the product of the hit rate times the false alarm rate. Preliminary thresholds were determined using a method of descending limits and then using the method of constant stimuli in 5 dB intervals around the initial estimate. Final thresholds were calculated based on at least two sessions that were within 3 dB of each other and rechecked after the complete audiogram was determined. If more than a 3 dB difference was detected, further testing was conducted. The test frequencies were 3 seconds in duration and ranged for the macaques from 8 Hz to 32 kHz in octaves, in addition to 0.012.5, 0.025, 36, and 40 kHz. The test frequencies for the human ranged from 4 Hz to 16 kHz, in addition to 18, 20, and 24 kHz. Test stimuli were presented with one of two loudspeakers: a 15-inch woofer for frequencies below 2 kHz and a high-frequency tweeter for all tones at 2 kHz and above.

The speaker position was varied to achieve an even sound field and maximize the intensity levels without producing undesirable distortion. Sound intensity levels were calibrated by placing a microphone in the position of the animals head and pointing directly towards the speaker. Testing was conducted in a double-walled acoustic chamber that contained additional sound attenuating materials to reduce acoustic reflections. As an added precaution, foam pads were placed under the woofer and testing cage to prevent the animals from responding to substrate vibrations produced by low-frequency sounds.

Appendix 37 presents the individual thresholds, species means and ranges. The mean range for all frequencies of the macaque audiograms (Figure 3.42A) was 5.4 dB with the highest variability at the high-frequencies (8.3 dB). The human audiograms (Figure 3.42B) showed more variability overall, with a mean range of 15.8 dB, but the highest variability was still at the higher frequencies (34 dB). This study was the first to examine the extreme low-frequency range of macaques and one of the monkeys could detect an 8 Hz tone at 85 dB SPL, while all could hear 12.5 Hz at 78 dB SPL. Although the average best frequency for all three monkeys was 4 kHz (1 dB SPL), this was only strictly true of one individual (#605). Monkey 286 showed two low points of equal sensitivity (1 and 4 kHz) while monkey 368 was slightly more sensitive at 16 kHz compared with 4 kHz. On the high-frequency side, the macaques averaged 89 dB SPL at 40 kHz, the highest frequency tested. The humans were able to be tested at higher intensity levels and it was found that they could hear a 4 Hz tone when the SPL was 101 dB. The best average threshold for the humans was -10 dB SPL at 2 and 4 kHz. Only

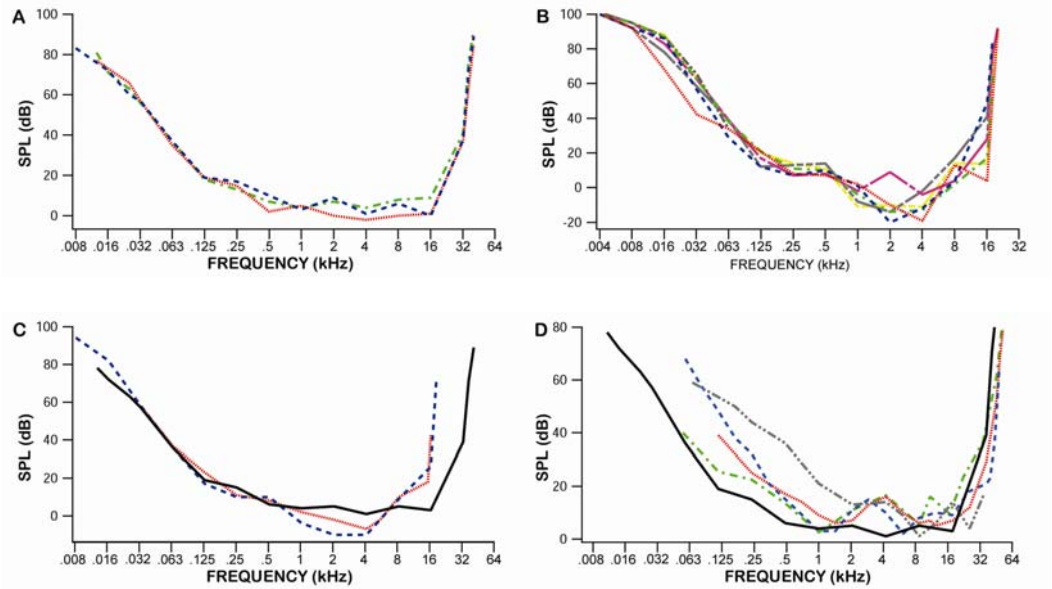

FIGURE 3.42 – **A**. *M. fuscata* individual audiograms from Jackson *et al*. 1999 (— ·— · — represents subject #286, ▪▪▪▪▪▪ represents subject #608, — — — represents subject #638). **B**. Individual human audiograms from Jackson *et al*. 1999 (——— — — — represent subject CC, ——— — — represents subject HH, ——— — represents subject JM, — ·· — ·· represents subject LH, — ·— ·— represents subject PH, — — — represents subject RH, and ▪▪▪▪▪▪ represents subject SM). **C**. *M. fuscata* (———) and human (— — —) species means compared with ISO human standard (▪▪▪▪▪▪). **D**. *M. fuscata* species mean (———) compared with macaque audiograms from Stebbins *et al*. 1966 (— ·— ·—), Pfingst *et al*. 1978 (▪▪▪▪▪▪), Smith and Olszyk 1987 (— ·· — ··), and Owren *et al*. 1988 (— — —).

three of the subjects responded at 20 kHz (91 dB SPL) and the average frequency for a 60 dB SPL tone was 17.6 kHz.

Figure 3.42C presents the mean audiograms for humans and macaques along with the ISO standard free-field audiogram. Jackson *et al*. (1999:3020) noted the good agreement between their human audiogram and the ISO standard at low- and high-frequencies but the fairly large discrepancy in the middle-frequencies where their threshold averaged 12 dB lower at 2 kHz. They suggested that this difference may be the result of the high individual variability in the region of best sensitivity (up to 29 dB at 2

kHz) but also acknowledged that there is a high level of variation at higher frequencies where their data agrees well with the ISO standard (Jackson *et al*. 1999:3020-3021). Jaskson *et al*. (1999:3021) pointed out that at lower frequencies the macaque and human audiograms are virtually identical, which they stated is similar to findings from other studies (*e.g*., Owren *et al*. 1988). However, the study by Owren *et al*. (1988), as well as most other studies comparing macaques to humans have found humans to have slightly better hearing sensitivity at lower frequencies (Behar *et al*. 1965; Pfingst *et al* 1975). Like all other studies on primate hearing, the monkeys show significantly better high-frequency sensitivity compared to humans. They used this data in support of the idea that differences in high-frequency hearing are explained by differences in interaural distance (Masterson *et al*. 1969) which have a "robust" relationship with each other producing a coefficient of determination of $r = 0.787$.

Compared with previous studies on Japanese macaque hearing (Owren *et al*. 1988; Smith and Olszyk 1997), the thresholds determined by Jackson *et al*. (1999) are considerably lower in the low-frequency range (Figure 3.42D). Although, the two previous studies did not use speakers, the authors suggest that this difference is due to the difficulties in calibrating headphones and not to differences in the transducer type *per se* (Jackson *et al*. 1999:3022). They suggested that audiograms determined in the free-field produce more consistent results across time and laboratories and that they test the hearing of the animal as a whole (including head and pinna effects) and not just the ear (Jackson *et al*. 1999:3022). While the second point is no doubt valid, the claim that headphones are more difficult to calibrate has been challenged by some (Stebbins 1971a; D. Smith 2003, pers. comm.). Also included in Figure 3.42D are the macaque audiograms determined by

Stebbins *et al*. (1966) and Pfingst *et al*. (1978) which the authors included to bolster their point, suggesting that they were more similar to their thresholds at lower frequencies than those of the other two *M. fuscata* studies despite being produced using headphones. However, it is obvious that at lower frequencies (125 Hz-1 kHz) the Pfingst *et al*. (1978) audiogram illustrates a closer affinity to the Owren *et al.* (1988) audiogram (mean difference = 6 dB) than that of Jackson *et al*. (1999) (mean difference = 11.5 dB). The Stebbins *et al*. (1966) audiogram follows both audiograms at different points, depending on the frequency. Furthermore, the Smith and Olszyk (1997) study used insert-earphones, which may have different response characteristics than headphones (it is only one of two studies on primates using this transducer type), and the studies by Stebbins *et al*. (1966) and Pfingst *et al*. (1978) investigated different species of macaques which could have slight differences in low-frequency sensitivity, all of which could confound this comparison. Therefore, it seems plausible that the disagreements between the Japanese macaque audiograms are at least as much a product of transducer type as errors associated with calibration procedures. The effect of transducer type on threshold estimates will be examined in more detail in section III.

LASKY, SOTO, LUCK and LAUGHLIN 1999

Lasky *et al*. (1999) measured distortion product otoacoustic emissions (DPOAE), auditory brainstem evoked response thresholds (ABR), and behavioral thresholds in 15 adult rhesus monkeys. The testing of the behavioral thresholds actually consisted of between seven and eleven 15 year old subjects. The ABR thresholds closely paralleled the behavioral thresholds at all frequencies except one (8 kHz), but were almost 20 dB

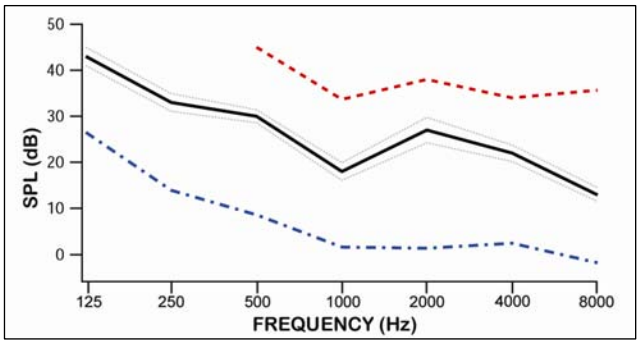

FIGURE 3.43 – Mean behavioral audiogram (———) with range in standard deviations (.....) and ABR audiogram (— — —) for *M. mulatta* from Lasky *et al*. 1999 compared with mean *M. mulatta* audiogram (— · — · —) from previous studies that tested their subjects using speakers (Harris 1943; Clack and Herman 1963; Behar *et al*. 1965; Fujita and Elliot 1965; Bennett *et al*. 1983).

lower (Figure 3.43). The behavioral thresholds were determined using a reaction-time procedure similar to previous studies except using a double-reward technique for correct responses (true positives and true negatives). The test frequencies ranged from 125 Hz to 8 kHz and were presented using two speakers positioned 46 cm to each side of the subject. Tonal intensity was calibrated using a condenser microphone positioned in the place of the monkey's head during testing. Testing was conducted in a sound attenuating booth, although it was not stated whether it was single or double-walled. The psychophysical method was a modified staircase procedure (using 3 dB intervals) where the actual starting value was randomly selected within a 30 dB range surrounding the expected threshold. The criteria for determining a threshold were considered to be "quite challenging" and resulted in a reduced number of subjects compared with the DPOAE and ABR measurements (Lasky *et al*. 1999:38). A threshold session for a single frequency consisted of three series that had to be within 6 dB of each other to count as a valid session and a series value represented the mean of four reversals in intensity

change. The final thresholds were the mean of two successive sessions that were within 3 dB of each other.

The mean threshold values and standard deviations are given in Appendix 38 and presented in Figure 3.43. The audiogram displays fairly normal contours with a peak at 1 kHz and a mid-frequency dip at 2 kHz. However, Laky *et al*. (1999:41) noted that the thresholds were about 10 dB higher than those from previous studies (Stebbins *et al*. 1966; Pfingst *et al*. 1978; Owren *et al*. 1988). In fact, controlling for transducer type (*i.e*., using only speaker studies), there is an average 19 dB difference between the mean *M. mulatta* speaker audiogram (Harris 1943; Clack and Herman 1963; Behar *et al*. 1965; Fujita and Elliot 1965; Bennett *et al*. 1983) and that of Lasky *et al*. (1999) (Figure 3.43). The authors suggested that the "strict threshold criteria, the complexity of the task, and the motivation of the subjects may be responsible for the elevation in threshold" (Lasky *et al*. 1999:41). However, the conditioning procedure was almost exactly the same as that used in other studies and the monkeys that did not meet the threshold criteria were excluded from the threshold determinations, so the anomalously high thresholds may be caused by other, yet to be identified factors (*e.g*., calibration procedures, testing chamber ambient noise, etc.).

HEFFNER 2004

The article by Heffner (2004) is a review of the sound localization data and a selected subset of the hearing sensitivity data for primates. This evidence is marshaled to support the theory that sound localization is the selective pressure on high-frequency hearing in smaller primates, and mammals in general, and is related to the need for

animals with smaller interaural distances to hear higher frequencies in order to localize sound using pinna cues and spectral differences between the ears (Masterson *et al*. 1969; Heffner and Heffner 1992; Heffner 2004:1115). Although no new data were presented from the Heffner laboratory, the review presented some unpublished data for *Eulemur fulvus* that was conveyed to the author via a personal communication from D. Sutherland and R. B. Masterson. No information was presented as to the psychophysical methods and testing conditions except that the data was apparently obtained using speakers. Attempts to obtain the full set of threshold data have been unsuccessful, but five parameters of hearing sensitivity were taken from Table 1 in the publication (Heffner 2004:1113) and these data are presented in Appendix 39.

SECTION III:

Problems with Comparing Audiograms

There are three main sources of error that could present difficulties when comparing the type of data presented in this chapter:

1. *Intra-individual variability* – The threshold values determined for an individual can sometimes deviate by several dB on either side of the determined threshold value due to threshold criterion and inter-ear differences;

2. *Intraspecific variability* – The threshold values used to generate a species mean audiogram might mask underlying variability caused by individual variation from numerous sources such as age and sex;

3. *Interlaboratory variability* – Differences between audiograms of the same species may be sizeable if obtained using different psycho-acoustical standards, conditioning procedures, and/or auditory equipment and calibration techniques.

These problems present the possibility that statistical evaluation may suggest differences in hearing performance that are not biologically meaningful or conversely could underestimate truly significant differences. Concerns such as these have led researchers to warn against emphasizing the subtle variations in primate audiograms (Fay 1988). However, through careful consideration of each one of these potential sources of error, it may be possible to enhance analytical power while having greater confidence that apparent differences in sensitivity represent true species distinctions.

Intra-individual Variability

An important factor to consider when evaluating intra-subject variability is the fact that the "final threshold" for a given frequency is actually the mean of several threshold estimates. Several of the studies established a threshold criterion that required the threshold estimates to be within a limited range before the data were averaged. A summary of the threshold range criterion is presented in Table 3.2. The values range from 3 to 10 dB with an average of 6 dB. Note that the two studies using a criterion of 10 dB took the average of a larger number of trials (the number in parentheses).This suggests that a single threshold determination could actually deviate by as much ± 3 dB around the given value. Several studies also reported information on the inter-session

Study	Threshold Criterion (dB)	Inter-Session Variability (dB)
Elder 1934		3.3
Fujita and Elliot 1965	5 (5)	
Behar *et al*. 1965		0.7 - 7.6 (4.2)
Clack 1966		4.8
Dalton 1968		0.88 - 1.14 (1)
Mitchell *et al*. 1970	6 (3)	
Green 1971	5 (3)	
Pugh *et al*. 1973		< 3
Beecher 1974		< 3
Pfingst *et al*. 1975		4
Bennett *et al*. 1983	6 (2)	5.2
Smith *et al*. 1987	10 (8)	
Owren *et al*. 1988	10 (5)	
Jackson *et al*. 1999	3 (2)	
Lasky *et al*. 1999	3 (2)	
Mean	**6**	**3.5**

TABLE 3.2 – Studies which published the acceptable range in intensity values (dB) for determining thresholds or measured the variability in final threshold estimates for more than one session. The number in parentheses in the second column is the number of trials used to determine the final threshold and the number in parentheses in the third column is the mean for the range in that cell.

variability for either a single subject or the species as a whole and are also included in Table 3.2. The range for these values is from 1 to 5.2 dB with an average of 3.5. The highest value (5.2 dB) from Bennett *et al*. (1983) was based on 3 measurements taken at approximate one year intervals which may have contributed to the high value. The data from Clack (1966) was also included although the thresholds for the "defective" ear were excluded above 1 kHz. These data, although based on a small sample, suggest that in practice a threshold estimate could vary by just under ± 2 dB.

Another issue that could contribute to intra-subject variability is the difference in sensitivity between the right and left ears. A handful of studies presented data on the individual thresholds for each ear in their subjects. The seminal primate hearing study by Elder (1934) was one such example and although he did not determine the absolute threshold values in his subjects, the relative differences are still a valid indicator of inter-

ear variability and these data are given in Appendix 1. The inter-ear variability for the three chimpanzees ranged from 3.1 to 4.3 dB with an average of 3.6 dB. The data presented by Smith and Olszyk (1997) for Japanese macaques (Appendix 36) illustrated a similar degree of variability with a range of 2.6 to 5.3 dB and a mean of 3.4 dB. As previously stated, Bennett *et al*. (1983) reported the differences between right and left thresholds were small and insignificant. In contrast, the inter-ear variability for Clack's (1966) macaques was quite substantial (Appendix 13 and Figure 3.16). The average variability for monkey c2 was 7.6 dB and for monkey c4 was 24.8 dB producing an average of 16.2 dB. This would seem to indicate that both subjects suffered from presbycusis although Clack only acknowledged a hearing loss in monkey c4. The only part of the audiograms that seems to be "normal" are the thresholds for monkey c2 from 125 to 1000 Hz that show an inter-ear variability of 2.5 dB. Taking this limited subset of Clack's data (1966) along with that of Elder (1934) and Smith and Olszyk (1997) suggests an estimate of inter-ear variability of around 3.2 dB.

Intraspecific Variability

Effects of Age on Threshold Values[26]

As early as the work of Elder it was recognized that older individuals often produce elevated threshold values, particularly at higher frequencies (Elder 1934:179). This was convincingly demonstrated by Bennett *et al*. (1983) for macaques and the report by Farrer and Prim (1965) added more evidence to the human literature on presbycusis and suggested the even the six year old chimpanzees may have suffered some high-

[26] This section focuses mainly on those studies involved with non-human primates although a large body of literature has been devoted to investigating age-related hearing loss in humans. The reader is referred to Glorig and Nixon for a seminal paper on this subject.

frequency hearing loss. However, as was previously mentioned, the seven year old chimpanzee in Elder's study (1935) responded to higher frequencies (33.5 kHz) than any of Farrer and Prim's subjects, while Elder's youngest chimpanzee (three years old) responded only to tones as high as 26.5 kHz. Therefore, the slight decrease in high-frequency sensitivity in the young chimpanzees of Farrer and Prim (1965) may have been an artifact of small sample size. And yet, in Seiden's study (1957), only the youngest individual could hear test stimuli at 35 kHz while all others showed a high-frequency limit closer to 30 kHz. In fact, subject #1 (the youngest) also has the lowest thresholds from 4 to 7 kHz, although at lower frequencies there does not appear to be any age-related effects (Figure 3.6B). This partially accounts for the relatively high variability at higher- (26.8 dB) and middle-frequencies (14.7 dB). Another example illustrating the effects of presbycusis is the middle-aged macaques in the study by Jackson *et al*. (1999). The oldest subject (17 years old) produced higher thresholds than the two 13 year-old macaques at all frequencies above 2 kHz. The two oldest humans (43 and 44 years old) from this study also had the highest thresholds of all human subjects at 16 and 18 kHz.

The final example of age-related hearing loss comes from the human subject from the study on chimpanzees by Kojima (1990). This individual was 42 years of age and had the lowest high-frequency limit of any human audiogram presented in this chapter. However, to provide one counter-example, the one adolescent in the study by Mitchell (1970) did not have thresholds that were any lower than those of the adult subjects in his study. At present, there does not seem to be enough data to determine at which age class presbycusis starts to have a significant influence on thresholds (which could be species specific). Although many of the studies did use young adults and adolescents it would

seem to be sensible to exclude all but the younger subjects when examining the upper limits of the hearing range whenever possible.

Intralaboratory Species Variability

Table 3.3 presents a tabulation of the intra-specific variability for all of the studies which presented individual threshold data. The mean range of absolute values for intra-specific thresholds of all studies was 8.4 dB with a range for individual studies from 1.9 to 18.5 dB. In light of the finding that the study with the lowest value tested only 2 individuals (Beecher 1974), it seems possible that lower levels of variability may be associated with only testing a few individuals. However, the study that presented data on six individuals (Fujita and Elliot 1965) had a mean range of 8.8 dB which is very close to the average and not near the upper limit as would be expected if more individuals resulted in higher variability. Furthermore, the range for studies that tested only 2 individuals was 1.9 to 13.6 dB (excluding the value of 16 dB for the GSR thresholds obtained for *M. mulatta* in the study by Dalton 1968). Therefore, this suggests that inter-subject variability is not directly related to the number of individuals tested.

When the mean for all studies is considered, the most variability occurred at the higher frequencies tested (9.2 dB), the mid-range frequencies showed the same value as the mean for all frequencies, and the lower frequencies showed the lowest variability (7.9 dB). However, when examining the studies individually (Table 3.3 - column 6), it appears that there is more variability in the low frequencies than in the mid-range frequencies, although the higher frequencies still produced the highest variability. These data suggest that on average thresholds vary by about ± 4.2 dB around the mean with

Species	# of Individuals	Mean Range (dB)	Low Range < 1kHz (dB)	Middle Range 1 - 8kHz (dB)	High Range > 8kHz (dB)	Range Order	Study
A. trivirgatus	2	1.9	2.7	1	2.1	L>H>M	Beecher 1974a
Ateles sp.	2	3.2	5.3	1.3	3[1]	L>H>M	Wendt 1934
C. jacchus	5	17.3	10.8	14.7	26.8	H>M>L	Seiden 1957
C. capucinus[2]	4	10.4	15[1]	9.3		L>M	Dalton 1968
C. aethiops	3	8.2	5.3	7.4	11.2	H>M>L	Owren *et al.* 1988
C. mitis	2	2.6	1.8	1.5	5.3	H>L>M	Brown & Waser 1984
C. neglectus	5	11.3	10.9	5.9	16.6	H>L>M	Owren *et al.* 1988
E. patas	2	10.1	7	5	27	H>L>M	Smith *et al.* 1987
G. sengalensis	2 (4)	5.2[3] (14.2)	7[3] (12)	6[3] (10)	4[3] (24)	L>M>H	Heffner *et al.* 1969
L. catta	4	18.5	14.7	13.8	26.3	H>L>M	Gillette *et al.* 1973
L. catta	4 (5)	10.5[4] (15.5)	12.3[4] (15.3)	8.3[4] (11.5)	11.5[4] (19.8)	L>H>M	Mitchell *et al.* 1971
E. fulvus	2	13.6	9.3	15.8	15.5	M>H>L	Mitchell *et al.* 1970
E. macaco	2	7.4	5.3	12	1.5	M>L>H	Mitchell *et al.* 1970
M. fasciculans	3	10.5	8	10.8	12	H>M>L	Stebbins *et al.* 1966
M. fasciculans	3	5.4	5	6.5	3[1]	M>L>H	Fujita and Elliot 1965
M. fasciculanis	2	7.9	7	8.3	9	H>M>L	Fujita and Elliot 1965
M. fuscata	3	5.4	3.6	6.3	8.3	H>M>L	Jackson *et al.* 1999
M. fuscata	5	13.5	14.6	10.3	15.3	H>L>M	Owren *et al.* 1988
M. fuscata	4	5.5	8.3	5	3.5	L>M>H	Smith & Olszyk 1997
M. mulatta	4	13	9.4	14.5	14.7	H>M>L	Behar *et al.* 1965
M. mulatta	2	8.1	9.9	8.1	7	L>M>H	Bennett *et al.* 1983
M. mulatta	2	9.8	14.3	12	3[1]	L>M>H	Clack 1966
M. mulatta[5]	2	16	10[1]	17.5		M>L	Dalton 1968
M. mulatta	4	8	10[1]	7.5		L>M	Dalton *et al.* 1969
M. mulatta	5	7.7	5.9	9.6		M>L	Harris 1943
M. mulatta	2	6.3	4.3	2.8	13	H>L>M	Pfingst *et al.* 1975
M. mulatta	4	10.2	11	10.3	7[1]	L>M>H	Fujita and Elliot 1965
M. mulatta	2	4.2	5	3.5	4	L>H>M	Fujita and Elliot 1965
M. nemestrina	2	6.4	4.2	7.7	4.8	M>H>L	Gourevitch 1970
M. simica	2	6	2.4	8.7		M>L	Harris 1943
N. coucang	2	7.3	4.8	8.5	9	H>M>L	Heffner & Masterson 1970
P. cynocephalus	3	8.1	6	12.3	6	M>L,H	Hienz *et al.* 1982
P. potto	2	13.6	18.5	20	1.7	M>L>H	Heffner & Masterson 1970
P. troglodytes	3	6.6	5.3	7.6		M>L	Elder 1934
P. troglodytes	2	6	8	6.8	3	L>M>H	Kojima 1990
S. sciureus	2	3.9					Beecher 1974b
S. sciureus	6	8.8	10	8.8	6.5	L>M>H	Fujita and Elliot 1965
S. sciureus	2	2	0.5	3	4	H>M>L	Fujita and Elliot 1965
S. sciureus	2	6.8[6] (6.5)	9.5	7.5[6] (11.5)	0.5	M>L>H	Fujita and Elliot 1965
S. sciureus	3	8.9	6.3	3.5	16.3	H>L>M	Green 1971
Mean		**8.4 (8.8)**	**7.9 (8.1)**	**8.4 (8.7)**	**9.2 (10)**	**H>L>M**	

TABLE 3.3 – Inter-subject variability for all studies which published individual thresholds. All data obtained using operant conditioning techniques unless otherwise noted. 1 = range based on only one frequency, 2 = galvanic skin response used to determine thresholds, 3 = range based on original two subjects (range for all four subjects in parentheses), 4 = subject # 2023 excluded from calculation, 5 = evoked cortical response used to determine thresholds, 6 = subject #10 excluded from calculation for 1 and 2 kHz.

slightly more variability at higher frequencies and slightly less at lower frequencies. Consequently, when comparing the mean values among species (which is necessitated when individual data are not presented) it would seem that differences that are smaller than 8.4 dB may not be biologically significant. On the other hand, if it is possible to include individual variation in a comparison between species, significant differences may still be found despite there being minor overlap in the ranges. Considering the sources of error discussed above associated with intra-individual and intra-specific variability, in addition to random individual variation and potential variation from sexual dimorphism, these values are reasonably small.

Inter-laboratory Variation

Monaural versus Binaural Thresholds

The modest amount of variation from inter-ear variability as well as the potential for the responses to auditory stimuli to be summed at higher levels of the auditory pathway could be confounding factors that influence comparisons of monaural versus binaural audiograms. Studies on humans have suggested that binaural measurements may show a slight advantage (0.8 – 2.6 dB decrease in threshold) over those determined monaurally (Fletcher and Munson 1933; Pollack 1948; Killion 1978). No non-human primate studies have addressed the problem of monaural versus binaural comparisons but two studies present limited data that may provide tentative clues. Fujita and Elliot (1965) measured monaural squirrel monkeys for the double-grill cage experiment and binaural squirrel monkeys for the bar-pressing avoidance experiment. This comparison holds constant the fact that both experiments used shock as a conditioning technique and

although the contours show some differences there does not appear to be a systematic trend in the absolute threshold values (Figure 3.12C). The binaural thresholds were slightly lower below 500 Hz and at 4 and 8 kHz but the monaural thresholds were lower at 1 and 2 kHz with both audiograms illustrating a similar threshold at 16 kHz. The mean difference for the two audiograms is only 2.2dB although the difference is as large as 11 dB at 500 Hz.

The other evidence comes from the less than ideal data produced by Clack (1966). In his study, the binaural audiogram of monkey c2 closely paralleled the thresholds of the right ear (and most sensitive at these frequencies) except at 4 kHz where the monaural (headphones) thresholds showed a strong mid-frequency dip. Similar trends were evident in subject c4 except the binaural threshold at 16 kHz was intermediate between the right and left monaural values. This agrees with Clack's statement that the binaural measurements tended to reflect the animals more sensitive ear and that the monaural measurements showed the 4 kHz notch (1966:1144). Perhaps the most suspicious aspect of these results is that the binaural audiograms are not lower than the monaural audiograms simply because they used speakers. Nonetheless, Clack's human subjects were tested monaurally and the only point at which their mean threshold values fall above those of the other human headphone audiograms was at 250 Hz (see below). These two limited examples seem to generally agree with the available data for humans, suggesting only a slight difference of around 2 dB between monaural and binaural determinations.

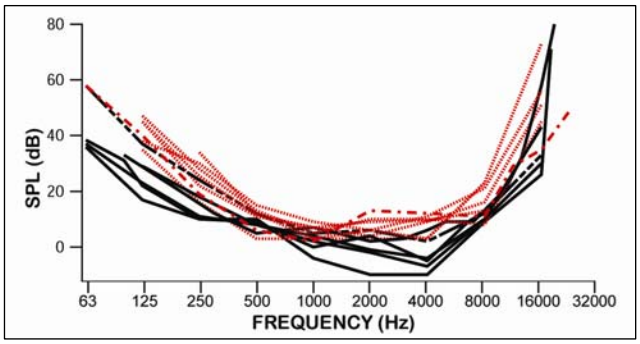

FIGURE 3.44 – Mean human audiograms comparing those that used speakers (———) versus those that used headphones (·····). Audiograms by Brown and Waser (— — —) and Owren *et al*. 1988 (— · — · —) were suggested to have elevated thresholds due to excessive ambient noise in their testing chambers.

Transducer and Conditioning Procedure Comparisons[27]

One of the biggest problems associated with comparing audiograms generated in different labs is the fact that the same testing procedures are rarely employed. Two of the largest potential sources of error are related to the type of transducer and the conditioning procedure. Figure 3.44 shows the audiograms for humans obtained in studies of non-human primates along with five other human audiograms that are commonly used in comparisons of primate hearing (Sivian and White 1933 open and closed-field; Dadson and King 1952; ISO free-field standard 1961; ANSI closed-field standard 1969). In these human comparisons, low-range refers to frequencies below 1 kHz, mid-range refers to frequencies between 1 and 4 kHz, and high-range refers to frequencies above 4 kHz. For the monkey comparisons (below), low-range is the same but mid-range refers to frequencies between 1 and 8 kHz, and high-range refers to all higher frequencies. This arbitrary division was made since the human data only goes up to 16 kHz while the monkey data goes as high as 40 kHz. The thresholds from the studies using speakers

[27] These data were presented at the Acoustical Society of America 150th Semi-annual Meeting, Minneapolis (Coleman 2005b).

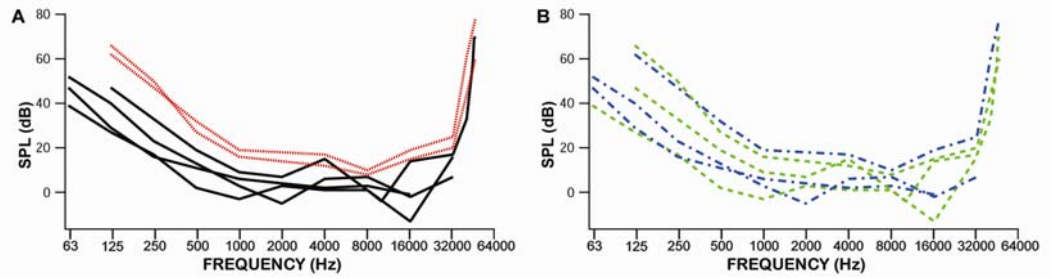

FIGURE 3.45 – **A**. Mean *S. sciureus* audiograms obtained using speakers (——) and headphones (▪▪▪▪▪▪). **B**. Same audiograms coded for positive (— — —) and negative (— ▪ — ▪ —) reinforcement conditioning procedures.

averaged 8.6 dB lower than those using headphones. The largest differences were at the higher frequencies (9.8 dB), the lower frequencies were only slightly less divergent (9.2 dB), and the mid-range frequencies showed the least differences (7.2 dB). Significant differences (one-tailed) were found between the two groups at 125 Hz (P = .001), 250 Hz (P = .004), and 4 kHz (P <. 001) using a Mann-Whitney U test. Another noteworthy difference between transducer types was that the lowest threshold (best frequency) for the average of the speaker studies was at 4 kHz, while that of the headphone studies was at 1 kHz although both mean audiograms show a broad region of good sensitivity between 1 and 4 kHz with the thresholds separated by 5 dB or less.

Figure 3.45A shows the audiograms for squirrel monkeys (*S. sciureus*). The thresholds from studies using speakers averaged 15.7 dB lower than those using headphones. The differences were greatest at lower frequencies (24.3 dB), less at higher frequencies (13.3 dB), and least at mid-range frequencies (10.5 dB). Significant differences (one-tailed) were found at nearly every frequency: 125, 250, and 500 Hz (P = .010); 1 and 2 kHz (P = .016); 4 kHz (P = .038); 16 kHz (P = .010); 32 kHz (P = .029). In this comparison, the audiograms obtained using headphones did not show a distinct mid-

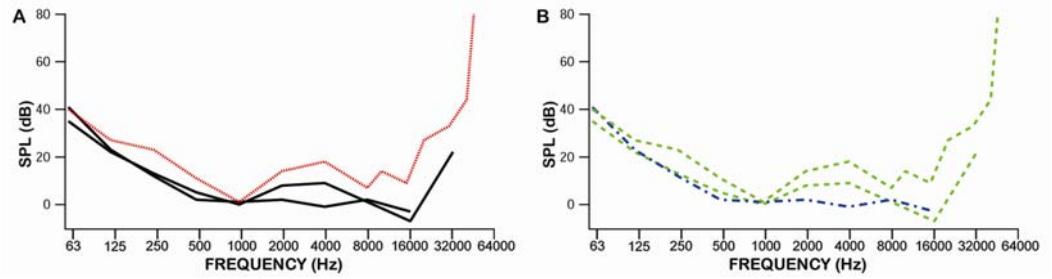

FIGURE 3.46 - **A**. Mean *M. fascicularis* audiograms obtained using speakers (▬▬▬) and headphones (▪▪▪▪▪▪). **B**. Same audiograms coded for positive (▬ ▬ ▬) and negative (▬ ▪ ▬ ▪ ▬) reinforcement conditioning procedures.

frequency dip, whereas those from speakers had a rise of 5.1 dB relative to the mean for the two peaks in sensitivity. Figure 3.45B shows the same audiograms except in this comparison they are separated by conditioning procedure: negative reinforcement (NR) and positive reinforcement (PR). The mean difference between the thresholds for each conditioning procedure was just 0.5 dB. At lower frequencies the differences averaged 1.7 dB, at higher frequencies the differences averaged 0.8 dB, and at mid-range frequencies the differences were 0.5 dB. A significant difference (two-tailed) was not detected at any frequency tested. The mid-frequency dip was slightly more pronounced in the PR audiograms (3.7 dB) compared with the NR audiograms (2.8 dB).

Figure 3.46 shows the audiograms for crab-eating macaques (*M. fascicularis*). The thresholds from the studies that used speakers averaged 8.5 dB lower than those from the study that used headphones. The differences were greatest at high frequencies (15.5 dB), intermediate at mid-range frequencies (7.3 dB), and lowest at low frequencies (6.1 dB). Significant differences were found at 0.25, 4, and 8 kHz ($P = .036$). Unlike the squirrel monkey comparison, the mean headphone audiogram showed a more pronounced mid-frequency dip (14 dB) compared with the mean speaker audiogram (7.3 dB). Figure

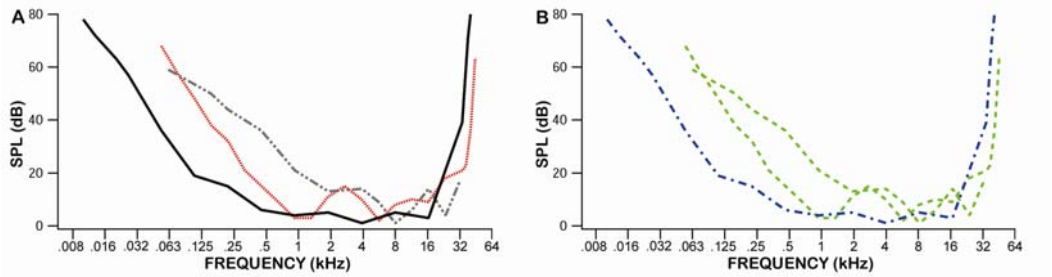

FIGURE 3.47 - **A**. Mean *M. fuscata* audiograms obtained using speakers (▬▬▬), headphones (▪▪▪▪▪▪), and insert-earphones (▬ ▪▪ ▬ ▪▪). **B**. Same audiograms coded for positive (▬ ▬ ▬) and negative (▬ ▪ ▬ ▪ ▬) reinforcement conditioning procedures.

3.46B illustrates that the single audiogram that used NR averaged 4.6 dB lower than the PR audiograms. The differences were greatest at mid-range frequencies (6.3 dB), slightly less at higher frequencies (6 dB) and smallest at lower frequencies (2.5 dB). Significant differences were found at 2 and 4 kHz (P = .036). The mid-frequency dip is quite evident in the PR audiograms (11.8 dB) but the NR audiogram shows only minor deviations (2 and 4 dB) from the lowest thresholds.

Figure 3.47 shows the audiograms for Japanese macaques (*M. fuscata*). Figure 3.47A shows the non-speaker studies separated into headphone and insert-earphone studies. The speaker audiogram averaged 6.7 dB lower than the headphone audiogram and 13.2 dB lower than the insert-earphone audiogram. When the headphones and insert-earphones are considered together, the results from the transducer and conditioning comparisons were identical since the one study that used speakers was also the only one to use NR (Jackson *et al*. 1999). The speaker / NR audiograms averaged 9.9 dB lower than the mean for the other audiograms although the non-speaker/ PR audiograms were actually 5.3 dB lower at the higher frequencies. The greatest differences were at lower frequencies (24.8 dB) while the mid-range frequencies showed a mean difference of 6.4

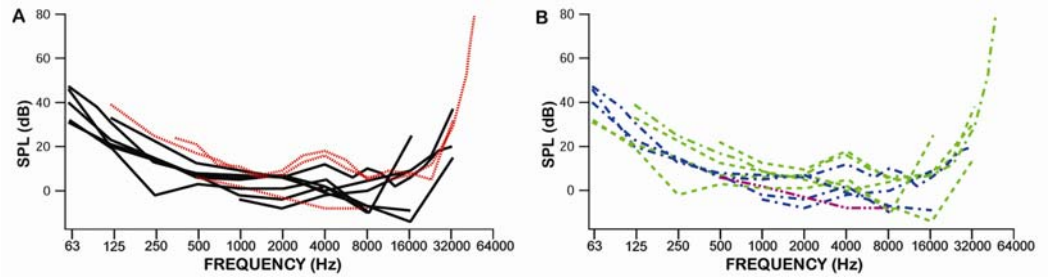

FIGURE 3.48 - Mean *M. mulatta* audiograms obtained using speakers (——) and headphones (▪▪▪▪▪▪). **B**. Same audiograms coded for conditioned suppression (— ▪ — ▪ ▪), positive reinforcement (— — —), and negative (— ▪ — ▪ —) reinforcement and conditioning procedures.

dB. Significant differences were found at 0.25, 0.5, 2 and 4 kHz (P = .036) and at 16 and 32 kHz (P = .036) despite the relatively small difference in the means at higher frequencies. The mid-frequency dip is most visible in the headphone audiogram (12.5 dB) but only minimally evident in the other two audiograms.

Figure 3.48 shows the audiograms for rhesus macaques (*M. mulatta*). The audiogram from Lasky *et al*. (1999) was excluded since it shows threshold values that are out of the range of all other macaques. Also the audiogram from Clack (1966) was not included because of the numerous problems discussed above. Similar to the previous comparisons, the audiograms produced using speakers were lower on average (7.1 dB) than the audiograms produced using headphones (Figure 3.48A). Lower frequencies showed the largest differences (12 dB), mid-range frequencies were less affected (4.8 dB), and higher frequencies even less so (4.3 dB). The mid-frequency dip averaged about 2 dB greater in the speaker audiograms. The NR audiograms had lower thresholds than the PR audiograms (Figure 3.48B), although the difference averaged only 2.2 dB. The differences in the mean thresholds were greatest at the high frequencies (6 dB) with less differences at mid-range (4.2 dB) and lower (1.6 dB) frequencies, although at lower

Species	Transducer (dB)	Variability	Dip	Conditioning (dB)	Variability	Dip
H. sapiens	8.6 (S)	Hi>Low>Mid	n/a	n/a	n/a	n/a
S. scuireus	15.7 (S)	Low>Hi>Mid	S>H	0.5 (NR)	Low>Hi>Mid	PR>NR
M. fascicularis	8.5 (S)	Hi>Mid>Low	H>S	4.6 (NR)	Mid>Hi>Low	PR>NR
M. fuscata	9.9 (S)	Low>Mid>Hi	H>S,E	9.9 (NR)	Low>Mid>Hi	PR>NR
M. mulatta	7.1 (S)	Low>Mid>Hi	S>H	2.2 (NR)	Hi>Mid>Low	PR>NR
Mean	**9.96 (S)**	**Low**	**split**	**4.3 (NR)**	**Low**	**PR**

TABLE 3.4 – Results from transducer and conditioning procedure comparisons. Second column shows the mean decrease in intensity for all frequencies between audiograms obtained with different transducer types and the number in parentheses shows type produced the lower values. Fifth column shows the mean decrease in intensity for all frequencies between audiograms obtained with different conditioning procedures and the number in parentheses shows procedure that produced the lower values. S = speakers, H = headphones, E = insert-earphones, NR = negative reinforcement, PR = positive reinforcement.

frequencies the NR audiograms are actually slightly higher than the PR audiograms. The mid-frequency dip was heightened about 6 dB more in the PR curves compared with the NR curves. When the Conditioned Suppression (CS) audiogram was included with the NR audiograms, the results remained virtually unchanged (mean difference of 2.7 dB).

Table 3.4 provides a summary of the results presented in the transducer and conditioning procedure comparisons. In all examples, the speaker studies were 7 to 16 dB lower than the studies using headphones. Although the differences were generally greater at lower frequencies, high frequencies showed the greatest variability in three cases and in one case the middle frequencies were most variable. The difference in threshold estimates from speakers compared with headphones was first noted by Sivain and White (1933) and has often been referred to as “the missing 6 dB” (Munson and Wiener 1952). Packer (1983) and others have suggested that headphones may mask frequencies below 1 kHz by physiological noise resulting in thresholds with higher SPL levels. However, this does not explain the elevated thresholds at mid-range and high frequencies. These differences are more likely due to the effects of head diffraction and the resonance of the

ear canal (Shaw 1974) and the fact that most headphone calibrations are conducted with the probe microphone close to the entrance of the ear canal and not at the eardrum itself (Killion 1978; Rudmore 1982). It is interesting to point out that the differences in the larger species (macaques and humans) were not much higher than the expected 6 dB, but the smallest species (squirrel monkeys) showed the greatest differences.

The mid-frequency dip appears to be unrelated to transducer type since the comparisons were divided as to which type produced a more pronounced loss in sensitivity. The differences related to conditioning procedure were much less marked than in the transducer comparison although the trend was for the NR audiograms to be slightly lower than the PR audiograms. The one case where there was a relatively large difference (*M. fuscata*) may be just as likely due to transducer type since the species groupings for both comparisons were the same. Differences of this magnitude (< 5 dB) fall within the intra-species range found in most studies, suggesting that conditioning procedure has an insignificant affect on threshold values at most frequencies. This finding supports evidence from other studies that have found relatively good agreement between audiograms regardless of the conditioning procedure (Fujita and Elliot 1965; Green 1975; Stebbins 1971; Stebbins 1975; Prosen *et al*. 1978; Heffner 2004). However, the mid-frequency dip was always more accentuated in the NR studies, which supports observations made by previous investigators (Fujita and Elliot 1965; Green 1971, 1975). It is interesting to note that there was a general trend for PR studies to uses headphones and for NR studies to use speakers. For the studies that employed PR, 13 used headphones and nine used speakers while eight of the NR studies used speakers compared with only three that used headphones (excluding those that used both

procedures). This may be a contributing factor to the finding that the NR studies produced slightly lower thresholds even though in most cases these differences were negligible.

Testing Chamber and Calibration Procedures

The final category of potential sources of error that will be discussed relates to the accurate measurement of sound pressure levels and the relationship to the perceived intensity by the test subject. Stebbins expressed the magnitude of the problem by stating "It is always extremely difficult to evaluate the characteristics of the sound field in relation to the physical position of the subject in any experimental arrangement. Precise measurement of the stimuli in physical units appropriate to the source of energy is essential if we are to make any quantitative statements about the sensory acuity of an organism" (1971:161). Regrettably, this is also one of the toughest obstacles to overcome, since there are few standardized protocols and various researchers have employed a wide array of different approaches. Table 3.5 summarizes the information from section II on the different types of acoustic enclosures and calibration procedures employed in each study.

Fortunately, it was recognized relatively early in the subfield of laboratory psychophysics that as many variables as possible must be controlled for in order to accurately specify the relationship between the physical stimulus and the sensory modality being investigated. In relation to determining absolute auditory thresholds, researchers quickly realized that the testing chamber must be as free from extraneous noise as possible so that low level test signals will not be masked and therefore

Investigators	Testing Chamber	Calibration Procedure
Elder 1934	Semi-soundproof room	Audiometer
Wendt 1934	Sound attenuating chamber	Human Standard
Elder 1935	Semi-soundproof room	Non-calibrated
Harris 1943	Sound attenuating chamber	Multiple-position average
Seiden 1957	Sound attenuating chamber	Multiple-position average
Clack & Herman 1963	Sound attenuating booth	?
Semenoff & Young 1964	Soundproof refrigerator (30dB)	Voltage readings
Fujita & Eliot 1965	Soundproof rooms	Multiple-position average
Behar *et al*. 1965	Double-walled soundproof room (45dB)	Highest reading from mutiple positions (Hot-spots)
Farrer & Prim 1965	Double-walled chamber (40 dB)	?
Stebbins *et al*. 1966	Double-walled soundproof room	Probe tube
Clack1966	Sound attenuating booth	Pinna position
Dalton 1968	?	?
Dalton *et al*. 1969	?	?
Bragg & Dreher 1969	Double-walled soundproof room	Non-calibrated
Heffner *et al*. 1969	Sound-treated acoutical chamber	Head position
Heffner & Masterson 1970	Sound-treated acoutical chamber	Head position
Gourevitch 1970	Double-walled chamber	Probe tube
Mitchell *et al*. 1970	Double-walled chamber	Pinna position with dummy animal
Mitchell 1970	Double-walled chamber	Pinna position with dummy animal
Mitchell *et al*. 1971	Double-walled chamber	Pinna position with dummy animal
Green 1971, 1975	Double-walled chamber (40-60dB)	Probe tube
Gillette *et al*. 1973	Double-walled chamber	Hot-spots
Pugh *et al*. 1973	Double-walled chamber	Probe tube
Stebbins 1973	Double-walled chamber	Probe tube
Beecher 1974a	Double-walled chamber w/cotton	Head position
Beecher 1974a	Double-walled chamber w/cotton	Head position
Pfingst *et al*. 1975	Double-walled chamber	Probe tube
Pfingst *et al*. 1978	Double-walled chamber	Probe tube
Lonsbury-Martin & Martin 1981	Double-walled chamber	Probe tube
Hienz *et al*. 1982	Double-walled chamber	Pinna position
Bennett *et al*. 1983	Sound attenuating booth (23dB)	Pinna position with dummy animal
Brown & Waser 1984	Semi-anechoic room (51dB)	Head position
Brown 1986	Semi-anechoic room (51dB)	Head position
Smith *et al*. 1987	Double-walled chamber	6cm³ coupler
Owren *et al*. 1988	Single-walled chamber	Probe tube
Kojima 1990	Double-walled chamber	6cm³ coupler
Smith & Olszyk 1997	Double-walled chamber	Artificial ear
Jackson *et al*. 1999	Double-walled chamber	Hot-spots
Lasky *et al*. 1999	Sound attenuating booth	Head position
Heffner 2004	?	?

TABLE 3.5 – Type of sound attenuating testing chamber used in each study and the method used to calibrate the intensity levels. See text for detailed information on calibration procedures.

undetectable. The general standard has become the usage of a double-walled commercially constructed sound attenuating chamber (Industrial Acoustics Corporation (IAC) is by far the most widely used). Some researchers have taken additional steps to minimize unwanted sounds by adding supplementary sound absorbing materials (*e.g.*,

Beecher 1974) and isolating the subjects from substrate vibrations (*e.g*., Heffner *et al*. 1969a; Jackson *et al*. 1999). However, some of the earlier studies as well as a few recent ones utilized less than ideal testing enclosures. In addition, some locations can have higher than average outside noise (nearby construction, highway noise, etc.) that could penetrate even the best constructed chambers. It might be possible to normalize the results from different studies if the ambient noise levels of the testing environments were given but this is rarely the case. In some instances, it may be possible to evaluate potentially problematic audiograms by comparing the results with other studies that have tested the same species. Of course, this assumes that the differences are not the result of other confounding factors. Two of the more recent studies where this approach may be applicable are those by Brown and Waser (1984) and Owren *et al*. (1988) and will be discussed below.

In both of the studies the non-human primates investigated have not been tested by other researchers (or using a different transducer type in the case of Owren *et al*. for *M. fuscata*), but they did determine thresholds for humans which may provide the best comparison since they represent the most commonly tested species. The human data from Brown and Waser (1984) have been highlighted in Figure 3.44. The position of this audiogram, particularly at the lower frequencies, falls within the range for the studies that used headphones supporting the notion of the authors that the low-frequency thresholds may be slightly higher than the actual values. Their testing chamber was simply a sound treated "semi-anechoic" room which had ambient noise levels that appear to be higher than those for the few studies that presented this information (Table 3.5). Therefore, it would seem unwise to compare the absolute threshold levels of *C. mitis* to those of other

studies although the relative values (see below) may still be valuable. The grey-cheeked mangabeys (*L. albigena*) in the study by Brown (1986) were also tested in the same laboratory, so these restrictions should also apply to this species.

The possibility that excessive ambient noise in the single-walled testing chamber used by Owren *et al*. (1988) might have affected the thresholds of their test subjects has already been discussed, but will briefly be revisited here. The human audiogram produced in their study has also been singled-out in Figure 3.44 and it falls right in the middle of the human audiograms produced using headphones at the lower and higher ranges, although it fluctuates between transducer-type groupings at the middle frequencies. Since this comparison has a larger sample size than the previous assessment (compared to Pfingst *et al*.'s humans), along with the other arguments presented above (see Owren *et al*. 1988 summary), there does not appear to be substantial evidence to exclude the data from Owren *et al*. (1988) from quantitative comparisons with other species. As present, it seems there is no reason to reject the results from most other studies as presenting tolerable levels of error from ambient noise unless there are additional reasons to question the data (see below).

The techniques used to calibrate the intensity levels of test stimuli have not achieved the same level of uniformity as with the usage of double-walled sound attenuating chambers (Table 3.5). Considering just the free-field studies, there have been numerous approaches employed such as averaging the intensity from numerous positions, using only the value from the most intense position (hot spots), measuring from the approximate position of the center of the head, measuring from the approximate position of the pinna, and using models of the subjects with microphones placed at the ear

position. While the last approach would intuitively seem to be the most precise (since it incorporates sound field disturbances caused by the animal itself), it has been used in only two laboratories (Mitchell 1970, Mitchell *et al*. 1970, 1971 and Bennett *et al*. 1983). A potential problem with the "hot-spot" approach is that it assumes that the animal will sample a sound from the most intense area so sampling away from this area will produce conservative (lower) threshold estimates. Even when the animals are relatively fixed in a single position their ears are still free to move which could cause variations in perceived intensity.

The calibration techniques for studies using headphones have not been quite as varied although there is still no standardized method. By far the most prevalent approach has been to use probe tube calibration. However, as the Pfingst *et al*. (1975) study demonstrated, there can still be some variation in thresholds, even when the same subject is tested (compare curves B and C, Figure 3.30C), presumably related to the type of headphone cushion. Most researchers now agree that the 6 cm^3 coupler is not suitable for use with most monkeys since it was designed to approximate the volume of the human ear. There is only one monkey audiogram that used the 6 cm^3 coupler (Smith *et al*. 1987), but as discussed above this audiogram illustrates thresholds that are in the opposite direction (elevated) of that expected if the calibration technique caused the unusually high thresholds. The Kojima (1990) study also used a 6 cm^3 coupler to calibrate intensity levels but the chimpanzee outer ear is larger than the human ear (Schultz 1969:134) so the result may be that the threshold values from this study slightly underestimate the chimpanzees' true sensitivity. It is difficult to evaluate the Japanese macaque audiogram

produced by Smith and Olszyk (1997) since they used a unique transducer and novel calibration procedure.

There appears to be no easy way of equating these apparently disparate calibration techniques. However, despite the potentially large inflation of error that different procedures could produce, the empirical data seems to suggest that the amount of variation introduced into threshold measurements is no larger than the average level of intra-species variation found in subjects tested in the same lab (Table 3.3). In fact, Stebbins has stated "It is true that most of the data, at least for absolute intensity thresholds, are in good agreement, and this promotes additional confidence in the procedures" (1971:171). With these reservations in mind, the application of a few general principles may help minimize undue variation. Obviously, studies that did not calibrate their data are to be avoided unless it is possible to adjust the thresholds based on a known standard and validate these adjusted values. It may be possible to discover spurious values by comparing the results with other studies (holding transducer-type constant) and exclude these data that appear unusually divergent (*i.e.*, outside the range of normal variability). When comparing headphone studies, only data that were calibrated using standardized probe calibration techniques would probably be the best to use.

SECTION IV

This section will focus on establishing sub-groupings of species mean audiograms that will provide a comparative dataset for phylogenetic interpretation and investigating the relationship between auditory sensitivity and morphological structures in later chapters. The evidence from the transducer-type comparison suggests that the data can be

grouped into two broad categories: headphone studies and speaker studies. Beyond defining an "optimal" set of audiograms for each category, "suboptimal" datasets will also be generated for the purpose of exploring the possibility that less than ideal audiograms may still provide useful information, albeit not as widely applicable to investigating the full range of hearing sensitivity. In finalizing the datasets of species mean audiograms, it is crucial to determine the compatibility of audiograms for the same species produced in different studies and attempt to fine-tune the data (*i.e*., subjects) to be included for determining various regions such as the high frequency limit.

Combining Data from Different Studies

There are seven species of non-human primates that have been tested in more than one laboratory: *E. fulvus*, *M. fascicularis*, *M. fuscata*, *M. mulatta*, *M. nemestrina*, *P. troglodytes*, and *S. sciureus*. Each will be considered in this order. The two studies that have published data on free-field audiograms for *E. fulvus* are Mitchell *et al*. 1970 and Heffner 2004. The mean audiogram from Mitchell *et al*. as well as the three data points provided by Heffner (connected to form a basic audiogram) are presented in Figure 3.49. Although Mitchell *et al*. acknowledged that their initial study underestimated the sensitivity of their subjects at most frequencies, the highest and lowest frequencies tested appeared to be unaffected. Despite the fact that these two audiograms have the same value at 2 kHz, the high- and low-frequency regions are quite different. The extrapolated high-frequency cut-off (at 60 dB SPL) for the Mitchell *et al*. data is 66 kHz while that from Heffner is 43 kHz. The extrapolated low-frequency cut-off (at 60 dB SPL) for the Mitchell *et al*. data is 46 Hz while that from Heffner is 73 Hz.

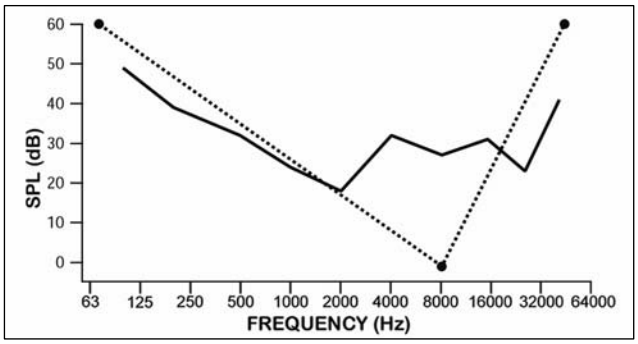

FIGURE 3.49 – *E. fulvus* species mean audiogram from Mitchell *et al*. 1970 (▬▬▬) compared with "basic" audiogram from data presented in Heffner 2004 (▪▪▪▪▪▪).

Therefore, these data will not be averaged. The limited data provided by Heffner will be put in the suboptimal category, primarily because no information is known about the specific procedures that were employed to derive these values.

The two *M. fascicularis* free-field audiograms (Figure 3.46) presented by Fujita and Elliot (1965) are in good agreement at most frequencies and have a mean difference at all frequencies of only 3.6 dB. Consequently, these data will be averaged and included into the optimal speaker category. The mean values of these two audiograms are given in Appendix 40. Although, there are two non-speaker audiograms for *M. fuscata* (Figure 3.47), the Smith and Olszyk (1997) audiogram used insert-earphones and calibrated the intensities with an artificial ear. Since the compatibility of this technique to the probe calibration method is unclear, only the data from Owren *et al*. (1988) will be used and will be included in the optimal headphone category.

Three laboratories have produced *M. mulatta* audiograms using headphones (Figure 3.50A). The audiograms produced by Pfingst *et al*. (1978) and Lonsbury-Martin and Martin (1981) are extremely similar but the audiogram from Dalton *et al*. (1969) illustrates much lower threshold values and is most sensitive at the mid-frequency dip

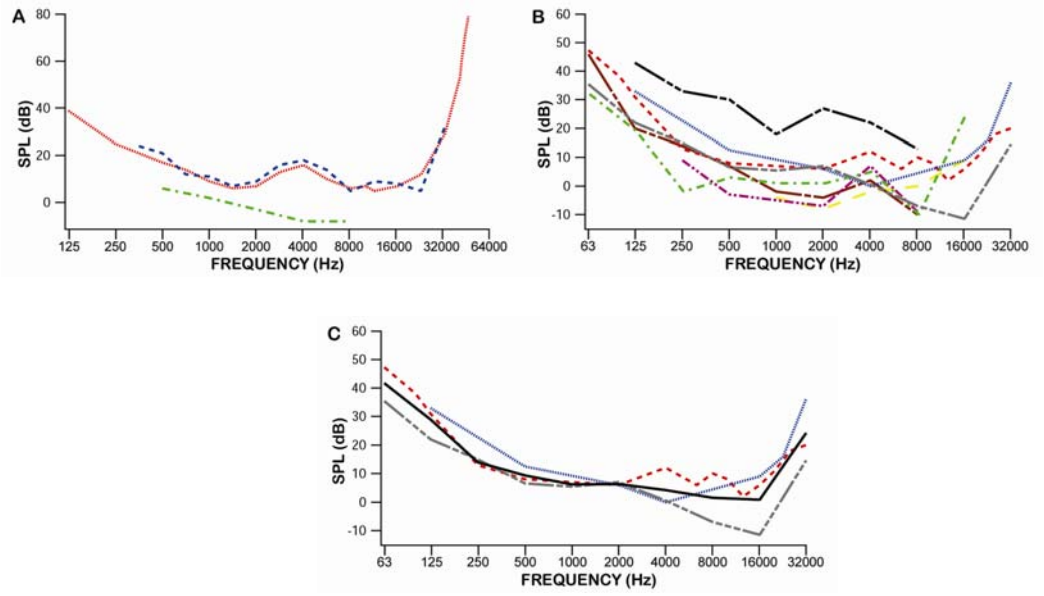

FIGURE 3.50 – **A**. *M. mulatta* audiograms obtained using headphones from Dalton *et al.* 1969 (▬ · ▬ · ▬), Pfingst *et al*. 1978 (▪▪▪▪▪▪), and Lonsbury-Martin and Martin 1981 (▬ ▬ ▬). **B**. *M. mulatta* mean audiograms obtained using speakers from Wendt 1934 (▬ · ▬ · ▬), Harris 1943 (▬▬▬ ▬), Clack and Herman 1963 (▬ ▬ ▬), Behar *et al*. 1965 (▬ ▬ ▬), Fujita and Elliot 1965 (▬▬▬ ▬ ▬ ▬), Clack 1966 (▬ ▪ ▬ ▪ ▪), Bennett *et al*. 1983 (▪▪▪▪▪▪), and Lasky *et al*. 1999 (▬▬▬ ▬ ▬). **C**. *M. mulatta* mean audiograms from Behar *et al*. 1965, Fujita and Elliot 1965, and Bennett *et al*. 1983 (coded as in Figure 3.50B) and *M. mulatta* speaker mean (▬▬▬) derived from these three studies.

evident in the other two audiograms. When all three audiograms are considered together, the mean range for all frequencies is 11.7 dB, but the value drops to 2.4 dB when Dalton *et al*. is excluded from the calculation. Therefore, the mean headphone *M. mulatta* audiogram (Appendix 41) will be based on the thresholds from Pfingst *et al*. and Lonsbury-Martin and Martin and will be placed in the optimal category.

In total, eight different laboratories have produced free-field audiograms for *M. mulatta* (Figure 3.50B) and there is considerable variability among the thresholds and contours, with a mean range for all frequencies of 27.2 dB! However, several of these audiograms present reasons to be suspicious of the results. As previously discussed, the

Lasky *et al*. (1999) audiogram falls well above all other rhesus macaque audiograms and for this reason was excluded from the transducer/conditioning procedures comparison. Even without this audiogram the mean range is still 18.1 dB but when the Wendt (1934) audiogram is removed (since the exact intensity levels were not determined), the value becomes 15.2 dB. The results from both Clack and Herman (1963) and Clack (1966) may also be doubtful since in the former case there was no mention of calibrating the test signals and in the latter the values were significantly below the humans in their study which is an atypical finding when comparing macaques to humans. Finally, Stebbins (1971:178) has suggested that Harris's (1943) data is anomalously low at 8 kHz (and at 1 and 2 kHz in fact). Removing these audiograms leaves the work of Behar *et al*. (1965), Fujita and Elliot (1965), and Bennett *et al*. (1983) (Figure 3.50C) which have a mean range of 10.7 dB (the Fujita and Elliot audiogram represents the mean of the reward and avoidance audiograms). This value is just over the mean for intra-specific variability (Table 3.3) and the average of these three audiograms (presented in Figure 3.50C) will represent the mean speaker *M. mulatta* audiogram (Appendix 42) in the optimal category.

The final macaque to consider is *M. nemestrina* which is represented by the audiograms from Stebbins *et al*. (1966), Gourevitch (1970), and Pugh *et al*. (1973) (Figure 3.51). Although the thresholds at mid-range frequencies are very similar, there is considerable discrepancy at higher and lower frequencies resulting in a mean range of 14.2 dB. Since the Pugh *et al*. audiogram is based on only one individual of unknown age and removing this subject from the range computation results in a value of only 5.6 dB, the mean headphone audiogram for *M. nemestrina* (Figure 3.51) will be based on

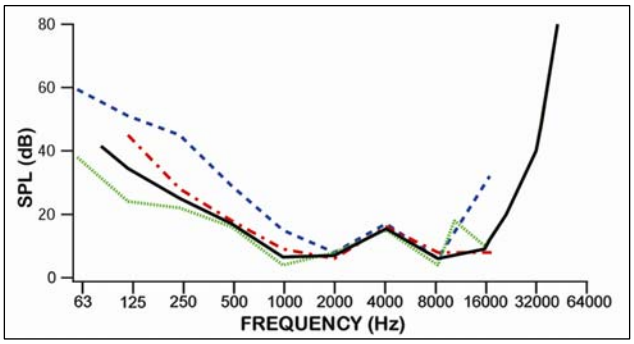

FIGURE 3.51 – *M. nemestrina* headphone audiograms from Stebbins *et al*. 1966 (▪▪▪▪▪▪), Gourevitch 1970 (▬ ▪ ▬ ▪ ▬), and Pugh *et al*. 1973 (▬ ▬ ▬) with mean *M. nemestrina* headphone audiogram (▬▬▬) derived from Stebbins *et al*. 1966 and Gourevitch 1970.

Stebbins *et al*. and Gourevitch. However, Stebbins *et al*. tested their macaques down to 63 dB compared to 125 Hz for Gourevitch's macaques and there is considerable difference between the intensity levels at lower frequencies. Therefore, the lowest frequency for the mean audiogram will represent an intermediate intensity and frequency (logarithmic mean) value between the respective lowest frequencies tested in each study (41.5 dB SPL at 87 Hz). This prevents the lower intensity, lower frequency value of the Stebbins *et al*. audiogram from causing the low-frequency slope to deviate abnormally (become much shallower from 125 to 63 Hz). The mean threshold values are given in Appendix 43.

There have been three laboratories that have contributed threshold data for *P. troglodytes*. Although the seminal non-human primate audiogram by Elder (1934) used a human standard for calibration, it is included here because it is suspected that the Kojima (1990) audiogram may have slightly underestimated the threshold values due to the usage of a 6 cm^3 coupler for calibration (see above). Figure 3.52 shows both audiograms and there is similarity in the contours although Elder's audiogram has lower thresholds at all

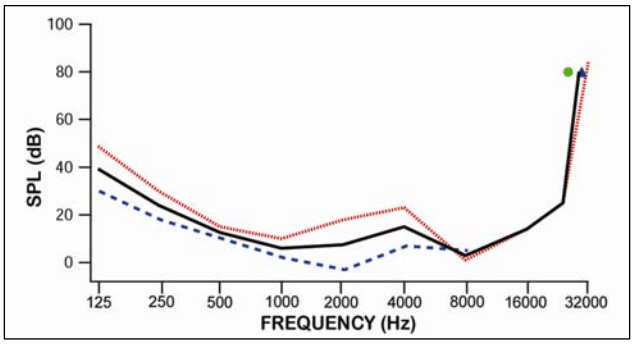

FIGURE 3.52 – *P. troglodytes* mean headphone audiogram (———) based on data from Elder 1934 (— — —), Elder 1935 (▲), Farrer and Prim 1965 (●), and Kojima 1990 (·····).

frequencies except 8 kHz. Since this difference is in the expected direction and the fact that the mean difference is 11 dB (a little high but still within the intra-specific range) these thresholds will be averaged. Also included in this figure are the high-frequency cut-off points determined by Elder (1935) and Farrer and Prim (1965). The high-frequency limits determined by Elder (assuming an 80 dB SPL) and Kojima are only about 1 kHz apart although the value determined by Farrer and Prim is about 4 kHz lower. However, since the exact SPL of the high-frequency limit from Elder is unknown, the high-frequency cut-off (at 80 dB SPL) will be taken as the average of the three values (which actually falls extremely close to the value determined by Elder). The mean audiogram (Appendix 44) derived from these averages is also presented in Figure 3.52 and will be tentatively placed in the optimal headphone category.

The two free-field audiograms for *S. sciureus* are presented in Figure 3.53. As in the *M. mulatta* evaluation, the reward and avoidance audiograms from Fujita and Elliot (1965) have been averaged. The mean difference between the audiograms is 10.2 dB, which is considered an acceptable level of intraspecific variation so these two

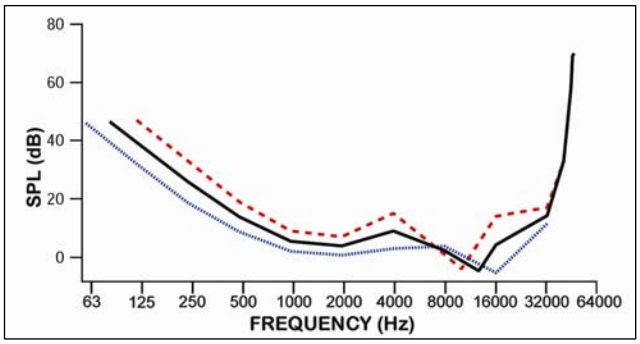

FIGURE 3.53 – *S. sciureus* mean speaker audiogram (▬▬▬) derived from Fujita and Elliot 1965 (▪▪▪▪▪▪) and Beecher 1974 (▬ ▬ ▬).

audiograms will be averaged to produce the mean speaker *S. sciureus* audiogram (Figure 3.53). However, similar to the case for *M. nemestrina*, Fujita and Elliot tested their subjects down to 63 dB compared with 125 Hz for Beecher's squirrel monkeys. Therefore, the lowest frequency for the mean speaker audiogram will represent an intermediate value between the lowest frequencies tested in each study (46.5 dB SPL at 87 Hz). The mean threshold values are given in Appendix 45 and will be included in the optimal speaker category.

The final adjustments that will be made will be to "fine-tune" the higher frequencies of species that appear to show some signs of presbycusis in certain individuals. There are only two audiograms to be included in the optimal category that require such an adjustment and were singled-out above in section III. The first is the study on *C. jacchus* by Seiden (1957). Subject #1 (the youngest in the group) shows thresholds that average 14 dB lower than those of the next lowest individual from 20 to 30 kHz and was the only marmoset to respond to 35 kHz. Therefore, the threshold values from 20 to 30 kHz will be calculated by averaging subject #1's thresholds with the mean of all other subjects. The highest frequency will be an intermediate value between #1's

threshold at 35 kHz and the mean of all other subjects at 30 kHz (72 dB SPL at 32 kHz), similar to the process used above to arrive at a low-frequency estimate for the mean audiograms of *M. nemestrina* and *S. sciureus*. This procedure should produce a conservative estimate that utilizes the results of the juvenile in the group but is not based exclusively on a single individual. The adjusted threshold values are given along with the original thresholds in Appendix 4.

As discussed above, the oldest subject (#286) in the *M. fuscata* study by Jackson *et al*. (1999) had higher thresholds at all frequencies above 2 kHz. However, the difference between #286's thresholds and the next highest values averages only 4 dB (2-8 dB) and removing these thresholds from the species mean calculation amounts to an average 2 dB decrease. Since these values are within the range of intra-individual variability, the thresholds for *M. fuscata* will not be adjusted.

ABSOLUTE THRESHOLD DATASETS

Optimal and Suboptimal Audiograms

Based on the foregoing analyses the following audiograms have been judged to present valid threshold estimates and will be included in the optimal audiogram datasets. The optimal speaker audiograms include: *Aotus trivirgatus* – Beecher 1974a; *Callithrix jacchus* – Seiden 1974 (adjusted); *Galago senegalensis* – Heffner *et al*. 1969a; *Lemur catta* – Gillette *et al*. 1973; *Macaca fascicularis* – based Fujita and Elliot 1965 mean; *Macaca fuscata* – Jackson *et al*. 1999; *Macaca mulatta* – mean based on Behar *et al*. (1965), Fujita and Elliot (1965), and Bennett *et al*. (1983); *Nycticebus coucang* – Heffner and Masterson 1970; *Perodicticus potto* – Heffner and Masterson 1970; *Papio*

cynocephalus – Hienz *et al*. 1982; *Saimiri sciureus* – mean based on Beecher 1974b and Fujita and Elliot 1965. The free-field audiogram for tree shrews (*Tupaia glis*) produced by Heffner *et al*. (1969b) will also be included in this group for the purpose of providing an outgroup. The suboptimal speaker group includes the above species in addition to: *Ateles paniscus* – Wendt 1934; *Cercocebus torquatus* – Wendt 1934; *Cercopithecus mitis* – Brown and Waser 1984; *Eulemur fulvus* – Heffner 2004; *Lophocebus albigena* – Brown 1984; *Macaca sinica* – Harris 1943; *Papio anubis* – Wendt 1934.

The optimal headphones audiograms include: *Cercopithecus neglectus* – Owren *et al*. 1988; *Chlorocebus aethiops* – Owren *et al*. 1988; *Macaca fascicularis* – Stebbins *et al*. 1966; *Macaca fuscata* – Owren *et al*. 1988; *Macaca mulatta* – mean based on Pfingst *et al*. (1978) and Lonsbury-Martin and Martin (1981); *Macaca nemestrina* – mean based on Stebbins *et al*. (1966) and Gourevitch (1970); *Pan troglodytes* – mean based on Elder 1934, Elder 1935, Farrer and Prim 1965, and Kojima 1990; *Saimiri sciureus* – Green 1971, 1975. *Erythrocebus patas* (Smith *et al*. 1987) is the only species that is added to form the suboptimal headphones group.

There are two primary approaches that are usually employed to analyze audiogram data. The first and more basic approach is to compare threshold values at individual frequencies in order to evaluate particular regions of sensitivity (*e.g*., 250 Hz for low-frequency comparisons). The other approach is to compare frequencies at a defined intensity level for different regions of the audiogram. Three of the more common parameters of this type are the high- and low-frequency cut-off points, customarily taken as the highest and lowest audible frequencies at either 60 or 70 dB SPL, and the range in octaves between these points. Another common measure of sensitivity is the frequency

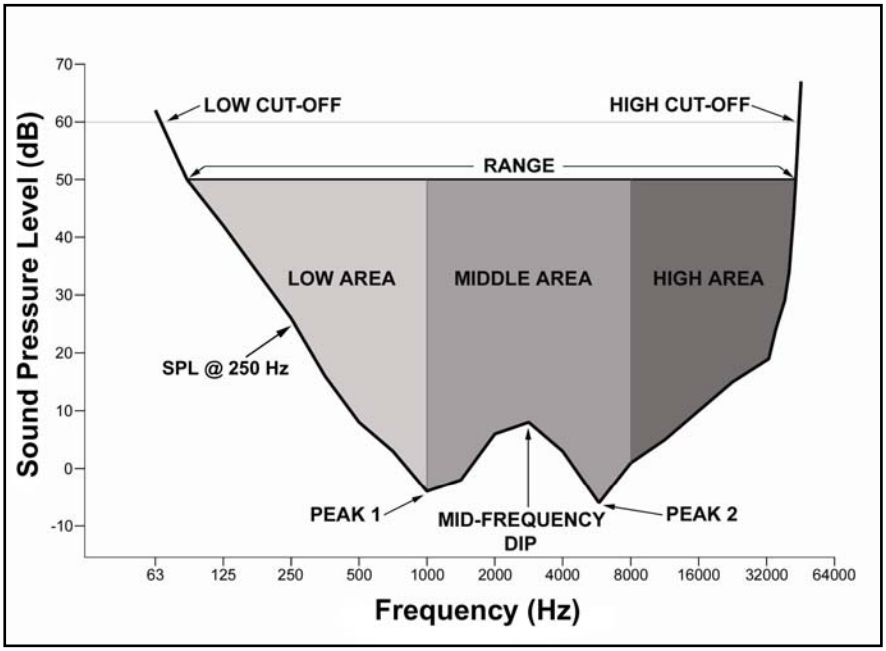

FIGURE 3.54 – Audiometric parameters measured on final audiogram datasets. Complete descriptions of each measurement given in text.

(or frequency range) with the lowest threshold, typically termed the "best frequency" (Masterson *et al*. 1969). A third less common approach is to measure the area of the audible field which is defined as the region bounded by the audiogram below an arbitrary intensity level such as 70 dB SPL (Masterson *et al*. 1969).

In this study, a modified combination of these approaches will be used due to the fact that few studies on primate audition have explored the entire range of hearing sensitivity. The list of auditory parameters that were measured are illustrated in Figure 3.54 and described below. The high- and low-frequency cut-off points were defined as the highest and lowest audible frequencies at 60 dB SPL. For species that were not tested up to this intensity level, extrapolated values were used as long as the species were tested at 49 dB SPL or higher. Even with this reduced threshold criterion, less than half of the species could to be evaluated at the low-frequency cut-off point. Therefore, the

Species	High Cut-off	Low Cut-off	250Hz	Peak 1	Dip	Peak 2	Total Area	Low Area	Mid-Area	High Area	Range
A. paniscus[1]			20dB	6dB @ 1kHz	26dB @ 4.1kHz	3dB @ 8.2kHz	2571	1088[3]	1131	352[3]	8.47[3]
A. trivirgatus	45kHz		24dB	5dB @ 2kHz	12dB @ 4kHz	-8dB @ 10kHz	3515	998[3]	1410	1107	9.11[3]
C. jacchus	28kHz[4]		24dB	0dB @ 2kHz	20dB @ 5kHz	-9dB @ 7kHz	3028	1072[3]	1372	584	8.95[3]
C. torquatus[1]			8dB	-5dB @ 2kHz	5dB @ 4.1kHz	-3dB @ 8.2kHz			1615		
C. mitis[1]	49kHz[4]	45Hz[4]	20dB	4dB @ 1kHz	6dB @ 2kHz	4dB @ 4kHz	3508	1189	1407	912	9.41
C. neglectus[2]	43kHz[4]	61Hz[4]	27dB	3dB @ 1.4kHz	15dB @ 2kHz	2dB @ 5.7kHz	3205	966	1335	904	8.54
C. aethiops[2]	45kHz	69Hz	26dB	-4dB @ 1.4kHz	8dB @2.8kHz	-2dB @ 5.7kHz	3520	1031	1510	979	8.74
E. patas[1,2]	31kHz	290Hz	63dB	23dB @ 1.4kHz	25dB @ 2.4kHz	14dB @ 8kHz	1541	229	867	455	6.19[3]
E. fulvus[1]	43kHz	72Hz				-1dB @ 8kHz					
G. senegalensis	65kHz[4]	70Hz[4]	44dB	30dB @ 500Hz	31dB @ 1kHz	-2dB @ 8kHz	2801	396	1188	1217	8.61
L. catta	58kHz	57Hz[4]	32dB	6db @ 2kHz	8dB @ 4kHz	3dB @ 8kHz	3137	803	1386	948	9.04
L. albigena[1]		54Hz	18dB	2dB @ 800Hz	6dB @ 2-4kHz	5dB @ 8kHz		1204	1429		
M. fascicularis			12dB	1dB @ 1kHz	4dB @ 2kHz	-5dB @ 16kHz		1542[3]	1504		
M. fascicularis[2]	42kHz		12dB	1dB @ 1kHz	18dB @ 4kHz	7dB @ 8kHz	3192	1292[3]	1209	691	10.07[3]
M. fuscata	34kHz	28Hz	15dB	4dB @ 1kHz	5dB @ 2kHz	1dB @ 4kHz	3813	1533	1478	802	9.65
M. fuscata[2]	41kHz	82Hz	32dB	3dB @ 1-1.4kHz	15dB @ 2.8kHz	2dB @ 5.7kHz	3025	839	1337	849	8.34
M. mulatta			14dB	6dB @ 1kHz	7dB @ 2kHz	1dB @ 16kHz		1331[3]	1434		
M. mulatta[2]	41kHz		25dB	7dB @ 1.4kHz	17dB @ 4kHz	6dB @ 8kHz	3035	917[3]	1248	870	9.05[3]
M. nemestrina[2]	35kHz		25dB	7dB @ 1kHz	16dB @ 4kHz	6dB @ 8kHz	3000	1023[3]	1282	695	9.13[3]
M. silnica[1]			12dB	-5dB @ 2kHz	3dB @ 4kHz			1517[3]	1688		
N. coucang	44kHz	83Hz	36dB			9dB @ 16kHz	2190	509	869	812	8.35
P. troglodytes[2]	27kHz		24dB	6dB @ 1kHz	15dB @ 4kHz	3dB @ 8kHz	2948	996[3]	1307	645	8.29[3]
P. potto	41kHz	135Hz	33dB	18dB @ 2kHz	24dB @ 4kHz	1dB @ 16kHz	2560	523	1039	998	7.79
P. anubis[1]			4dB	-1dB @ 2kHz	29dB @ 4.1kHz	-10dB @ 8.1 kHz			1315		
P. cynocephalus	41kHz		19dB	3dB @ 1kHz	7dB @ 2kHz	-1dB @ 8kHz	3739	1355[3]	1463	921	9.25[3]
S. sciureus	44.2kHz		26dB	4db @ 2 kHz	9dB @ 4kHz	-5dB @ 12.7kHz	3449	974[3]	1409	1066	9.16[3]
S. sciureus[2]	41kHz	140Hz	47dB			8dB @ 8kHz	2280	409	1132	739	7.39
T. gilis	60kHz		47dB			-5dB @ 16kHz	2806	358[3]	1158	1290	7.92

TABLE 3.6 – Audiometric parameters measured on final audiogram datasets. See Figure 3.54 and text for details on measurements. 1 = sub-optimal dataset, all species without a 1 are from the optimal datasets; 2 = headphone studies, all species without a 2 used speakers; 3 – based on an extrapolated intensity value of 40 dB SPL or higher; 4 = based on an intensity value of 49 dB SPL or higher.

intensity level (dB) at 250 Hz was taken as an additional index of low-frequency sensitivity. Since primate audiograms are often bimodal in shape, the region of best sensitivity was assessed by taking the frequency and intensity of the two peaks surrounding the mid-frequency dip in sensitivity where applicable. The audible area was estimated by measuring the area bounded by the audiogram below 50 dB SPL (using Sigma Scan 5.0 image measurement software). Each audiogram was scaled to the same ordinate and abscissa ranges and calibrated using the intensity values along the ordinate axis. The total audible area was subdivided into high (< 8 kHz), middle (1 to 8 kHZ), and low (> 1 kHz) regions. One advantage to using areal subdivisions such as these over more traditional measures of regional sensitivity is that they incorporate data from multiple threshold values and not just one arbitrarily defined point. Extrapolated values were used for species that were tested to within 10 dB of the upper bound (*i.e.*, 40-49 dB SPL). The total range of sensitivity was measured as the number of octaves between the highest and lowest audible frequency at 50 dB SPL. The values derived from these measurements are given in Table 3.6.

RELATIVE THRESHOLD DATASETS

Human Biological Reference Line

One approach that attempts to mitigate problems associated with comparing audiograms obtained using different procedures and testing environments is to use the "human biological reference level" (Brown and Waser 1984). In this method, human intensity values are used to normalize the values of the non-human subjects in the study: positive values indicate less sensitivity than humans and negative values indicate more

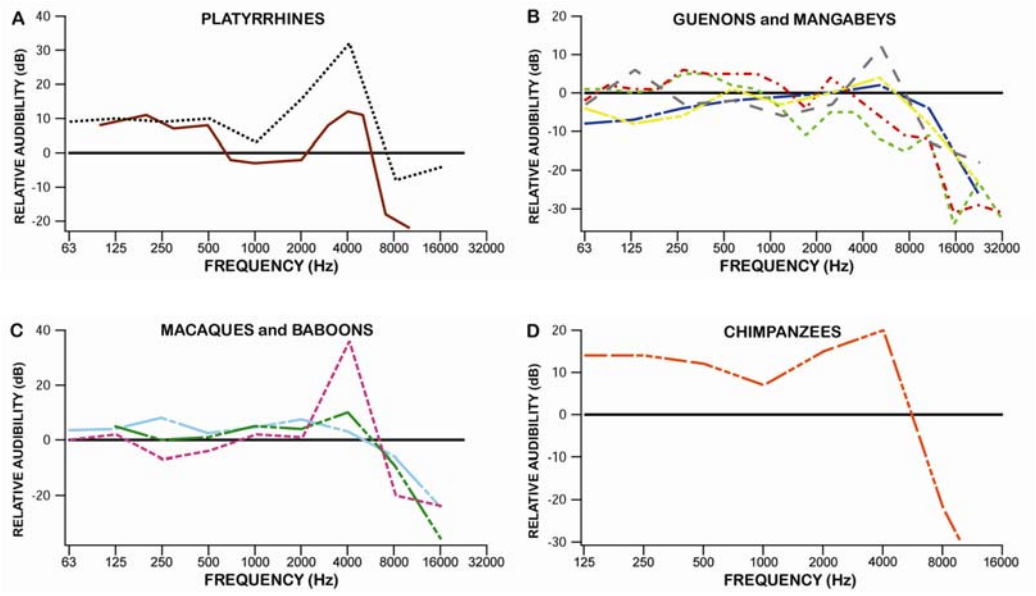

FIGURE 3.55 – Relative audibility functions for all non-human primates that were tested along with human subjects in the same testing environment. Absolute values were normalized relative to the human subjects in the study. Positive values indicate less sensitivity at that frequency compared to humans and negative values indicate better sensitivity. **A**. Platyrrhines – *A. paniscus* (▪▪▪▪▪▪) and *C. jacchus* (——) functions. **B**. Guenons and Mangabeys - *C. torquatus* (— — —), *C. mitis* (— — —), *C. neglectus* (— · — · —), *C. aethiops* (— — —) and *L. albigena* (— — — —). **C**. Macaques and Baboons – *M. fuscata* (— — —), *M. mulatta* (— — —), and *P. anubus* (— — —). **D**. *P. troglodytes* (— — — —).

sensitivity than humans at a given frequency. The method requires that both human and non-human subjects were tested in the same study using the same acoustical apparati and procedures and assumes that humans measured in different studies have approximately the same hearing sensitivity contours (even though the human audiograms in separate studies may have different threshold values). The major drawback of this method is that it does not allow the investigation of frequencies above the range of human hearing (>16-20 kHz).

Figures 3.55A-D show the relative audibility (normalized data) of the 11 different species that have been tested along with human subjects. Figure 3.55A illustrates the

relative audibility functions for two platyrrhines (*C. jacchus* and *A. paniscus*.) and overall the functions showed much agreement. Below 500 Hz, the platyrrhines were less sensitive than humans, from 500 Hz to 2 kHz their sensitivity was similar to humans, above 2 kHz to about 6 kHz their sensitivity was inferior, and above this frequency their sensitivity became markedly superior. Figure 3.55B shows the functions for five medium-sized Old World monkeys (mangabeys and guenons). *C. mitis* and *L. albigena* showed slightly better hearing than humans below 500 Hz, similar sensitivity from 500 Hz to around 6 kHz, and superior hearing above this range. *C. aethiops* and *C. neglectus* showed equal sensitivity to humans below 250 Hz, less up to around 1 kHz, and increasingly better sensitivity above 1 kHz. *C. torquatus* fluctuated around the human line (0 dB) until above 6 kHz where it showed the same pattern as the other monkeys (*i.e.*, better hearing). Figure 3.55C shows the functions for three medium- to large-sized Old World monkeys (baboons and macaques). The *M. fuscata* function represents the mean of two studies (Owren *et al*. 1988; Jackson *et al*. 1999) and the *M. mulatta* function represents the mean of three studies (Wendt 1934; Behar *et al*. 1965; Pfingst *et al*. 1978). The two macaque functions showed similar contours: slightly inferior hearing up to about 5 kHz and then progressively better sensitivity at higher frequencies. The baboon function was also similar except for the marked dip at 4 kHz which may reflect a measurement artifact (also evident in the *A. paniscus* and *C. torquatus* curves from the same study). Figure 3.55D illustrates the inferior sensitivity of *P. troglodytes* below 6 kHz but at higher frequencies the chimpanzees appeared extremely more sensitive than humans.

Low Sensitivity (63 - 500 Hz)	Middle Sensitivity (1 - 4 kHz)	High Sensitivity (8 - 16 kHz)
C. mitis (-5.3)	*C. aethiops* (-7)	*P. troglodytes* (-40.5)
L. albigena (-4.3)	*C. jacchus* (-3)	*C. jacchus* (-24.5)
P. anubis (-2.3)	*C. neglectus* (0)	*M. mulatta* (-22.5)
C. torquatus (-0.5)	*C. mitis / L. albigena* (0.3)	*P. anubis / C. neglectus* (-20.5)
M. mulatta / C. aethiops (2)	*C. torquatus* (0.7)	*C. aethiops* (-17)
C. neglectus (2.5)	*M. fuscata* (5)	*L. albigena* (-15.5)
M. fuscata (4.5)	*M. mulatta* (6.3)	*M. fuscata* (-15.3)
C. jacchus (8.7)	*P. anubis* (12.3)	*C. mitis / C. torquatus* (-15)
A. paniscus (9.5)	*P. troglodytes* (14)	*A. paniscus* (-5)
P. troglodytes (13.3)	*A. paniscus* (16.3)	

TABLE 3.7 – Results from the human biological reference line comparison. Numbers in parentheses represent the SPL level for a frequency region above (positive numbers) or below (negative numbers) the human subjects tested in the same study. Positive values indicate less sensitivity than humans and negative numbers indicate better sensitivity than humans.

Table 3.7 gives a summary of the results from the human biological reference line comparison. A few of the notable observations will be discussed. These data suggest that most anthropoids are less sensitive to low-frequency sounds than are humans. A few of the exceptions, *C. mitis* and *L. albigena*, have been noted to specialize on low-frequency vocalizations (Brown 1986). Surprisingly, *P. troglodytes* appear to have the worst low-frequency sensitivity despite being the largest species in the comparison. Most species were also less sensitive than humans to mid-range frequencies with the exceptions of *C. aethiops* and *C. jacchus*. At the highest frequencies tested (8 and 16 kHz), all species showed greater sensitivity than humans. *P. troglodytes* and *C. jacchus*, the largest and smallest species compared, respectively, showed the best high-frequency hearing while *A. paniscus* showed the worst. In fact, *A. paniscus* was at or near the bottom of the list in all three frequency ranges. All other species illustrated relatively similar high-frequency sensitivity, with a range of only 7.5 dB. The extremely low value for chimpanzees (-40.5 dB) is probably the result of the fact that the human data from Kojima 1990 was based on

one middle-aged individual (42 years old) and this human audiogram showed the lowest high-frequency sensitivity of any presented in this chapter.

Intra-Laboratory Comparisons

In addition to using human threshold data as a reference for inferring sensitivity, the studies that examined multiple species also offer the opportunity for limited inter-specific comparisons. Since these datasets are for subjects tested under the exact same conditions they eliminate problems associated with different conditioning techniques, calibration procedures, and other factors that can lead to inflated variability. Out of the ten laboratories that tested more than one species, seven found significant differences between the species tested and these results will be briefly discussed. The most notable distinction in Wendt's study was the finding that spider monkeys had inferior hearing over the entire frequency range compared with the three Old World monkey species (mangabeys, baboons and macaques). Similarly, Fujita and Elliot's study found their New World species (squirrel monkeys) to be less sensitive at lower frequencies compared with the macaques, regardless of the type of reinforcement (Figure 3.56A and B). The rhesus macaques were also more sensitive at the best frequency (16 kHz) than were the

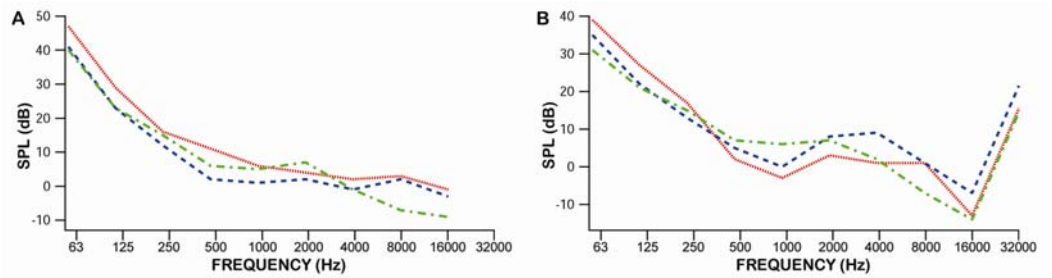

FIGURE 3.56 – *S. sciureus* (▪▪▪▪▪▪), *M. fascicularis* (— . — . —), and *M. mulatta* (— — —) from Fujita and Elliot 1965. **A**. Audiograms obtained using positive reinforcement. **B**. Audiograms obtained using negative reinforcement.

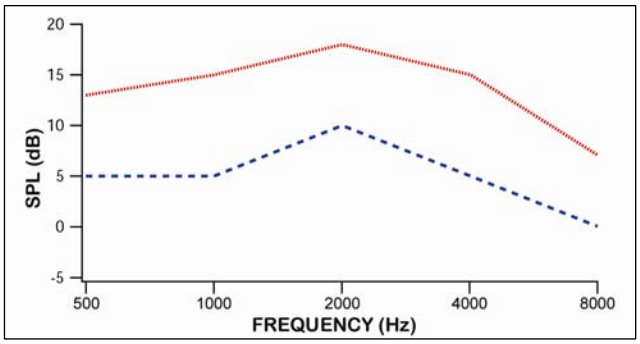

FIGURE 3.57 – GSR audiograms for *C. capucinus* (▪▪▪▪▪▪) and *M. mulatta* (▬ ▬ ▬) from Dalton 1968.

crab-eating macaques. The GSR data from Dalton's study (1968) also seems to suggest that platyrrhines (*C. capucinus*) are less sensitive at lower frequencies than Old World monkeys (Figure 3.57). The largest drawback of these three studies is that the Old World monkeys were generally larger than the platyrrhines in each study. Within New World monkeys, Beecher's owl monkeys were more sensitive than squirrel monkeys over the entire range but particularly at lower frequencies. Among the catarrhines in Owren *et al*.'s study, the vervets were more sensitive at their best frequency and showed a higher upper range than either the de Brazza's monkeys or Japanese macaques. The studies by Heffner and colleagues (1969, 1970) indicated that the galagos had the best high-frequency hearing of the lorisoids tested and that lorises were markedly less sensitive at the mid-range frequencies compared with the other two species. Lastly, the brown lemurs in Mitchell's studies (as well as the data published by Gillette 1973 and Heffner 2004) suggest a reduced high-frequency capacity compared with other lemuroids. These findings are summarized in Table3.8.

The relative (Tables 3.7 and 3.8) and absolute (Table 3.6) data sets established in this chapter present two different lines of evidence that can be used to investigate

Researchers	Findings
Wendt 1934	*A. paniscus* less sensitive than *C. torquatus*, *P. anubis*, and *M. mulatta*
Fujita and Elliot 1965	*S. scuireus* less sensitive than macaques at low frequencies
Fujita and Elliot 1965	*M. mulatta* more sensitive than *M. fascicularis* at 16 kHz
Dalton 1968	*C. capucinus* less sensitive than *M. mulatta* (500 Hz to 8 kHz)
Beecher 1974	*A. triveragtus* more sensitive than *S. scuireus*
Owren *et al*. 1988	*C. aethiops* more sensitive than *C. neglectus* and *M. fuscata* at 2 kHz
	and high frequency cut-off
Heffner *et al*. 1969	*G. senegalensis* more sensitive than *N. coucang* and *P. potto* at high frequencies
	N. coucang less sensitive than *G. senegalensis* and *P. potto* at middle frequencies
Mitchell *et al*. 1970	*E. fulvus* less sensitive than *E. macaco* and *L. catta* at high frequencies

TABLE 3.8 – Studies which found significant differences between the species investigated in that study (or same laboratory using the same methods).

relationships between form and function in the primate auditory system. The relative values can be used to address the general question of whether differences in morphology are reflected in differences in hearing sensitivity. However, the smaller sample sizes and the fact that the intensity values are not specified in absolute SPLs limit the overall utility of these data sets. The absolute data on the other hand can be used to address a wider spectrum of questions. In addition to testing the basic correlation between morphology and sensitivity, absolute values can be used to evaluate specific auditory theories and the capacity for using morphological structures to predict hearing sensitivity. Using form to predict function can be a useful tool for estimating sensitivity in fossil taxa. These topics are discussed in detail in chapters VII and VIII.

CHAPTER 4

Research Design

The preceding reviews of auditory functional morphology (Chapter 2) and primate hearing sensitivity (Chapter 3), make it apparent that we are still a long way from having a complete understanding of the basic principles governing auditory function. This dissertation seeks to answer three fundamental questions aimed at addressing this problem with a focus on an understudied group of highly diverse mammals, namely primates. First, ***are differences in primate auditory morphology correlated with differences in hearing sensitivity?*** The middle ear is of particular interest, since its multifarious nature has led to the application of numerous mechanical models and predictions pertaining to hearing function. Yet, a small group of researchers still contend that middle (and outer) ear morphology has little to do with the shape of an animal's audiogram (Heffner 1983; Ruggero and Temchin 2002; Overstreet and Ruggero 2002). Second, ***do significant relationships between form and function agree with expectations from auditory theory?*** The various ideas to be tested include those that posit strong ties between specific structures (*e.g.*, bullar volume, ossicular and tympanic membrane size) and particular hearing patterns (*e.g.*, increased low-frequency sensitivity). Third, ***are associations between morphology and function precise enough to allow auditory***

function to be predicted in extinct taxa? Since we now realize that differences exist between various clades of extant primates, it becomes of interest to try and track these changes through time by examining fossils representing pivotal nodes in the evolution of the order. These predictive equations could also potentially be useful for examining extant species for which hearing sensitivity is as yet unmeasured. These three elemental questions were addressed with nine comparisons broadly grouped into the four hypotheses that follow.

SPECIFIC HYPOTHESES TO BE TESTED

Hypothesis 1) Variation in primate auditory morphology is correlated with variation in hearing sensitivity. This hypothesis was tested by analyzing correlations between the audiometric variables defined in Chapter 3 and a variety of morphometric variables that seem to influence hearing sensitivity (described below). The basic analysis compared all primate taxa that have had their hearing sensitivity tested (full and optimal datasets) and for which morphological data could be attained.

Hypothesis 2) Distinctions in hearing sensitivity should be reflected in differences in ear morphology. Based upon predictions from audiogram analyses (Chapter 3), subsets of the morphometric dataset were compared to test for significant differences in auditory morphology. In the first comparison, three species of lorisoids were compared with three species of platyrrhines in an attempt to control for differences in overall body size and middle-ear configurations. A handful of other comparisons were made between taxa that had their hearing tested in the same laboratory but appeared to show variations in hearing performance. These include testing the observation drawn from the studies by Wendt

(1934) and Fujita and Elliot (1965) that New World monkeys are slightly inferior to Old World monkeys in low-frequency sensitivity. Comparisons were made between *Cebus* and *Macaca* and between *Ateles* and *Macaca*. More subtle distinctions in sensitivity were also tested by comparing *Aotus* with *Saimiri*, *Lemur catta* with *Eulemur fulvus*, and *Galago senegalensis* with the other lorisoids.

Hypothesis 3) Relationships between primate hearing sensitivity and middle ear morphology agree with expectations from auditory theory. This hypothesis was evaluated by comparing the results from the comparisons outlined above with predictions from previous auditory research. The theories tested include: 1) animals that are theoretically more efficient at impedance matching (*e.g.*, PTR's) should show greater hearing sensitivity; 2) inertial effects from ossicular mass limit high-frequency hearing; 3) bullar volume largely control the stiffness of the middle-ear and consequently should have an influence on low-frequency sensitivity; 4) tympanic membrane and stapedial footplate area strongly influence the overall shape of the audiogram.

Hypothesis 4) Correlations between morphological structure and hearing sensitivity allow the basic hearing patterns of fossil taxa to be investigated. This idea was tested by using a jack-knife procedure to test the precision of using morphometric variables to predict audiometric variables.

Measurements Taken and Validation Experiments

The auditory measurements that were taken include the dimensions of the pinna, the areas of the tympanic membrane and stapedial footplate, the lever arm lengths of the malleus and incus, the masses of all three ossicles, the volume of the middle ear cavity

and all related diverticuli, several measurements of the external surface of the tympanic bulla and temporal bone, and the length of the basilar membrane. These structures were selected because they have been implicated as exerting a strong influence on an animal's hearing sensitivity (see Chapter 2 - Dallos 1973; Webster and Webster 1975; Fleischer 1978; Moore 1981; Rosowski 1994; Puria *et al*. 1997). Furthermore, most of these are either made of or attach to bone permitting them to be measured in dried and fossilized specimens. The majority of the taxa examined were selected because their hearing sensitivity has been tested. However, numerous other species without audiograms were assayed in order to investigate allometric, ontogenetic, and phylogenetic patterns in auditory morphology.

Pinna Area and Shape

Due to the concern that drying and storage of museum skins may distort the size and shape of the outer ear, pinna dimensions were taken on cadaveric specimens and a few anesthetized animals. Specimens were measured only if the outer ear appeared to be representative of the position and shape in the living animal. Measurements of the maximum height and width of the pinna were taken to the nearest millimeter using the landmarks shown in Figure 4.1. Since many primate taxa do not have a true ear lobe (Schultz 1969), subaurale was determined as the most inferior aspect of the outer ear as it extends laterally from the side of the head. These measurements were used to calculate two morphometric variables: the area of the lateral pinna margin (A_p) and an index of pinna shape (S_p). A_p was computed using the formula for an ellipse ($\pi * r_1 * r_2$) and S_p was computed by dividing pinna height by pinna width.

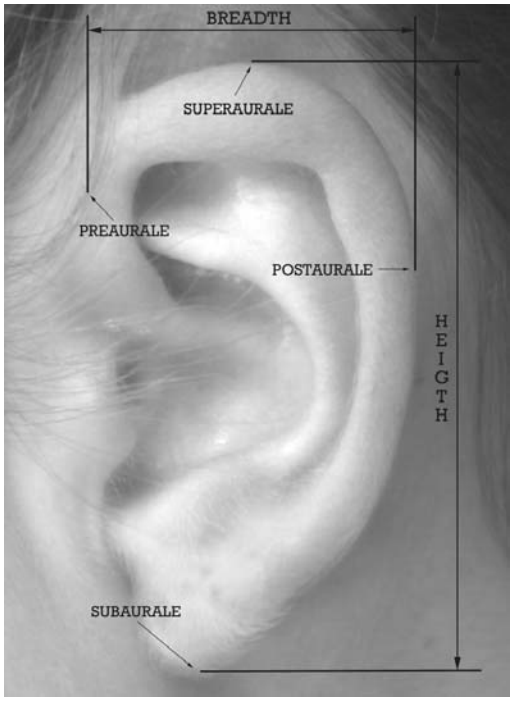

Figure 4.1 – Measurements taken on outer ears.

Tympanic Membrane Area

The surface area of the tympanic membrane (A_{tm}) was estimated using one of two procedures. In both procedures, the measurements were taken on the tympanic ring, and not the membrane itself, since the tympanic membrane is deteriorated in most dried (museum) specimens. For the majority of specimens, a casting technique was used similar to that employed by Masali *et al*. (1992). Specifically, an endocast was produced that preserved the impression left by the tympanic ring, and measurements were taken from digital images of the endocast (Figure 4.2). The molds were made by injecting a low viscosity molding gel (polyvinylsiloxane – Coltène President Plus Jet light body) into the lateral aspect of the middle ear cavity (a minimum of two molds per ear were produced). The molds were then removed and sectioned under a microscope along the line of

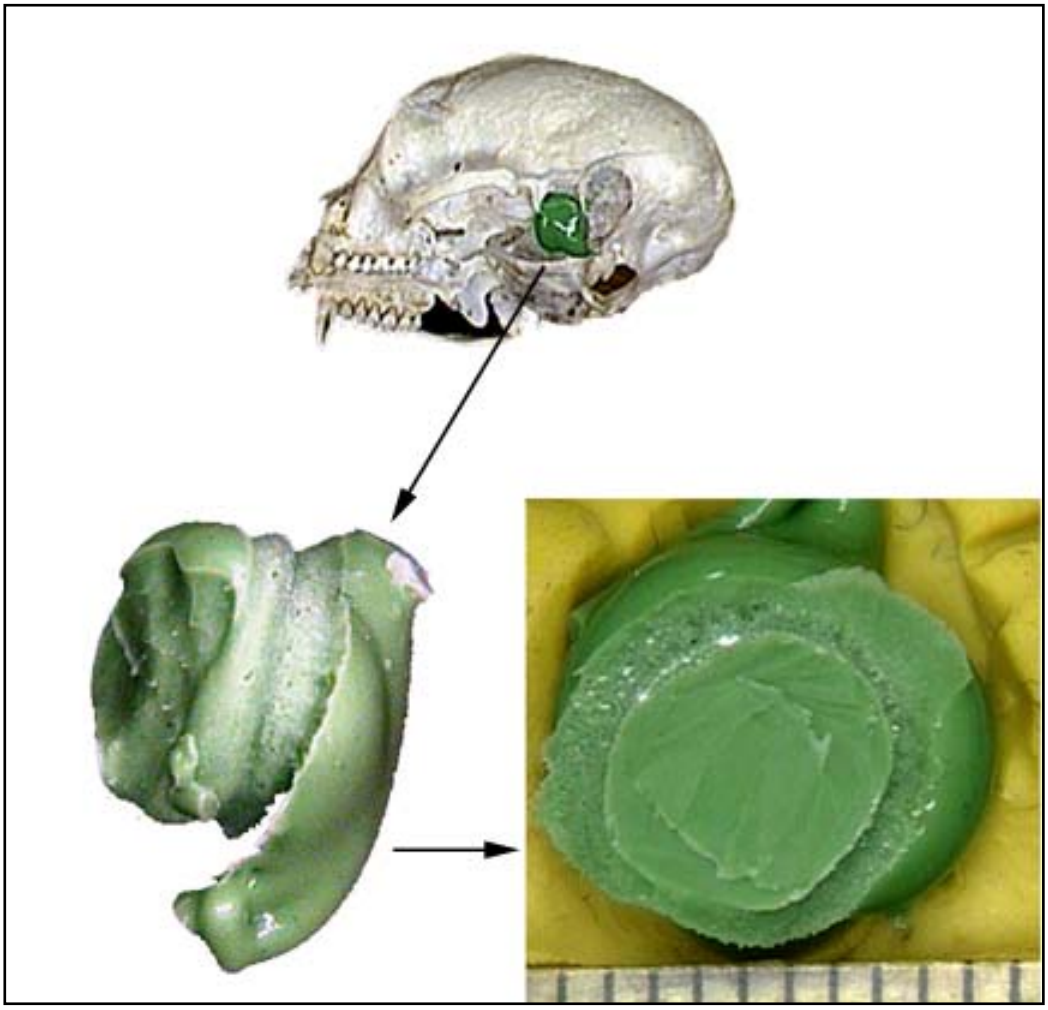

Figure 4.2 – Endocasts preserving an impression of the tympanic ring were created by injecting molding gel into the lateral aspect of the middle ear cavity. These casts were then sectioned and measured as described in the text.

attachment of the tympanic membrane (*sulcus tympanicus*). The sectioned molds were then digitally photographed, along with a scale placed in the same plane as the cut edge of the mold, at a distance at least 12 times the maximum dimension to be measured in order to minimize the effects of parallax (Spencer and Spencer 1985). Digital images were imported into Sigma Scan Pro 5.0 image measurement software, calibrated, and the A_{tm} calculated by tracing the perimeter.

This procedure was chosen over traditional methods which calculate area based on two perpendicular axes because it allowed the measurement of tympanic rings that are not fully visible externally, created a mold that can be repeatedly measured, and permitted deviations from round outlines to be incorporated into the estimate. Replication experiments were carried out to evaluate the precision of this technique and incorporated the potential variation associated with angle of the lens, parallax, and calibration and measurement error. Non-significant differences were found between A_{tm} for two different measurements of the same specimens (paired-samples T-test: $n = 54$, $p = 0.623$).

The one shortcoming of this technique was that it did not allow endocasts to be produced in species with a bony ear canal such as Old World monkeys and apes (expect in a few damaged specimens). Therefore, in order to obtain estimates of A_{tm} for these taxa, a second procedure was employed using high-resolution X-ray computed tomography (HRXCT). HRXCT scans were obtained for a select group of species and used to produce three-dimensional models of the ear region. Measurements of the tympanic ring were then taken on the models. More details about the HRXCT scanning protocols, thresholding techniques, and measurement procedures are given below.

Stapedial Footplate Area

The surface area of the stapedial footplate (A_{sf}) was estimated using one of three methods. In the first method, A_{sf} was measured from digital photographs of the actual footplate. The stapedes were carefully aligned (footplate parallel to the lens of the camera) on a piece of modeling clay, digitally photographed and measured in a manner similar to that described for A_{tm}. Repeated measurements on the same specimens using

this method produced non-significant differences (paired-samples T-test: n = 18, p = 0.538). In order to increase the sample size for A_{sf} (stapedes are relatively rare in museum collections), a second method was used that measured the oval window as a proxy for the stapedial footplate. Although it seems logical that one could use oval window dimensions to approximate A_{sf}, to my knowledge the correlation between A_{sf} and oval window area has not been tested. To investigate this relationship, the oval window was measured in a sub-sample of specimens that also had stapedial footplates available. Although the oval window may be slightly larger than the stapedial footplate, the slope between these two sets of measurements did not exclude isometry ($r^2 = 0.973$, slope = 1.011 ± 0.055, n = 41), justifying the usage of oval window area in the absence of a stapes. A third technique used HRXCT to estimate A_{sf} and will be described below.

Ossicular Lever Arm Length

Mallear and incudal lever arms lengths (LA_m and LA_i, respectively) were estimated using the same digital measurement techniques described above for A_{tm} and A_{sf}. The bones were positioned so that the presumed axis of rotation and the lever arms were as close to parallel to the axis of the lens as possible. The lever arm lengths were then measured by first drawing a line representing the axis of rotation from the short process of the incus through the anterior process of the malleus (Figure 4.3). Perpendicular lines were then drawn from the axis of rotation to the tips of the manubrium and long process of the incus. One limitation of this method is that it requires that the malleus and incus be articulated in order to establish the axis of rotation. Unfortunately, many ossicles in museum collections are loose and the

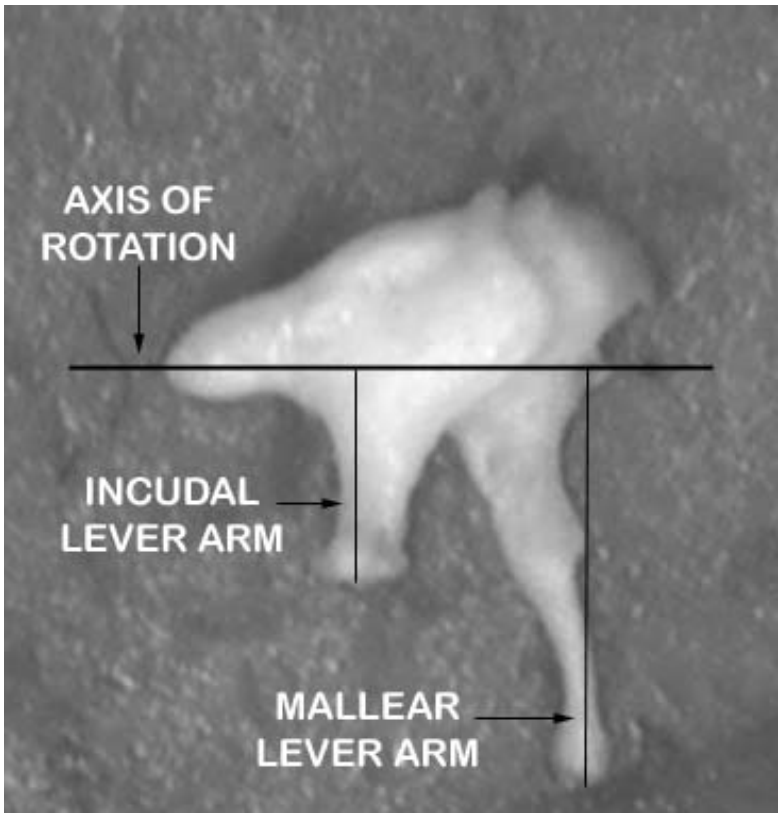

Figure 4.3 – Ossicular lever arm lengths were measured by taking a digital image of articulated malleus-incus pairs, drawing a line representing the axis of rotation, and then measuring the perpendicular distance from the axis of rotation to the tips of the manubrium of the malleus and long process of the incus.

malleus-incus complex rarely remains intact. However, it was suspected that the complex saddle-shaped articular surfaces of these bones would permit a good reconstruction of the orientations of the malleus and incus relative to each other in their natural positions. To test this idea, articulated malleus-incus pairs were removed from specimens in the Stony Brook Comparative Anatomical Museum and measured as described above. Next, the pairs were gently separated and re-articulated on a piece of clay, photographed and re-measured. No differences were found between the articulated and re-articulated measurements (paired T-test: $n = 24$, $p = 0.885$).

Ossicular Mass

Ossicular mass was measured to the nearest 0.01 mg for all three ear bones using a Cahn model D electrobalance, generously loaned to me by Dr. Michael LaBarbera at the University of Chicago. Although this is an older, non-digital balance (Figure 4.4), it had the advantage of being portable which allowed it to be easily transported to the various museums that house the specimens. The balance was allowed to warm up for more than one hour before measurements began and calibrated before each usage using a 10 mg OIML class E2 leaf weight. The calibration was continually checked every few specimens to detect any drift. All specimens were weighed three times and the mean of all three measurements was taken as the final value. If the malleus and incus were still articulated their combined mass was measured. Ossicles that had visible soft-tissues still attached (*e.g.*, ligaments, pieces of the tympanic membrane) were not weighed.

Figure 4.4 – Cahn microbalance used to measure ossicular mass.

To evaluate the precision of the ossicular mass measurements, 50 specimens were measured on two different days (and consequently with different calibrations). These paired sets of measurements were found to be highly consistent, varying by no more than 0.02 mg (Table 4.1), and a paired-samples T-test detected no significant differences ($p = 0.795$). Another concern with measurements on the order of micrograms is that their mass could be affected by moisture, lipid deposits, or even dust. To investigate this potential source of error, a drying and cleaning experiment was performed on 12 ossicles from the Stony Brook Comparative Anatomical Museum collections.

Specimen	Mass 1	Mass 2		Specimen	Mass 1	Mass 2
68225	1.88	1.89		211599	1.47	1.47
73432	0.17	0.17		215056a	2.65	2.67
76471	3.62	3.63		215056b	3.87	3.86
78562	4.09	4.07		239851	3.88	3.88
78653a	2.84	2.84		246658a	2.69	2.69
78653b	4.24	4.25		246658b	1.85	1.85
78653c	4.30	4.32		255860	1.72	1.73
93075	3.82	3.80		66346	1.84	1.84
93712	4.41	4.40		98767	3.42	3.41
98338	0.85	0.85		108172	2.09	2.08
100522a	4.11	4.09		134473	1.35	1.34
100522b	4.06	4.04		135471a	1.18	1.18
103653	3.69	3.71		135471b	1.54	1.54
133626a	0.36	0.36		150723	1.53	1.52
133626b	0.34	0.34		153089	1.30	1.29
139830	10.51	10.52		NAt4	4.29	4.28
187936	5.14	5.13		83651	3.08	3.08
211460a	2.26	2.26		83964	4.52	4.54
211460b	3.60	3.59		199694	6.73	6.71
211466	5.92	5.92		257397	3.43	3.44
211477	3.16	3.17		518587	2.08	2.09
211479	2.51	2.51		573934	2.56	2.57
211480	3.95	3.94		582737	2.44	2.45
211543	6.40	6.39		NSg6	0.17	0.17
211595	0.19	0.19		211603	1.52	1.53

Table 4.1 – Ossicular mass estimates (in milligrams) for 50 specimens measured on two different occasions. Non-significant differences were found between the paired sets of measurements.

Specimen	Ossicle	Mass 1	Mass 2	% diff	Mass 3	% diff
NSg 6	stapes	0.14	0.15	7		
NSg 1	incus	1.46	1.46	0	1.46	0
NAl 8	malleus	4.51	4.45	1		
NPt 10	malleus	2.53	2.52	0		
NSm 7	incus	2.11	2.09	1	2.04	3
NCh 2	stapes	0.43	0.44	2	0.43	0
NAt 8	stapes	1	1	0		
PGa 2	malleus	1.27	1.24	2		
NAl 5	incus	7.93	7.76	2	7.68	3
NAt 20	malleus	4.46	4.42	1	4.38	2
NCb 10	incus	4.15	4.12	1	4.08	2
NCb 3	stapes	0.34	0.34	0		
mean % diff				2		2

Table 4.2 – Results from an experiment evaluating the effects of moisture and non-organic materials on determining ossicular mass (in milligrams). The Mass 1 measurements represent the initial starting weight, Mass 2 are the weights after a drying procedure, and Mass 3 are the weights after using a chemical solvent and then another drying procedure.

The experimental procedure was as follows: First the ossicles were weighed in the manner described above. Next, the ossicles were placed in a Barnstead / Thermolyne mechanical convection oven and heated at 58° C for 68 hours, followed by a second weighing. Then the ossicles were submerged in an organic solvent (xylene) for 10 hours and then dipped in a 100% ethanol for 2 hours to remove any excess solvents. The bones were then dried again for 12 hours in the convection oven and weighed a final time.

Non-significant differences were found between the first and second sets of measurements ($p = 0.073$) and the average difference for all specimens was only 2% (Table 4.2). However, one specimen (NSg 6) did show a difference of 7%, but this is probably an artifact of measurement error since the second measurement was actually heavier than the first (by 0.01 mg). Statistics were not computed comparing the last set of

measurements because half of the bones were damaged during the cleaning process[28]. However, the final mass measurements for the remaining six specimens were reduced by no more than 3% from their initial starting weight (Table 4.2). Therefore, although moisture and extraneous material may add a marginal amount of mass to the ossicles, the finding that the measurements varied by less than 5% was considered an acceptable level of possible error.

Computed-Tomography Protocols

The remaining groups of measurements were all taken on either scans or three-dimensional models produced using HRXCT. The scanning protocols, thresholding techniques, and validation experiments will be described first before the actual measurements are outlined. All scanning of extant specimens was done at the University of Texas High-Resolution X-ray CT facility in collaboration with Drs. Matthew Colbert and Richard Ketcham. These scans were taken with a 68-µm slice thickness and 68-µm interslice spacing. This level of resolution was chosen in order to minimize the effects of partial-volume averaging that might occur when measuring small structures such as trabecular bone which is commonly found in the middle ear cavities of some primate taxa (previous studies have indicated that trabecular thickness generally ranges from 200 µm to 800 µm - Mullender *et al*. 1996; Fajardo and Müller 2001). The images were reconstructed from 1000 views and the field of view was 64 mm yielding a pixel size of 62.5 µm (1024 X 1024 pixel matrix). The final images were 16-bit TIFF files. The image stacks were imported into ImageJ 1.35f (NIH), cropped, converted to 16-bit signed files

[28] The ossicles were not damaged by the solvent but by the usage of a vortex genie touch mixer which was initially part of the experimental procedure. Since this process appeared to be too violent for the fragile bones (small pieces were broken off), it was not used for the remaining, undamaged six specimens.

(to be compatible with the measurement software), and saved as raw stacks. The image stacks were then loaded into 3D Slicer 2.6, where all measurements were taken.

One of the biggest challenges in using CT data is determining the appropriate threshold value that represents the boundaries of the structure under investigation. Because the viewer control settings (window and leveling values) can greatly affect the visual appearance of images (particularly the edges of structures), basing the threshold value on the apparent (visual) boundaries can yield erroneous results (Koehler *et al*. 1979; Baxter and Sorenson 1981). One approach that has received increasing popularity is the half-maximum height (HMH) approach which calculates the threshold value as the mean of the maximum and minimum gray scale values along a row of pixels that spans the boundary transition (Ulrich *et al*. 1980). This method (using regular CT images) has been found to produce accurate measurements of modern human vertebrae (Ullrich *et al* 1980; Baxter and Sorenson 1981; Seibert *et al*. 1981; Eubanks *et al*. 1985) as well as of extant and fossilized materials (Spoor *et al*. 1993). More recently, Fajardo *et al*. (2002) used HRXCT to accurately reconstruct and measure the trabecular architecture of long bones (trabecular bone volume and mean trabecular plate number). They also found that it was important to sample the appropriate region of interest (ROI) because bone types of different density (cortical versus trabecular) yield different HMH values (Fajardo *et al*. 2002).

One of the limitations of these studies is that the HMH protocol and validation measurements were applied to individual slices. However, when a researcher wishes to take measurements on three-dimensional models created from CT, a global threshold value must be applied to the entire dataset. One potential concern is that applying a global

threshold to a dataset of dozens or hundreds of slices may not accurately represent the real morphology of various structures. Thus, this analysis sought to investigate the effects of taking linear measurements on three-dimensional models using a modified version of the HMH protocol[29].

To examine the accuracy of the thresholding protocol, measurements were taken from HRXCT data and compared with measurements taken on dried specimens. The oval window was selected as the variable of interest because it represents a relatively small structure and also because it is possible to obtain these measurements on the dried skulls of certain taxa with a reasonable amount of accuracy. A Zeiss Discovery V.12 stereo digital microscope was used to take the measurements on the dried specimens (hereafter referred to as Zeiss-based measurements).

Two different threshold values were used to construct the models, one following a modified HMH protocol and the other by visually adjusting the threshold value until the threshold boundaries appeared to correspond to the image boundaries. The HMH protocol used here is a modified version of the protocol outlined by Fajardo *et al*. (2002). The threshold value was determined by calculating the HMH for a row of pixels that crossed the bone-to-air transition around the circumference of the oval window for 10 randomly selected slices. The mean value of the 10 HMH values was then taken as the threshold for the entire stack. Table 4.3 presents the measurements taken on 14 primate specimens representing a wide range of body sizes. In all cases, the measurements made using the HMH protocol were in close agreement with those made on the dried specimens (Zeiss-based). A paired-samples T-test found there to be a non- significant difference between

[29] The results from this comparison were published in the American Journal of Physical Anthropology (Coleman and Colbert 2007).

Genus	Spec #	Zeiss Length	HMH Length	Visual Length	Zeiss Width	HMH Width	Visual Width	Zeiss Area	HMH Area	Visual Area
Alouatta	Nal 13	1.90	1.88	1.78	0.95	0.92	0.80	1.42	1.36	1.12
Aotus	Nao 1	1.30	1.28	1.11	0.63	0.60	0.43	0.64	0.60	0.37
Aotus	77299	1.31	1.30	1.15	0.64	0.67	0.56	0.66	0.68	0.50
Callithrix	15915	1.22	1.19	0.89	0.59	0.60	0.38	0.57	0.56	0.27
Callithrix	133688	1.16	1.18	1.14	0.64	0.63	0.56	0.58	0.58	0.50
Cebus	Ncb 9	1.67	1.65	1.56	0.85	0.86	0.78	1.11	1.11	0.96
Erythrocebus	19003	1.96	1.97	1.73	0.80	0.80	0.67	1.23	1.24	0.91
Erythrocebus	34852	2.09	2.09	1.94	0.92	0.93	0.88	1.50	1.53	1.34
Galago	81458	1.16	1.14	0.90	0.57	0.60	0.43	0.52	0.54	0.30
Macaca	103730	1.87	1.90	1.79	0.72	0.77	0.67	1.06	1.15	0.94
Nycticebus	183827	1.16	1.16	1.12	0.67	0.70	0.65	0.61	0.64	0.57
Perodicticus	52704	1.15	1.15	1.08	0.66	0.66	0.57	0.60	0.60	0.48
Perodicticus	52700	1.34	1.30	1.24	0.71	0.73	0.64	0.75	0.75	0.62
Saimiri	NSm 7	1.29	1.29	1.15	0.62	0.58	0.45	0.63	0.59	0.41
percent diff			1	11		3	21		3	37
mean diff			0.02	0.14		0.02	0.11		0.03	0.19
max diff			0.04	0.33		0.05	0.21		0.09	0.32

Table 4.3 – Oval window measurements taken using three different procedures as described in the text. Length and width measurements are in millimeters (mm) and areal measurements are in mm^2. The last three rows show the differences between the Zeiss-based values and the HMH and Visual thresholding protocol values.

the two sets of data (length $p = 0.217$; width $p = 0.414$; area $p = 0.745$). The average difference for oval window length was about 1% and the mean difference in absolute terms was 0.02 mm with a maximum difference of 0.04 mm. For oval window width, the average difference was 3% with a mean difference of 0.02 mm and a maximum difference of 0.04 mm. Oval window area showed a similar pattern with an average difference of 3%, a mean difference of 0.02 mm^2 and a maximum difference of 0.09 mm^2.

In contrast, the measurements made using the visually determined threshold values were consistently smaller than the other two measurement sets, and were found to be significantly different from the Zeiss-based measurements for all three variables ($p < 0.001$). The average difference for oval window length was 11%, the mean absolute

difference was 0.14 mm, and the maximum difference was 0.33 mm. Oval window width showed an even larger difference of 21%, with a mean absolute difference of 0.11 mm and maximum difference of 0.21 mm. Oval window area illustrated the largest discrepancies averaging 37% smaller than the Zeiss-based calculations, with a mean absolute difference of 0.19 mm^2 and a maximum difference of 0.32 mm^2. The larger disparities displayed by the area calculations are most likely the product of compounding the errors associated with the length and width measurements. When comparing the HMH-based boundaries with the apparent boundaries (Figure 4.5), the HMH boundaries were nearly always within the apparent bone-to-air transition. Therefore, an oval window

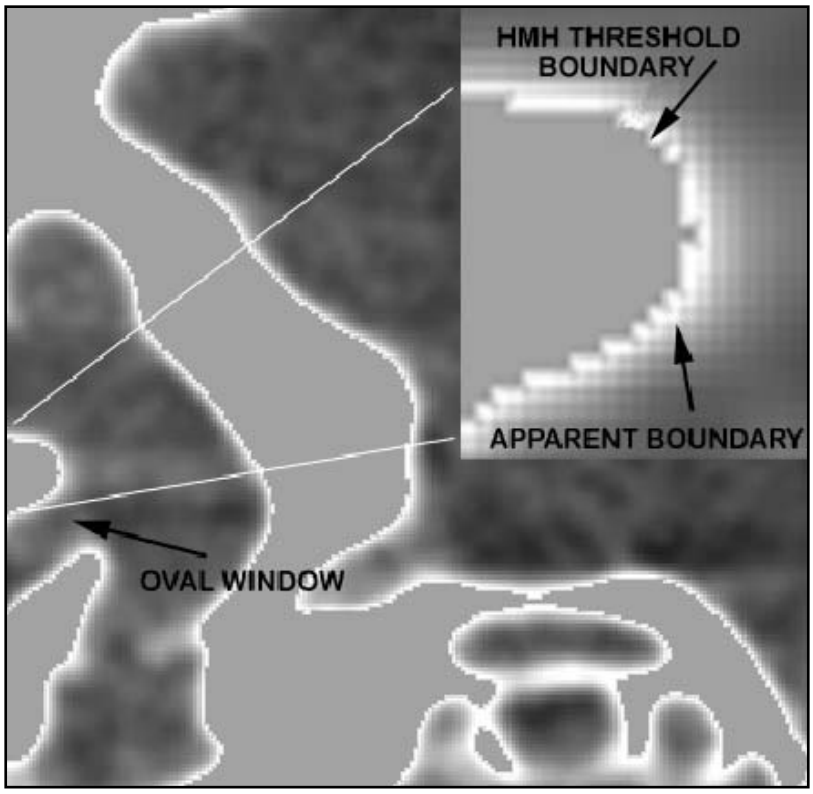

Figure 4.5 – A representative CT slice of the oval window illustrating the difference between the HMH-based threshold and the apparent (visually-based threshold) bone-to-air boundary. Using the visually-based threshold protocol often results in underestimating the measurement values.

measurement from one bone boundary to an adjacent bone boundary using the HMH protocol will be larger and this explains why the visually-based threshold measurements were generally smaller. A similar directional trend between HMH and visually determined protocol measurements was also found for other auditory structures such as the volume of the middle-ear cavity and the length of the cochlea (Table 4.4).

In general, the difference between Zeiss-based measurements and the HMH-based measurements were on the same order as the size of the voxel dimensions, where as the dissimilarity with the visually-based measurements was an order of magnitude larger. These results agree with previous studies that found problems with visually adjusted thresholding protocols, but add confidence to the HMH procedure for estimating a global threshold value for a particular region of interest. Therefore, all measurements derived from HRXCT data were made using the HMH protocol as defined above and the ROI was shifted depending on the measurement being taken (see below).

Genus	Spec #	HMH V_{me}	Visual V_{me}	HMH L_c	Visual L_c
Aotus	NAo1	0.40	0.31	23.74	20.14
Callithrix	NCx 1	0.15	0.13	20.62	19.73
Lemur	22912	0.58	0.55	21.73	19.74
Lemur	100596	0.78	0.77	21.30	19.74
Lemur	100821	0.66	0.65	20.30	18.33
Nycticebus	112991	0.84	0.83	23.27	22.35
Nycticebus	101508	0.29	0.28	17.41	16.26
Nycticebus	183827	0.46	0.46	23.16	22.12
Perodicticus	52704	0.28	0.26	21.97	20.93
Perodicticus	52700	0.43	0.36	20.12	18.31
Perodicticus	52699	0.40	0.38	21.01	17.56
percent diff			8		9
mean diff			0.03		1.76
max diff			0.09		3.60

Table 4.4 – Middle ear cavity volume (V_{me}) and cochlear length (L_c) measurements taken using the visually-based and HMH-based thresholding protocols. V_{me} values are in ml^3 and L_c values are in mm. The last three rows show the difference between the two protocols for both structures.

Middle-Ear Cavity Volume

Cavity volumes were measured by "filling" the spaces within the middle ear using the change island function in 3D Slicer. The ROI used to determine the threshold value was either a region of trabecular bone (10 random slices) or the bullar walls for taxa without trabeculae. Neurovascular tubes (*e.g.*, carotid canal, facial canal) were excluded from the measurements. In taxa with multiple cavities, the individual volumes were estimated for each cavity. The demarcation between the epitympanic sinuses and the tympanic cavity proper was estimated as the point within the epitympanic recess approximately corresponding to the position normally occupied by of the head of the malleus and the body of the incus. This point was chosen since it was estimated to represent the most constricted volume of air between these two cavities while the ossicles are intact. In lorisiforms, the beginning of the MAC was judged as the point where the supracochlear duct opened into the epitympanic sinus. For all anthropoids, the opening of the AAC (*apical aperture*) into the Eustachian tube (or occasionally into the tympanic cavity itself) was used as the inter-cavity boundary. The volume of the Eustachian tube (see below) was included with the volume of the tympanic cavity proper.

Since the specimens used for scanning were dried skulls it was necessary to seal-off certain holes that are typically closed in living animals. The holes normally filled by the tympanic membrane, secondary tympanic membrane (round window), and stapedial footplate were digitally closed-off by drawing boundary lines on each slice between relevant bony structures (*e.g.*, *crista tympanica*). Specimens with intact tympanic membranes were periodically evaluated under magnification to validate the attachment areas of taxa with different ring configurations. The Eustachian tube was closed-off at the

rostral bony end where it articulates with the cartilaginous part. This may slightly underestimate the functional volume of the Eustachian tube since a small portion of the cartilaginous part most likely remains patent under all conditions (*i.e.*, even when the membranous tube is not being opened by palatal muscles). However, since the contribution from this part is probably trivial and is not normally preserved in dried specimens, it was ignored when estimating Eustachian tube volume.

The other middle-ear structures measured using HRXCT included the dimensions of the oval window and two perpendicular axial measurements of the tympanic ring. The ROI's used for determining threshold values were the inner circumference of the oval window and the tympanic ring, depending on the measurement. Both pairs of measurements were taken on 3D models using the fiducials[30] module, as described above.

The final structure measured using HRXCT was the length of the cochlea (L_c) which was used as a proxy for length of the basilar membrane. Although basilar membrane length is best estimated by measuring the length of the bony spiral lamina along the inner circumference, the lamina is often incomplete in dried specimens and rarely present at all in fossilized specimens. Therefore, as a proxy for basilar membrane length, the outer circumference of the scala media was measured on 3D models (the cochlea-air boundary was used to determine the HMH value). Although cochlea length probably overestimates basilar membrane length, it is assumed that these two measurements are proportional. The measurements were taken by placing fiducials at

[30] Fiducials are markers that can be placed on three-dimensional digital models.

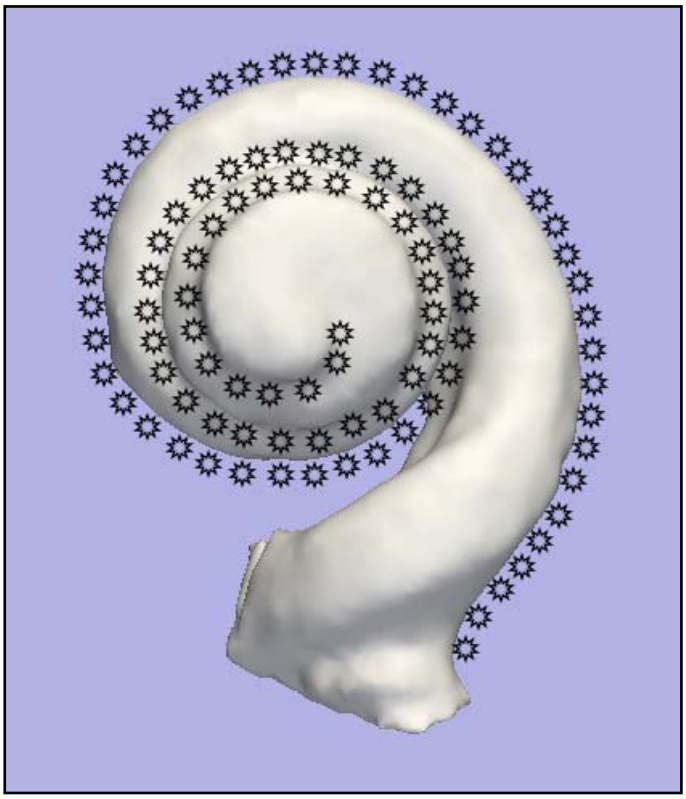

Figure 4.6 – Image of a CT generated 3-D cochlea model illustrating the approximate placement of fudicial points along the outer spiral used to measure cochlear length.

the smallest possible intervals[31] along the outer circumference of the cochlea starting at the distal edge of the round window and continuing until the approximate location of the helicotrema (Figure 4.6). The distances between all the fiducial points were then measured and summed. This procedure was repeated twice for each specimen.

Final Morphometric Variables

Based on the measurements described above, a total of 22 morphometric variables were derived. Many of these are simply the individual measurements themselves,

[31] The intervals between points averaged less than 0.5mm and generally a minimum of 35 points were used.

although several derivative variables were also generated. These included using A_{tm} and A_{sf} to calculate the areal convergence ratio (ACR) which was computed by simply dividing A_{tm} by A_{sf}. In a similar way, an ossicular lever arm ratio (LAR) was calculated by dividing LA_m by LA_i. These four measurements were also used to calculate the overall transformer ratios (PTR and ITR) described in Chapter 2. Two variations of the PTR and ITR were generated, one using the full area of the tympanic membrane (PTR_{fa}, ITR_{fa}) and the other assuming an effective area that is 2/3 that of the anatomical area (PTR_{ea}, ITR_{ea}).

Ossicular mass was evaluated using the values for the individual bones (malleus mass = M_m; incus mass = M_i; stapes mass = M_s). In addition, M_m and M_i were combined to produce a single value for the mass of the malleus-incus complex (M_{mi}). Also included in this group were the malleus-incus pairs that were still articulated when measured. Finally, the mass of the entire ossicular chain (the bones at least) was computed by summing the individual masses (M_{mis}). In reality, the M_{mis} is very similar to the M_{mi} since the stapes weighs so much less than either of the other two bones. Still, this variable was included to investigate the possibility that this small amount of additional mass has functional implications. The final derivative variables relate to the volume of the tympanic cavities. The first three variables consider the volumes of the individual cavities (tympanic cavity proper = V_{tc}; epitympanic sinus = V_{es}; accessory cavity (MAC and AAC) = V_{ac}). In addition, the combined volume of all middle-ear cavities was calculated (V_{me}).

One question to be considered when combining individual variables to produce derivative variables is whether to use a mean value (*i.e.*, species mean) for each individual structure or to only use the values produced by specimens with all relevant

Genus	Ratio 1	Ratio 2	% diff		Genus	Ratio 1	Ratio 2	% diff
Alouatta	1.573	1.575	0.2		*Hapalemur*	2.012	2.024	0.6
Aotus	1.707	1.714	0.4		*Indri*	1.899	1.905	0.3
Arctocebes	2.014	2.015	0.0		*Lagothrix*	1.724	1.724	0.0
Ateles	1.637	1.652	0.9		*Lemur*	2.105	2.105	0.0
Avahi	2.078	2.080	0.1		*Leontopithecus*	1.846	1.851	0.3
Brachyteles	1.596	1.607	0.7		*Lepilemur*	2.354	2.336	0.8
Callicebus	1.793	1.796	0.2		*Macaca*	1.671	1.669	0.1
Callimico	1.785	1.785	0.0		*Microcebus*	1.962	1.970	0.4
Callithrix	1.823	1.832	0.4		*Nycticebus*	2.072	2.085	0.6
Cebuella	1.838	1.841	0.2		*Pan*	1.415	1.483	4.8
Cebus	1.606	1.610	0.3		*Perodicticus*	2.088	2.089	0.1
Cercocebus	1.607	1.616	0.6		*Pithecia*	1.718	1.720	0.1
Cercopithecus	1.700	1.710	0.5		*Propithecus*	1.843	1.856	0.7
Chiropotes	1.812	1.820	0.4		*Saguinus*	1.840	1.856	0.9
Chlorocebus	1.831	1.831	0.0		*Saimiri*	1.691	1.697	0.3
Erythrocebus	1.717	1.743	1.5		*Tupaia*	1.910	1.915	0.3
Eulemur	1.818	1.818	0.0		*Varecia*	1.811	1.821	0.5
Galago	2.255	2.259	0.2		mean % diff			0.5

Table 4.5 –A comparison of ossicular lever arm ratios (mallear lever arm length / incudal lever arm length). Ratio 1 was derived using genus means for each bone individually and Ratio 2 was derived by using only specimens that had both bones present.

structures present. Although it would seem advisable to use only the latter, this could severely limit sample sizes, particularly when the derivative variable is the product of several variables (because few specimens will have all structures intact). This was the case in a study on subfossil lemur post-crania by Walker (1967). He found that the single specimen of *Archaeolemur majori* with a complete skeleton produced very similar indices (brachial, crural, and intermembral[32]) to the indices produced using the means for each element from a sample of partial skeletons. To further examine this issue, two sets of genus mean ossicular lever arm ratios were compared. The first set was calculated using only specimens for which both bones were present and the second set was

[32] Brachial index = radius length / humerus length; crural index = tibia length / femur length; intermembral index = (humerus length + radius length) / (femur length + tibia length)

calculated by taking the genus mean for mallear lever arm length and dividing it by the genus mean for incudal lever arm length.

Table 4.5 shows the two sets of ratios for 35 genera. A regression of these two sets of ratios showed a tight relationship ($r^2 = 0.997$) with a slope just below the isometric slope of 1 (slope = 0.968 ± 0.20). A paired samples T-test found the ratios to be significantly different ($p = 0.001$), and Table 4.5 shows that the second set of ratios was nearly always higher[33]. However, since the mean difference for all genera was less than 1 percent and no genus showed an absolute difference of more than 5 percent, all derivative variables will be calculated using the means for each individual element in order to maximize the number of taxa that can be used in the forthcoming analyses (a few species do not have a single specimen with all variables present).

[33] It is unclear to the author why the second set of ratios was nearly always higher.

CHAPTER 5

Introduction

Comparative biologists interested in a wide range of questions often use some measure of size to "scale" a particular trait of interest (*e.g.*, brain size) so that taxa of different sizes can be compared. This type of comparative analysis has been termed "body size allometry" (Smith 1993) and should not be confused with studies that aim to investigate the relationship between the shape and size of a particular structure. Despite over a century of awareness that size must often be considered when studying biological systems (Dubois 1894; Thompson 1917), there remains much to be learned as to the appropriate variable(s) to use when adjusting for differences in size. Body mass is often considered the most fundamental measure of the size of an individual (Clutton-Brock and Harvey 1983; Hens *et al.* 2000), and many studies have used mass as a size variable to evaluate the relative size of other structures *(e.g.*, Jungers and Olsen 1985). However, body mass data are unavailable for a large proportion of museum specimens and are never available for fossils. In the absence of such data, researchers have used a variety of morphological proxies for body mass ranging from single linear measurements to the geometric mean of multiple measurements (*e.g.*, Mosimann 1970; Gordon 2004).

Scientists investigating aspects of cranial morphology often use some approximation of cranial size to scale other variables based on the notion that the overall size of an individual is less relevant than head size for investigating particular questions (Hylander 1985; Langenbach and Weijs 1990). This type of analysis might be more appropriately termed "head size allometry" or more generally just "size allometry". One such approach involves using a single morphological measurement that is assumed to be independent of the variable of interest (Kay 1981; Schleich and Vassalo 2003) or in an attempt to "hold constant" one variable in a multifarious functional system (Bouvier 1986; Ravosa 1991; Vinyard *et al*. 2003). Another approach is to calculate the geometric mean of multiple measurements.

One concern with using methods such as these is that the size measurements are often chosen indiscriminately, without an adequate understanding of the functional or scaling relationships between the size variables and the trait being investigated. Consequently, it remains unknown whether the results have been influenced by the particular size variable used. The few cranial studies that have been critical when selecting the appropriate size variable generally have been limited to investigations of the dentition (Martin 1983; Macho 1994; Grine 2002). The aim of the research presented here was to investigate the relationships between numerous size variables and two well-studied functional characters found in the head (orbit size and mandibular robusticity) in an attempt to gain new insights into how different measurements and combinations affect size variable performance in head size allometry[34]. These principles were then used to guide the selection of the appropriate size variable that will be used in later chapters.

[34] These data were presented at the American Association of Physical Anthropologists 72nd Annual Meeting, Arizona State University, Tempe, Arizona. (Coleman 2003)

Experimental design

Two analyses were undertaken to investigate the influence of using different size variables for size adjustment in biomechanical comparisons. Testing the ability of various size measures to recover known biomechanical relationships will be used as one standard of performance. The first analysis examined the relative size of the bony orbit and the second analysis looked at the robusticity (thickness) of the mandible. These two traits were chosen because each has a substantial body of theoretical and empirical knowledge that could be used to develop a null hypothesis about the expected outcome from functional comparisons. For example, smaller-bodied nocturnal mammals have been found to have relatively larger orbits than diurnal ones (Kay and Cartmill 1977; Heesy and Ross 2001), and primates that feed primarily on hard or fibrous foods generally have more robust mandibles than animals that feed on soft foods (Daegling 1992; Anapol and Lee 1994). The relative sizes of these traits were determined by dividing their size by numerous types of size variables. For example, the relative size of the orbit (O^{REL}) was calculated using the formula:

(5.1) $$O^{REL} = (\sqrt{\text{orbital area}}) / \text{size variable}$$

where orbital area is calculated using the radii of the height (r_h) and width (r_w) of the bony orbit (orbital area = $\pi * r_h * r_w$). This calculation assumes that the inner circumference of primate orbits are more rounded than rectangular in shape. Similarly, a size ratio for the mandibular corpus (MC^{ROB}) was calculated using the formula:

(5.2) MC^{ROB} = corpus width / size variable

where corpus width is taken as the maximum thickness (width) at the second molar.

New World monkeys (platyrrhines) were the research group for this study because they offer a wide range of body sizes and dietary specializations, and are also the only anthropoid family to include a nocturnal genus. A total of 385 adult specimens representing 12 of 16 New World monkey genera (Table 5.1) were examined from the

Genus	Species	Number of Specimens	Activity Cycle	Dietary Category
Alouatta (Alo)	*caraya*	9	Diurnal	Hard/Fibrous
	seniculus	19		
Aotus (Aot)	*azarae*	22	Nocturnal	Soft
	nancymae	15		
	trivirgatus	2		
Ateles (Ate)	*paniscus*	25	Diurnal	Soft
Cacajao (Cac)	*calvus*	14	Diurnal	Hard/Fibrous
	melanocephalus	9		
Callicebus (Cal)	*moloch*	23	Diurnal	Soft
	personatus	4		
	torquatus	10		
Callithrix (Ctx)	*jacchus*	3	Diurnal	Soft
	albifrons	15		
Cebus (Ceb)	*apella*	46	Diurnal	Hard/Fibrous
	capucinus	48		
Chiropotes (Chi)	*satanas*	19	Diurnal	Hard/Fibrous
Lagothrix (Lag)	*lagotricha*	12	Diurnal	Soft
Pithecia (Pit)	*monachus*	10	Diurnal	Hard/Fibrous
	pithecia	10		
Saguinus (Sag)	*fuscicollis*	6	Diurnal	Soft
	midas	3		
Saimiri (Sai)	*boliviensis*	22	Diurnal	Soft
	sciureus	39		

Table 5.1 - Taxa for which cranial measurements and behavioral data were gathered. Dietary data taken from the literature: Baldwin and Baldwin (1981); Boubli (1994); Eisenberg (1989); Emmons and Feer (1990); Ferrari and Ferrari (1989); Freese and Oppenheimer (1981); Hershkovitz (1977); Hershkovitz (1985); Janson and Boinski (1992); Julliot and Sabatier (1993); Kinzey (1992); Kinzey and Norconk (1993); Peres (1994); Robinson *et al*. (1987); Strier (1992); Terborgh (1983); van Roosmalen and Klein (1988).

collections at the American Museum of Natural History, the National Museum of Natural History (Smithsonian), and the Field Museum of Natural History. Thirty-three cranial dimensions were taken on each specimen to the nearest 0.1mm using digital calipers (Table 5.2). Additional information such as body mass and total body length were also

Region/ Apparatus	Measurement	Abbr.	Osteometric Landmarks
Full Skull	Skull Length	SL	Prosthion - Inion
	Skull Width	SW	Zygion - Zygion
	Skull Height	SH	Vertex - Chord connecting Gonion
Neural	Neurocranial Length	NL	Nasion - Inion
	Neurocranial Width	NW	Euryon - Euryon
	Neurocranial Height	NH	Basion - Vertex
Facial/Visual	Facial Width	FW	Ectoconchion - Ectoconchion
	Facial Height	FH	Prosthion - Nasion
	Orbital Depth	OD	Orbitale Inferiorus - Anterior Optic Canal
	Orbital Width	OW	Ectoconchion - Maxillofrontale
	Orbital Height	OH	Orbitale Inferiorus - Orbitale Superiorus
	Interorbital Width	IW	Maxillofrontale - Maxillofrontale
Facial/ Masticatory	Palate Length	PL	Prosthion - Staphylion
	Palate Width	PW	Ecotmolare - Ecotmolare
	Symphyseal Width	MW	Pogonion - Posterior Symphyseal Border
	Symphyseal Height	MH	Infradentale - Gnathion
	Corpus Width	CW	Mandibular Corpus Width at M2
	Corpus Height	CH	Superior - Inferior Border of Corpus at M2
	Ramus Height	RH	Gonion - Condyle of Ascending Ramus
Temporal/ Masticatory	Zygomatic Arch Length	ZL	A - P distance of Zygomatic Arch (Internal)
	Zygomatic Arch Width	ZW	Width at mid-Zygomatic Arch
	Zygomatic Arch Height	ZH	Height at mid-Zygomatic Arch
	Postorbital Constriction	PC	Minimum Neural Width Posterior to Orbits
Cranial	Ant. Skull Length	PB	Prosthion - Bregma
	Post. Skull Length	IB	Inion - Bregma
	Ant. Cranial Length	NB	Nasion - Bregma
	Ant. Cranial Height	BB	Basion - Bregma
	Post. Cranial Length	BI	Basion - Inion
	Post. Cranial Width	AA	Asterion - Asterion
Basicranial	Ant. Basicranial Length	BP	Basion - Prosthion
	Post. Basicranial Length	IO	Inion - Opisthion
Basicranial/ Auditory	Interaural Distance	EE	Ectotympanic - Ectotympanic
	Petrosal Length	AP	Asterion – Anterior Tip of Petrosal

Table 5.2 - Cranial measurements taken on each specimen.

gathered from the field notes. These head and body measurements were used either independently or in combination (to calculate a geometric mean) as size variables that can be classified into three main categories (Table 5.3). These size variables were designed to explore how different regions, combinations, and functional systems interact to influence biomechanical and allometric comparisons.

The first category is termed universal size variables (**USVs**) and simply uses total body length and the cube root of body mass as size variables. The second category is referred to as global size variables (**GSVs**) and consists of measurements that generally span the entire surface of the skull. Included in this category are three individual

Category	Size Variable (total variables)	Measurements Used
USV	Body Mass (1)	Cube Root of Body Mass
	Body Length (1)	Length from Rostrum to Tip of Tail
GSV	Skull Length (1)	SL
	Skull Width (1)	SW
	Skull Height (1)	SH
	VAMNO 1 (1)	FW, EE, PW, NW, SL
	VAMNO 2 (1)	VAMNO 1 + OD, BI, PL, NH, SW
	VAMNO 3 (1)	VAMNO 2 + FH, BB, RH, NL, SH
	Geoskull (1)	NL, NW, NH, OD, OH, PL, PW, RH
	Additive Sequence (g^{AS}1-23 = 23)	SL+ SW, +SH, +NL, +NW, +NH, +PB, +FW, +BP, +IB, +AA, +AP, +RH, +PC, +OD, +IO, +EE, +BB, +FH, +PL, +PW, +ZL, +MH, +IW
RSV	Individual Measurements (33)	NL, NW, NH, FW, FH, OD, OW, OH, IW, ZL, ZW, ZH, PC, PL, PW, MW, MH, CW, CH, RH, PB, IB, NB, BB, BI, AA, BP, IO, EE, AP
	Orbital Region G-Mean Combos (g^{O}2.1-5.1 = 26)	FW, OD, OW, OH, IW in all non-repetitive g-mean combos of 2, 3 and 4 (plus all 5)
	Masticatory Region G-Mean Combos (g^{M}2.1-6.1 = 56)	PL, PW, MW, MH, CH, RH in all non-repetitive g-mean combos of 2, 3, 4 and 5 (plus all 6)
	Random Obital G-Mean Combos (g^{RO}2.1-28.12 = 168)	All measurements except OW, OH, Body Mass and Body Length used in 12 random combinations of 2, 4, 6, … up to 28
	Random Masticatory G-Mean Combos (g^{RM}2.1-28.12 = 168)	All measurements except CW, Body Mass and Body Length used in 12 random combinations of 2, 4, 6, … up to 28

Table 5.3 - Size variables used to evaluate orbital area and mandibular thickness. Terms in parentheses show the coding for each size variable group. For example, g^{O}2.1 represents the first orbital region g-mean combination in the series using 2 measurements, g^{O}3.2 represents the second orbital region g-mean combination using 3 measurements, and so on. The final number in parentheses is the total number of variables for that variable group.

measurements; skull length (prosthion-inion), skull width (bi-zygion), and maximum skull height, which were used independently as size variables. Next, three groups of measurements were taken to sample dimensions from different regions of the skull to calculate a geometric mean (g-mean) of skull size. These three groups are termed VAMNO (1, 2 and 3) for the acronym formed by the regions sampled (Visual, Auditory, Masticatory, Neural, and Overall size). VAMNO 1 uses one measurement from each region (for a total of five) to calculate a g-mean value for each specimen and focuses on measurements that can be taken on damaged and distorted skulls, such as fossils. VAMNO 2 adds a second measurement from each region, for a total of 10 in the g-mean calculation. The additional measurements were selected in an attempt to represent a dimension that has an orthogonal vector to the previous measurement from that region. VAMNO 3 adds a third dimensional measurement from each region (15 total).

The next series of GSVs consists of an additive sequence of measurements used to calculate a sequence of g-mean values where the first combination in the series uses two measurements, the second combination adds a third measurement to the calculation, and so on. This string of 24 measurements alternates between length, breadth, and height estimates and was selected in an order that attempts first to capture the overall size of the skull and then to incorporate increasingly finer detail. This group of 23 g-mean combinations is termed the "additive sequence". The last global size variable is called Geoskull and used an estimate of volume as a proxy for head mass. Volume was used to estimate mass because these two variables have been found to show an isometric relationship across most mammals (Jungers 1984). The name derives from the fact that it uses simple geometric shapes to represent the different components of the skull that

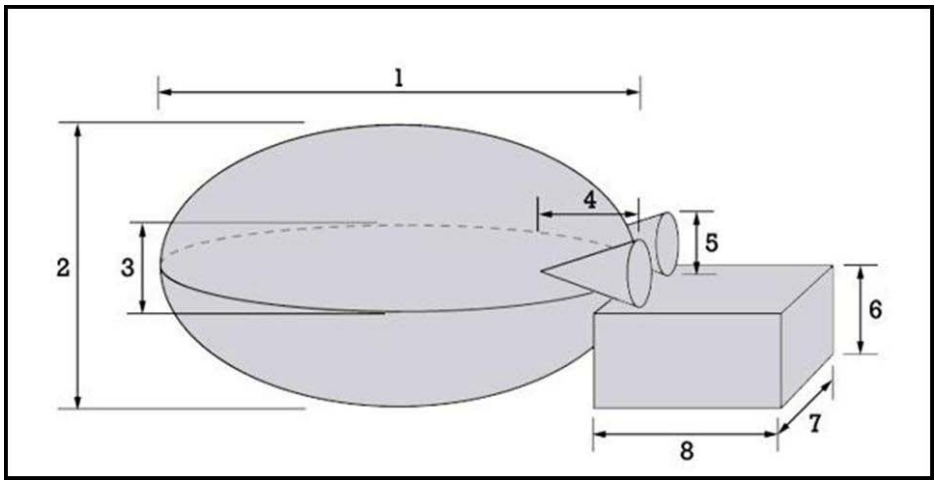

Figure 5.1 - Simple geometric representation of the main contributing components to the mass of the skull (termed Geoskull). Eight measurements were used to estimate total skull volume: 1 – neural length (NL); 2 – neural height (NH); 3 – neural width (NW); 4 – orb orbital depth (OD); 5 – orbital height (OH); 6 – mandibular ramus height (RH); 7 – palate width (PW); 8 – palate length (PL). Details as to exact volumetric calculation techniques given in text and more information on individual measurements given in Table 2.

appear to contribute the most to its total mass. The total volume is calculated by summing the volumes of an ellipsoid representing the neurocranium, two cones representing the orbits, and a rectangular prism representing the rostrum (Figure 5.1). The cube root of total volume was then used as a size variable.

The final category of scaling factors is termed regional size variables (**RSVs**), and includes all of the individual measurements (excluding the three used as GSVs and the trait being examined), as well as random and selected combinations to calculate g-means, which are then used as size variables. The random combinations for experiment 1 were constructed by generating random sequences of non-repeating numbers with values from one to 31 in combinations of 2, 4, 6, up to 28. Twelve sequences were generated for each combination for a total of 168 sequences. The random numbers were generated using the research randomizer form available online at www.randomizer.org. Each measurement

was then assigned a number (*e.g.*, prosthion-inion = 1), except orbital width and orbital height, so that the sequence of numbers was transformed into a sequence of measurements. These 168 sequences of measurements were then used as the variables in geometric mean combinations. This procedure was carried out again for experiment 2, except by generating random sequences of non-repeating numbers up to 32 and excluding only corpus width from the g-mean calculations. The final RSVs consist of measurements only from the region being investigated excluding the trait itself (because orbital area is a derivative variable, both orbital width and height were used). For example, experiment 1 used all five measurements from the orbital region and experiment 2 used six measurements from the masticatory region (excluding those from the temporal region). All non-repetitive combinations of these variables were used in geometric mean calculations, resulting in a total of 26 orbital RSV combinations and 56 masticatory combinations.

All of these size variables (USV, GSV, and RSV) were used to analyze the relative size and scaling relationships of orbital area and mandibular thickness. In the first simulation, the relative size of the orbits was analyzed by performing pair-wise independent samples T-tests between *Aotus* and all other New World monkeys, with the expectation that this nocturnal genus should show relatively larger orbits than the other genera. One concern with using all New World taxa in the comparison is that the distinction in relative orbit size between nocturnal and diurnal species becomes less clear when skull length exceeds 75 mm in mammals due to overlap in the respective distributions (Kay and Cartmill 1977). However, examination of the data used to define this relationship shows that *Aotus* has relatively enormous orbits, falling well above the

average distribution. Therefore, distinctions in orbit size should remain obvious between *Aotus* and other anthropoids at skull sizes larger than 75 mm (*Ateles* has the longest skull length in this sample with a generic average of 117 mm).

In the second simulation, the robusticity of the mandible was analyzed in three different comparisons, all based on the assumption that primates that feed primarily on hard or fibrous foods will have relatively thicker mandibles than ones that are mainly soft-fruit frugivorous. First, a comparison was made at the infraordinal level incorporating all of the specimens investigated in this study. The "robust" group (Table 4.1) consists of folivorous monkeys (*Alouatta*) and ones that consume seeds as at least 20% of their annual diet. The "non-robust" group consists of monkeys that are primarily soft-fruit frugivorous. Second, an inter-generic comparison was made within atelines between one of the most frugivorous New World primates (*Ateles*) and one of the most folivorous New World primates (*Alouatta*). Last, an intra-generic comparison was made between *Cebus apella* and *C. capucinus*. Previous research has revealed that *C. apella* has a relatively thicker mandibular corpus than *C. capucinus*, which is presumably related to the processing harder objects (seeds) in the diet of *C. apella* (Daegling 1992).

Next, scaling relationships were examined by comparing the coefficients of determination (r^2) between orbital area or mandibular thickness and all the scaling variables. Because there are hundreds of results to compare from each experiment, these results are presented in bivariate plots with the r^2 values plotted on the y-axis and the number of measurements used to calculate the size variable plotted on the x-axis. Different types of size variables are coded to aid in interpretation.

Group	Scaling Variable	Measurements	Genera
Individual	Total Body Length	Nose-to-Tail	Cal
	Facial Width	FW	Ceb, Cac, Chi
	Orbital Width	OW	Alo, Ate, Ceb, Pit, Chi, Cac, Lag
	Orbital Height	OH	Alo, Ate, Ceb, Pit, Chi, Cac, Lag
	Interorbital Width	IW	Ceb, Cac
	Corpus Height	MH	Sai
	Ramus Height	RH	Sag
	Zygomatic Width	ZW	Cal, Ctx
	Zygomatic Height	ZH	Ctx, Sag, Sai
	Post. Skull Length	IB	Lag, Pit
Random	$g^{RO}2.5$	CH, ZH	Ctx, Sag, Sai
	$g^{RO}2.9$	NW, AP	Chi
	$g^{RO}2.10$	MW, RH	Sai
	$g^{RO}4.2$	NL, FW, OD, AP	Chi, Lag
	$g^{RO}4.4$	OD, IB, BP, AP	Lag
	$g^{RO}4.6$	FW, FH, IW, CW	Sai
Orbital	$g^{O}2.1$	FW, IW	Cac, Ceb
	$g^{O}2.3$	FW, OH	Cac, Chi, Sag
	$g^{O}2.4$	OD, IW	Chi
	$g^{O}2.5$	OH, IW	Cac, Ceb
	$g^{O}2.6$	OD, OH	Sag
	$g^{O}2.7$	FW, OW	Ate, Cac, Ceb, Pit
	$g^{O}2.8$	OW, IW	Cac, Ceb
	$g^{O}2.10$	OW, OH	All except Lag
	$g^{O}3.1$	FW, OD, IW	Chi
	$g^{O}3.2$	OD, OH, IW	Chi
	$g^{O}3.4$	FW, OD, OH	Cac, Ceb
	$g^{O}3.5$	FW, OW, IW	Cac, Ceb
	$g^{O}3.7$	OD, OW, IW	Chi
	$g^{O}3.8$	FW, OW, OH	Cac, Chi
	$g^{O}3.9$	OW, OH, IW	Cac, Ceb
	$g^{O}4.1$	OD, OW, OH, IW	Chi
	$g^{O}4.3$	FW, OW, OH, IW	Cac, Ceb
	$g^{O}4.4$	FW, OD, OW, IW	Chi
	$g^{O}4.5$	FW, OD, OH, IW	Chi
	$g^{O}5.1$	FW, OD, OW, OH, IW	Chi

Table 5.4 - List of size variables from simulation 1 that did not produce significant differences in orbital area between nocturnal (*Aotus*) and diurnal taxa.

Results

Simulation1: Nocturnal vs. Diurnal

Table 5.4 presents a summary of the size variables that did not produce significant differences in O^{REL} between *Aotus* and the other platyrrhines. The first notable observation is that there does not appear to be a systematic bias in the results associated with the size of the taxa investigated. If non-significant differences were the result of overlap in the nocturnal and diurnal distributions at the top of the size range, then one would expect the larger genera to show a greater number of non-significant results. However, the two largest genera, *Ateles* and *Alouatta*, account for only seven of the 80 comparisons producing non-significant results. Also suggestive was the finding that the relationship between the number of non-significant comparisons and size (as measured by prosthion-inion length) for each genus is non-significant (Figure 5.2). Although these results do not appear to be related to size, there appears to be some phylogenetic influence on the results. Over half of the non-significant comparisons were concentrated in only three genera (*Cebus* = 13; *Chiropotes* = 16; *Cacajao* = 15), suggesting that these clades have either relatively larger orbits than most other platyrrhines (except *Aotus* in most cases) or that they share some other trait (*e.g.*, durophagy) that is influencing the analysis. Even when these three taxa are excluded from the comparison, there still appears to be an essentially flat relationship (no change) between skull size and number of non-significant results.

Considering USVs, body mass always proved to be an adequate size adjuster for orbital area, but in one comparison total body length was not able to sort nocturnal from the diurnal taxa (*Aotus* vs. *Callicebus*). All of the GSVs produced significant differences

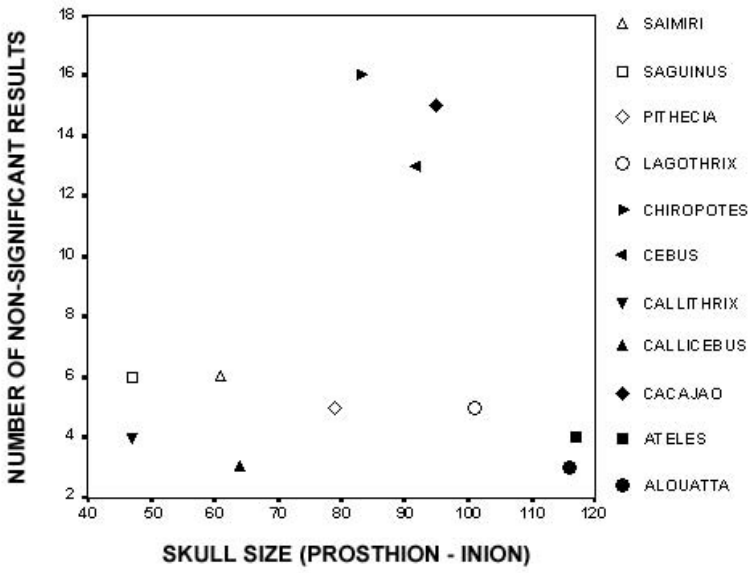

Figure 5.2 - Bivariate graph showing the number of non-significant results from experiment 1 plotted by skull size for each genus.

in O^{REL} regardless of combination or phylogenetic comparison. However, the RSVs did not perform as well, particularly for the orbital region g-mean combinations. In fact, 20 of the 26 orbital g-means produced results that suggested similarly sized orbits between *Aotus* and diurnal primates in at least one of the pair-wise comparisons. All six orbital g-means that consistently produced significant differences used orbital depth (OD) as one of the variables, even in the case ($g^{O}3.10$) where the other two variables were orbital width (OW) and orbital height (OH). When using individual measurements as the size variable, four of the five orbital region measurements did not always show *Aotus* to have relatively larger orbits with the exception of orbital depth. The other single measurements that were not successful at sorting primates with different activity cycles include corpus height (CH), ramus height (RH), zygomatic width (ZW), zygomatic height (ZH), and

posterior skull length (IB), four of which are related to the masticatory apparatus. The results of the random sequence g-mean combinations seem to be related to the number of measurements used and the relationship of the individual measurements themselves to orbital area. For example, all combinations that used six measurements or more produced significant differences in O^{REL} between *Aotus* and all other genera. However, three combinations using two measurements produced non-significant results and all contained a measurement that performed poorly when used individually as a size variable. This pattern is repeated in the three combinations using four measurements, and each one of these combinations also used a measurement from the orbital region.

Next, the coefficients of variation (CV) for the size ratios (O^{REL}) were compared (Figure 5.3A). The CV value represents the average CV for both groups from all of the pair-wise comparisons. In some cases, only the average for a group (*e.g.*, individual measurements) is presented, although individual standout values are still reported. Total body length had the highest coefficient of variation (CV = 8.88%), whereas the three VAMNO combinations produced the lowest (2.82-3.15%). Mass (6.49%) and the average for all the individual measurements (7.01%) also showed relatively high values. The three lowest CVs for the individual measurements are from the orbital region (OW = 2.13%; OH = 2.14%; FW = 2.94%). This is not surprising because all three of these variables are expected to strongly covary with orbital area. The individual measurements with the highest CVs include zygomatic width (ZW = 23.75%), zygomatic height (ZH = 17.38%), interorbital width (IW = 13.42%), posterior basicranial length (IO = 12.80%), corpus height (CH = 9.64%), and ramus height (RH = 9.47%). All of these variables except IO

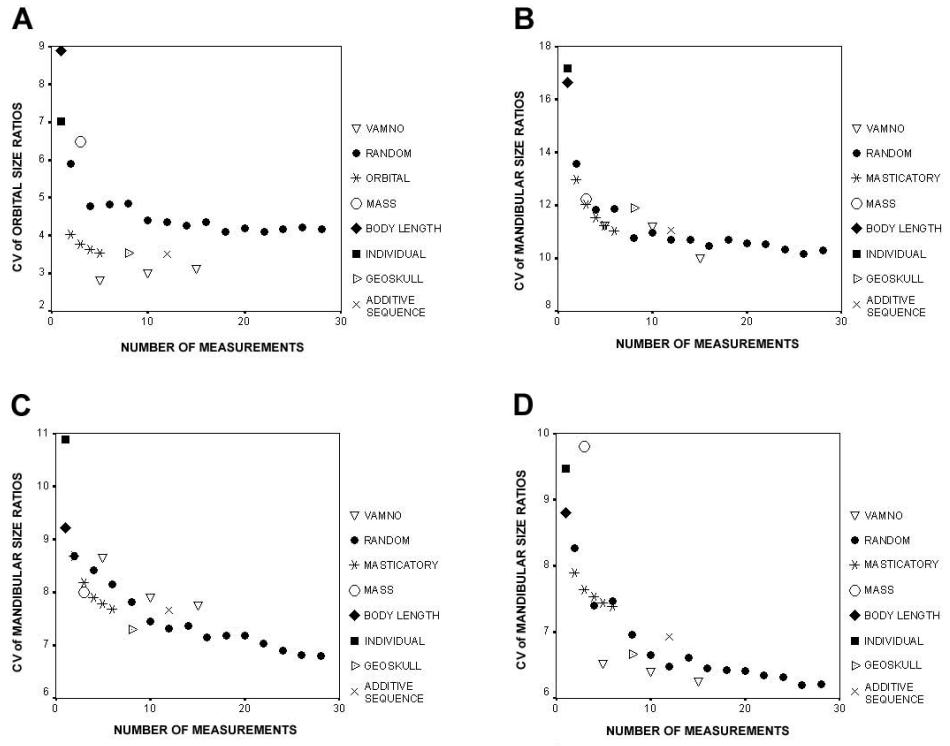

Figure 5.3 - Bivariate graphs plotting CV values of size ratios against the number of measurements used to calculate size variables. A – CV values for orbital size ratios from experiment 1 (nocturnal vs. diurnal). B – CV values for mandibular size ratios from experiment 2a (hard vs. soft object feeders, all platyrrhines). C – CV values for mandibular size ratios from experiment 2b (*Alouatta* vs. *Ateles*). D - CV values for mandibular size ratios from experiment 2c (*C. apella* vs. *C. capucinus*).

were among the individual measurements that resulted in non-significant differences in O^{REL} and are among the smallest measurements taken on each skull.

Figure 5.4A presents the results from the 269 different linear regression analyses that plotted orbital area against all the scaling variables used in simulation 1. This figure shows the number of measurements used to calculate the size variables on the x-axis against the r^2 values on the y-axis. The individual measurement size variables show the widest range of values with petrosal length (AP r^2 = .210) having the weakest

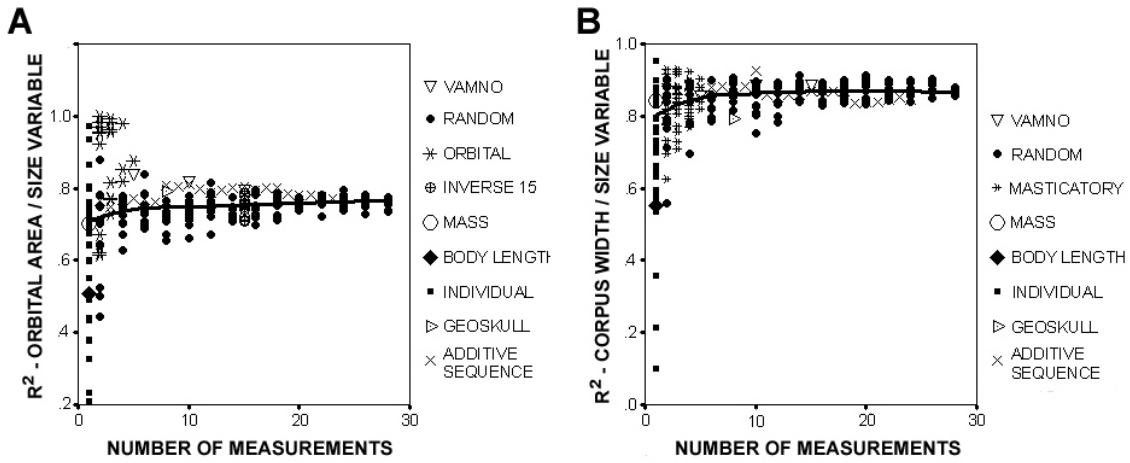

Figure 5.4 - Bivariate graphs showing number of measurements against coefficients of determination (r^2) from linear least squares regressions for all size variables. A – r^2 values from analyses regressing orbital area against all 269 size variables from experiment 1. B - r^2 values from analyses regressing mandibular corpus thickness against all 299 size variables from experiment 2. Best fit line based on lowess line fitting method.

relationship with orbital area while orbital region variables generally show the strongest relationship (OW r^2 = .973; OH r^2 = .972; FW r^2 = .936; OD r^2 = .867). Likewise, orbital region g-mean combinations show consistently high r^2 values ranging from .616 ($g^O2.4$ = $\sqrt{}$(OD * IW)) to .992 ($g^O3.8 = \sqrt[3]{}$(FW * OW * OH)). All of the GSVs show comparatively similar r^2 values ranging from .749 to .841, and these values are generally close to the best-fit line with the minor exceptions of VAMNO 1 and 2, which show slightly higher r^2 values compared with other GSVs. In fact, the additive sequence g-means follow the best-fit line almost perfectly.

The most evident pattern from this graph is the narrowing of values with increasing number of measurements. This narrowing appears to "level off" at around 14 measurements and the limited spread of r^2 values remains fairly constant up to 28 measurements. One possible explanation of this pattern is that as the number of

measurements increases, the g-means increasingly use similar combinations of variables resulting in the convergence of results. It is also possible that at a certain number of measurements, the relationships between the independent and dependent variables become relatively consistent regardless of the individual measurements used to produce the size variable. To help differentiate these possibilities, six new random g-mean combinations were generated with 15 measurements each. Next, the inverse of each of these combinations was calculated using the 15 unused measurements for each combination (orbital height, orbital width, and skull height were excluded to give a total pool of 30 measurements to sample from). These 12 combinations are termed "inverse 15" and are illustrated in Figure 5.4A. Both the "original" and their "inverse" combinations produce r^2 values that are within the narrow ranges produced by random combinations using 14 and 16 measurements. This supports the idea that the narrowing of r^2 values is not just the product of progressively sampling from the same pool of measurements.

Simulation 2A: Hard vs. Soft Object Feeders

Table 5.5 presents a summary of the size variables that did not produce significant differences in MC^{ROB} between the primates that feed on hard or fibrous objects and those that eat softer foods. Only six size variables proved to be ineffective at discriminating hard versus non-hard object feeders when comparing the entire platyrrhine sample. All of the ineffective variables were RSVs and include symphyseal width (MW), plus five combinations of masticatory region g-means. Symphyseal height (MH) is a common component to all five g-means, while symphyseal width (MW) is a component in three.

Group	Size Variable	Measurements	Comparison
Individual	Interorbital Width	IW	2b
	Symphyseal Width	MW	2a, 2b, 2c
	Symphyseal Height	MH	2b
	Corpus Height	CH	2c
	Zygomatic Width	ZW	2b, 2c
Random	$g^{RM}2.6$	OD, ZW	2c
	$g^{RM}2.7$	SW, RH	2b
	$g^{RM}2.8$	ZW, BB	2c
Masticatory	$g^{M}2.3$	PL, MH	2a
	$g^{M}2.8$	MW, MH	2a, 2b
	$g^{M}2.9$	MW, CH	2c
	$g^{M}2.13$	MW, RH	2c
	$g^{M}2.14$	MH, RH	2a, 2c
	$g^{M}2.15$	CH, RH	2b, 2c
	$g^{M}3.4$	PL, MW, MH	2a
	$g^{M}3.10$	MW, MH, CH	2c
	$g^{M}3.11$	PL, PW, RH	2b
	$g^{M}3.12$	PL, MW, RH	2b
	$g^{M}3.14$	PL, CH, RH	2b
	$g^{M}3.15$	PW, MW, RH	2b, 2c
	$g^{M}3.17$	PW, CH, RH	2b, 2c
	$g^{M}3.18$	MW, MH, RH	2a, 2c
	$g^{M}3.19$	MW, CH, RH	2b, 2c
	$g^{M}3.20$	MH, CH, RH	2b, 2c
	$g^{M}4.3$	PL, PW, MW, RH	2b
	$g^{M}4.5$	PW, MW, MH, RH	2b
	$g^{M}4.6$	MW, MH, CH, RH	2b, 2c
	$g^{M}4.7$	PW, MH, CH, RH	2b
	$g^{M}4.8$	PL, MH, CH, RH	2b
	$g^{M}4.10$	PL, MW, MH, RH	2b
	$g^{M}4.11$	PW, MW, CH, RH	2b, 2c
	$g^{M}4.13$	PL, PW, CH, RH	2b
	$g^{M}4.14$	PL, MW, CH, RH	2b, 2c
	$g^{M}5.2$	PW, MW, MH, CH, RH	2b
	$g^{M}5.3$	PL, MW, MH, CH, RH	2b
	$g^{M}5.4$	PL, PW, MH, CH, RH	2b
	$g^{M}5.5$	PL, PW, MW, CH, RH	2b
	$g^{M}5.6$	PL, PW, MW, MH, RH	2b
	$g^{M}6.1$	PL, PW, MW, MH, CH, RH	2b

Table 5.5 - List of size variables from simulation 2 that were non-significant.

The average CVs of the size ratios for each group of scaling variables are presented in Figure 5.3B. The average for all the individual measurement CVs proved to be the highest (16.36%) followed closely by total body length (16.63%), whereas VAMNO 3 produced the lowest CV (10.05%). The CV values for all the other groups generally fell between 10.5% and 12%, except the slightly lower values produced by the random g-mean combinations that used a larger number of measurements (≥ 16). The values for the individual measurements producing the lowest CVs include skull width (SW = 10.60%), symphyseal height (MH = 10.76%), symphyseal width (MW = 11.15%), skull length (SL = 11.43%), and interaural distance (EE = 11.56%). Those with the highest values include petrosal length (AP = 35.76%), zygomatic arch width (ZW = 26.43%), ramus height (RH = 25.52%), zygomatic arch height (ZH = 24.90%), and interorbital width (IW = 24.03%). In this comparison, no clear relationship is apparent linking CV values with the ability to classify hard versus soft object feeders, although this may be influenced by the low number of non-significant results.

Simulation 2B: *Alouatta* vs. *Ateles*

Comparing folivores with frugivores, numerous RSVs resulted in non-significant differences in relative corpus width (MC^{ROB}) between *Alouatta* and *Ateles*. Four of these were individual measurements and included interorbital width (IW), symphyseal width (MW), symphyseal height (MH), and zygomatic arch width (ZW). In addition, one random combination g-mean produced non-significant results ($g^{RM}2.7$). Among masticatory region g-means, 23 of the 56 combinations were ineffective as a relative size adjuster. The most common measurement used in the g-mean combinations was ramus

height (23 combinations), followed by corpus height (16), symphyseal width (15), palate width (13), palate length (12), and symphyseal height (12). The only five-measurement masticatory region g-mean that produced significant differences in MC^{ROB} was $g^{M}5.1$, which did not include ramus height in its calculation.

The CV values for each group of scaling variables used in the *Alouatta* vs. *Ateles* comparison are presented in Figure 5.3C. Once again the average for the individual measurements had the highest CV values (10.89%). The five measurements with the lowest values were skull length (SL = 7.87%), anterior skull length (PB = 8.15%), palate length (PL = 8.48%), skull width (SW = 8.50%), and anterior basicranial length (BP = 8.61%), whereas the five with the highest values were zygomatic width (ZW = 22.68%), zygomatic height (ZH = 20.04%), interorbital width (IW = 15.93%), ramus height (RH = 13.67%), and posterior basicranial length (IO = 13.60%). Two of these variables with the highest CVs (ZW and IW) also produced non-significant results when used individually as a size variable. The lowest CV values were produced by the group of random g-means using 28 measurements. Among the purposefully constructed scaling variables, geoskull had the lowest CV value (7.30%). In this comparison, the VAMNO g-means showed values that were in the middle of the range, although the values decease with increasing numbers of variables (VAMNO 1 = 8.65%, VAMNO 2 = 7.91%, and VAMNO 3 = 7.77%). A similar pattern is apparent in the masticatory region g-means, with decreasing values ranging from 8.68% – 7.68%.

Simulation 2C: *C. apella* vs. *C. capucinus*

As in the previous masticatory comparisons, all USVs and GSVs produced significant differences in relative mandibular corpus width (MC^{ROB}) between *C. apella* and *C. capucinus*. However, numerous RSVs were not successful at finding differences in MC^{ROB}. Three individual measurements produced non-significant results and all were related to the masticatory apparatus: symphyseal width, corpus height, and zygomatic width. Zygomatic width was also a component of both of the random g-mean sequences that produced non-significant results. Overall, 14 of the 56 mandibular region g-means suggested no difference in corpus thickness. Of the six variables used to create these g-means, ramus height was the most common measurement (12 combinations), followed by symphyseal breadth (10) and corpus height (9). Palate length (2) and width (3) as well as symphyseal height (5) appeared less often in the combinations producing non-significant results.

The CV values for the *C. apella* vs. *C. capucinus* comparison are presented in Figure 5.3D. In this comparison, body mass has the highest value (9.80%), followed by the average for the individual measurements (9.46%). The measurements with the highest values are zygomatic arch width (ZW = 22.47%), posterior skull length (IB = 17.04%), zygomatic arch height (ZH = 15.95%), anterior cranial length (NB = 15.26%), and interorbital width (IW = 12.20%). The measurements that resulted in the lowest CV values are skull length (SL = 6.23%), neural length (NL = 6.38%), palate width (PW = 6.72%), interaural distance (EE = 6.85%), and skull height (SH = 7.10%). The variable with the lowest value is the average for the random g-means using 26 measurements (6.20%) followed closely by VAMNO 3 (6.27%). In fact all three VAMNO combinations

and geoskull produced relatively low CVs. A fact not obvious from Figure 5.3D is that the lowest and highest CV values for the additive sequence are $g^{AS}4$ (6.31%) and $g^{AS}5$ (9.15%), with the only difference between these two combinations being the addition of neural width (NW) to the g-mean calculation in $g^{AS}5$.

Figure 5.4B shows the results from the 299 different linear regression analyses plotting mandibular corpus width against the scaling variables used in experiment 2. Overall, these results share several similarities with the results from experiment 1. Again, the individual measurements show the widest range of r^2 values with posterior skull length (IB r^2 = .102), petrosal length (AP r^2 = .215), and interorbital width (IW r^2 = .358) showing the lowest values but with skull width (SW r^2 = .952), symphyseal height (MH r^2 = .899), and symphyseal width (MW r^2 = .869) showing the highest values. The narrowing of values with increasing number of measurements up to approximately 14 is also similar to the pattern illustrated in Figure 5.4A. Mass and the majority of GSVs show a fairly narrow range of r^2 values with a range between .757 and .891, close to the best-fit line. Unlike experiment 1 however, the RSVs close to the trait of interest (masticatory region g-means) are not as separated from the average spread of values. The r^2 values for the majority of the size variables are higher in this experiment than in the orbital comparison and suggest that the masticatory apparatus has a disproportionately strong influence on many aspects of primate skull shape. Despite the fact that many of the variables show a strong relationship with corpus width, masticatory region g-means still produced the highest r^2 values of any size variable category.

Discussion

Overall, many of the size variables performed perfectly at sorting biomechanically defined groups of New World monkeys. GSVs always produced the predicted differences and, in all cases except one, the USVs worked adequately as size variables as well. In contrast, numerous RSVs failed to produce the results predicted by *a priori* expectations in both the orbital and masticatory comparisons. Several interesting patterns are revealed by both the non-significant and significant results from these comparisons, and these help provide a basic framework for understanding and using various types of size variables.

The most widespread characteristic shared by many of the unsuccessful RSVs was their relative topographic position. In particular, the size variables that were anatomically close to the trait of interest (Ex. 1 - orbital region and Ex. 2 - masticatory region) dominated the lists of ineffective size variables (Tables 5.4 and 5.5). These include individual measurements, local g-mean combinations, and random g-mean combinations that included measurements from the region being investigated. One interpretation of this pattern is that measurements that are spatially close to the variable of interest may be functionally or pleiotropically linked to that variable, thereby showing a strong tendency to covary with it. Martin has proposed that when two variables are strongly dependent, one variable will be less effective in determining the relative size of the other (1983, 1985). This situation begins to approach the condition of dividing a trait by itself (or a multiple). This phenomenon is illustrated by the finding that single measurements and combinations from the orbital region show the strongest relationship with orbital area (Figure 4.4A) and the measurements and combinations related to the

masticatory apparatus show the strongest relationship with mandibular corpus width (Figure 5.4B).

One additional point further underscores the pattern that strongly covarying structures are of doubtful utility when used as size variables. Although the pitheciins (*Cacajao*, *Chiropotes* and *Pithecia*) are classified here as "hard object" feeders because of the high percentage of seeds and nuts in their diet, this dietary category may be somewhat of an oversimplification. Kinzey and Norconk (1990) have classified all three pitheciin genera as sclerocarpic foragers, characterized by the mastication of relatively soft and pliable seeds by the posterior dentition after a fruit's hard pericarp (*e.g.*, Manilkara fruit) has been opened with the anterior dentition. Furthermore, Martin *et al*. (2003) found the pithecines to have relatively thin-enameled molars and stated that the posterior dentition is specialized for the mastication of pliable and soft seeds rather than hard food items. Yet, despite the evidence that the posterior teeth do not show signs of morphological specializations for durophagy (*i.e.*, thick enamel), this group still appears to have a robust mandibular corpus (Figure 5.5). The robusticity of the corpus may not be due to the stresses induced by the posterior dentition but instead to the stresses produced by the anterior dentition (possibly to prevent a weak link between the hard object processing teeth and the ramus). Regardless of exactly why the mandibular corpus is robust in this group, corpus thickness showed a strong relationship with symphyseal width ($r^2 = .869$), and symphyseal width proved to be an ineffective size variable in each of the three mastication comparisons.

These findings strongly support the conclusion reached by Smith in a study examining categories of allometry in masticatory studies where he stated, "The general

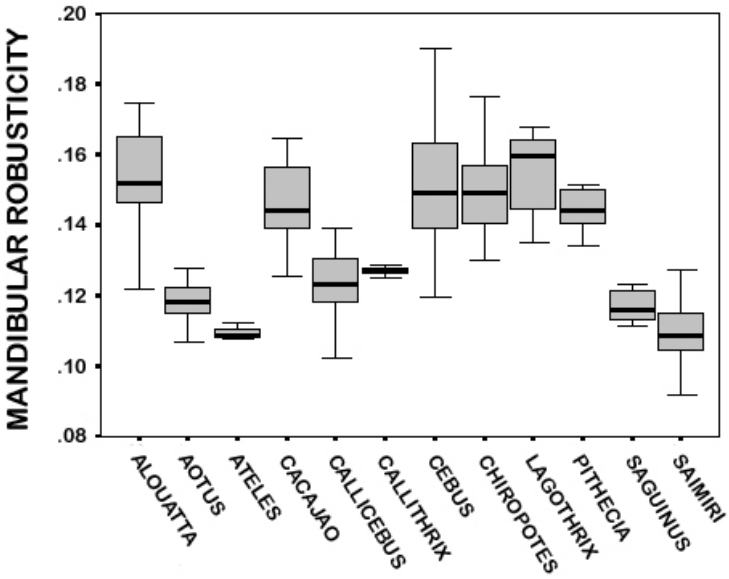

Figure 5.5 - Mandibular robosticity for each genus calculated using VAMNO 2 as the size variable in the MC^{ROB} size ratio (described in text).

principle is to avoid a size measure that might function as part of a covarying system with the dependent variable, but instead use a functionally and anatomically remote feature that is strongly related to body size", (1993:180). However, apparently not all variables that are "anatomically remote" work equally well as size variables, and by further examining the ones that produced non-significant results it may be possible to extend this general principle. The ineffective remote variables include total body length, posterior skull length (IB), corpus height (CH), ramus height (RH), zygomatic width (ZW), zygomatic height (ZH), $g^{RO}2.5$, $g^{RO}2.9$, and $g^{RO}2.10$ for the orbital comparison and interorbital width (IW) for the masticatory comparison. The majority of these variables share the property of resulting in high CV values when used as a size variable. All other things being equal, higher amounts of variation will reduce the statistical power of a

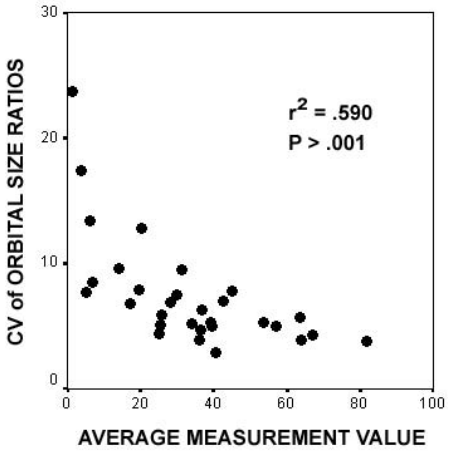

Figure 5.6 - CV values of orbital size ratios derived using individual measurements plotted against the average value (for all specimens) for the individual measurements themselves. A significant negative relationship was observed using quadratic least squares regression ($r^2 = .590$; $p < .001$).

comparison and require considerable differences between means in order to establish statistical significance. Many of these variables (excluding body length) also represent the smallest measurements taken on each skull suggesting that there may be a relationship between measurement size and the CV value of the size ratio. This is supported by the finding that when the mean values of the individual measurements were regressed against the orbital comparison size ratio CV values, a significant negative relationship was detected (Figure 5.6; $p < 0.001$; $r^2 = 0.590$). A possible explanation for this finding may be that larger measurements are less influenced by measurement error, particularly when the smaller measurements are close to the significant digit (*i.e.,* >10.0 in this study). In addition, larger measurements generally have a wider range of absolute values than smaller measurements, giving them the potential to more precisely track differences in size. For example, the range of values for interorbital width (IW) in *Aotus*

is 4.5 - 7.5 mm while the range for skull length (SL) is 59.2 – 67.5, a range greater than 5.0 mm.

The finding that GSVs always produced significant results may be explained partially by the two principles just outlined. That is, anatomically remote and larger measurements generally perform well as size variables. GSVs rarely use small measurements or ones close to the region of interest and when they do, it is always part of a g-mean combination using 5 or more measurements (*e.g.*, VAMNO). The general coalescence of values illustrated in Figures 4.4A and 4.4B suggest that beyond a certain number of measurements (certainly by 12 to 14), individual measurements have little impact on the relationship between the size variable and the trait of interest. Therefore, a size variable using a relatively large number of measurements appears to have the ability to dilute the negative impacts imposed by covarying structures or relatively small measurements. Furthermore, using more measurements seems to increase statistical power by reducing the variance as suggested by the finding that CV values generally decrease with an increasing number of measurements (Figure 5.3A-D). Also of interest was the observation from experiment 2C that there was a relatively large increase in CV value when the additive sequence went from four to five measurements. This provides evidence that g-mean combinations with five or fewer measurements have still not reached the potential to dilute problematic variables, at least in this particular case. Last of all, it may be possible to compare the results in a general way from different studies as suggested by the stability of the relationship (r^2) between that dependent and independent variables at higher numbers of measurements. The "inverse 15" g-mean combinations (Figure 4.4A) are particularly illuminating in this regard, showing that two groups of 15

completely different measurements have similar relationships with the independent variable. VAMNO 3 is well-constructed to take advantage of all of these principles (15 medium-to-large measurements taken from multiple regions of the skull) and had among the lowest CV value in every comparison as well as an r^2 value that fell within the "convergence zone".

In certain instances, it may not be possible to collect an extensive swath of measurements due to the fragmentary or incomplete condition of the material (*e.g.*, Kirk and Kay 2004). In such cases, the measurements used to calculate the size variable must be carefully selected. If some dimensions of overall size are still preserved (such as in a dorso-ventrally distorted fossil), selecting one or several broad measurements would appear to perform adequately based on the comparisons presented here. For example, the three individual measurement GSVs (SL, SW, and SH) were always successful at sorting groups, and furthermore, skull length and skull width consistently showed low CV values, although rarely lower than those produced by the VAMNO g-means (*e.g.*, Exp. 1 – SL = 3.79%, SW = 5.35%, VAMNO 3 = 3.15%; Exp. 2a – SL = 11.43%, SW = 10.60%, VAMNO 3 = 10.05%). Still, it must be kept in mind that measures such as skull length will be influenced strongly by rostral length and therefore this trait has the potential to incorporate a strong functional signal in taxonomic groups with particular dietary specializations. For example, although New World monkeys are not characterized by extreme rostral elongation, certain Old World monkeys (*e.g.*, papionin cercopithecines) do exhibit relatively long snouts which may reduce the usefulness of skull length as a size variable essentially free of functional signals. The same argument

does not necessarily apply to skull width, suggesting it may be among the most useful single-measurement size variables.

If only a region of the specimen is preserved (*e.g.*, the face, a tooth), it may not be possible to use any broad multi-region measurements. In this case, it seems that the safest strategy would be to select a relatively high number of non-redundant measurements, taking care not to sample too many relatively small variables or ones that are potentially linked to the trait being evaluated. This basic principle has been used to reject a number of size variables that were used in studies of enamel thickness. Specifically, Martin (1985) and Grine (2002) argued that using overall crown dimensions to scale enamel thickness is to be avoided because crown dimensions incorporate a component of enamel thickness in their measurements. In relation to scaling orbital area in fragmented specimens, orbital depth consistently worked well as a size variable, singly and with other measurements.

Summary

The primary goal of this study was to identify and supplement general principles related to selecting morphological measurements to be used as proxies for skull size. Although caution must be applied when extending these principles beyond the specific group for which they were developed, several common trends were observed, regardless of the biomechanical or phylogenetic comparison, suggesting their general applicability to a wide range of questions and taxonomic groups. When the material is moderately complete, three general principles can be applied which appear to produce consistent and statistically powerful results:

● Avoid using measurements that covary strongly or are functionally linked to the trait being investigated by sampling anatomically remote regions of the skull;

● Larger measurements often produce a size ratio with a lower coefficient of variation than smaller measurements (relative to the significant digit of measurement), increasing statistical power; and

● Use a relatively high number of measurements (≥12) to calculate a geometric mean of skull size in order to dilute individual measurements that may confound the analysis.

In this analysis, the size variables in the GSV category generally followed these principles and always produced the expected results when used in functional comparisons. In particular, the VAMNO g-mean combinations performed quite well and used numerous, relatively large measurements from various skull regions. When the preservation of the material precludes gathering measurements from the entire skull, the following amendments may be useful:

● If only one (or a few) measurements is (are) used, broad dimensions that span more than one anatomical region are most desirable (*e.g.*, basicranial width);

● If measurements are only available from the region being investigated, collect as many non-redundant measurements as possible, minimizing ones that are patently functionally linked with the specific trait of interest (*e.g.*, mandibular measures when evaluating mandibular robusticity).

Based upon these findings, a VAMNO combination will be used as a size variable in latter chapters to investigate auditory structures in taxa of different sizes. Fourteen measurements will be used in total including three from the visual system region (orbital

height, orbital depth, and facial width), two from the auditory region (petrosal length and interaural distance), three from the masticatory region (palate length, palate width, and ramus height), three from neural region (neurocranial height, neurocranial length, and neurocranial width), and three overall measurements (skull length, skull width, and facial height).

CHAPTER 6

Introduction

One of the final steps necessary before analyzing the functional relationships of the primate auditory system is to investigate the variability of individual structures at different analytical levels. The main goal was to determine the degree to which subgroups of data could be pooled in order to increase sample sizes and potentially eliminate problems associated with taxonomic uncertainty. Moreover, examining the amount of variation in morphology is an interesting evolutionary question in-and-of itself. In the words of Ernst Mayer "The availability of variation is the indispensable prerequisite of evolution and the study of the nature of variation is therefore a most important part of the study of evolution" (2001:88). The focus of this chapter will be on examining ontogenetic, sexual, and phylogenetic differences in auditory morphology as well as head and body size in a select sample of primate taxa.

Materials and Methods

Two genera that warrant particular attention in regard to taxonomic ambiguity are owl moneys and squirrel monkeys since both of these genera had their hearing sensitivity tested before they were split up into multiple species in 1983 and 1984, respectively

(Hershkovitz 1984; Costello *et al*. 1993). No information was published on the original geographic location of the test subjects so their exact species identification remains unclear. In addition, data on ontogenetic, sexual, and/or intra-generic variation has been collected on six other New World monkey genera (*Alouatta*, *Ateles*, *Cacajao*. *Callithrix*, *Cebus*, and *Pithecia*), one Old World monkey (*Macaca*), three lemuroids (*Eulemur*, *Lemur*, *Varecia*), and two lorisoids (*Galago* and *Perodicticus*). These genera represent a broad taxonomic sample with a wide range of sizes and display varying amounts of both intra-specific and intra-generic sexual dimorphism (Smith and Jungers 1997).

Sexual identification and body mass data were gathered from the field notes compiled by the original collectors, as well as skin and skeletal labels associated with the specimens. Species identification was based on updated taxonomic revisions and, in the case of *Aotus* and *Saimiri*, verified using locality information. Specimens were excluded if their species designation was unclear. Skull size was determined by taking the geometric mean of fourteen skull measurements as defined in Chapter V. The ontogenetic age of individuals was arbitrarily defined into three broad categories using dental eruption patterns: **age-class 1** was defined as specimens demonstrating the eruption of all permanent teeth; **age-class 2** as specimens with some but not all post-canine dentition erupted, and **age-class 3** as specimens with no evidence of permanent post-canine eruption. Specimens in class 3 were also visibly smaller in overall size and lacked full or partial fusion of most cranial sutures. These assessments were made on digital photographs of the maxillary dentition taken on each specimen.

The morphometric parameters to be compared include the surface area of the tympanic membrane (modeled as a disk) and the mallear and incudal lever arm lengths

and masses. The tympanic membrane is of interest since very little data are available relating to the growth of the tympanic ring (and tympanic membrane) or differences in the size of adult forms in primates. However, Khanna and Tonndorf (1969) found the area of the tympanic membrane to show a strong correlation with body weight in a sample of mammals ranging from mice to elephants. Correlations have also been found between tympanic membrane area and body mass ($r = 0.83$, $p < 0.01$) within different breeds of dogs (Heffner 1983). Because the ossicles are formed in perichondral bone, and consequently lack epiphyseal growth centers, Hershkovitz stated that they are fully ossified and adult in size at all post-natal stages (1977). Still, this does not preclude them from remodeling and potentially adding mass or density throughout ontogeny. It has also been noted that the malleus shows considerable morphological variation reflective of assorted taxonomic relationships (Segall 1943, 1947; Hershkovitz 1977) and this could have implications on both lever arm length and mass. What's more, the sizes of the auditory ossicles generally scale with negative allometry against both body size (Rosowski 1994) and head size (Herskovitz 1977; Nummela 1997) across mammals. All of these allometric relationships could result in significant differences within species that have high levels of sexual dimorphism or within genera that show a wide range in body size between species.

In most cases, only a few specimens were available from the subadult categories 2 and 3, thereby preventing statistical evaluation of the ontogenetic data. In order to investigate possible trends, the data will be presented visually as box-plots and comments made comparing means, inter-quartile and total ranges. For the sexual dimorphism and intra-generic investigations, analysis of variance (ANOVA) was used for comparisons

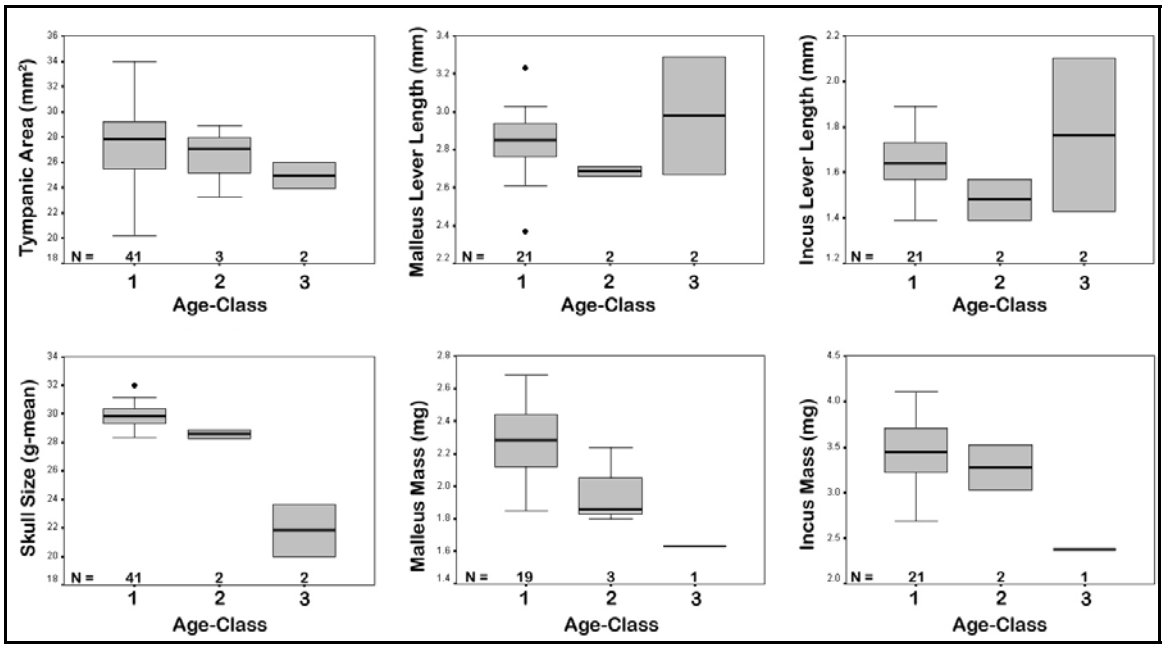

Figure 6.1 – Box-plots of ontogenetic comparisons for *Aotus azarae*. Age-class 1 is the oldest group and age-class 3 is the youngest group: see text for further details.

where the sample sizes were 10 or greater or using nonparametric statistics for smaller sample sizes. All data[35] used in parametric statistical comparisons were log-transformed due to the finding that the variables often illustrated considerable skewness and kurtosis.

Results: ANTHROPOIDS

Aotus

The small sample sizes of age-class 2 and 3 specimens preclude statistical evaluation in *Aotus*, but there are several age-related trends in certain parameters that are suggestive of ontogenetic differences. Figure 6.1 shows box-plots of the auditory variables and skull size in *A. azarae* for each age-class. There appears to be a progressive increase in tympanic membrane size going from age-class 3 to 1, although there is still

[35] All mass and area data were transformed (*e.g.*, cube root) to be comparable to linear measurements.

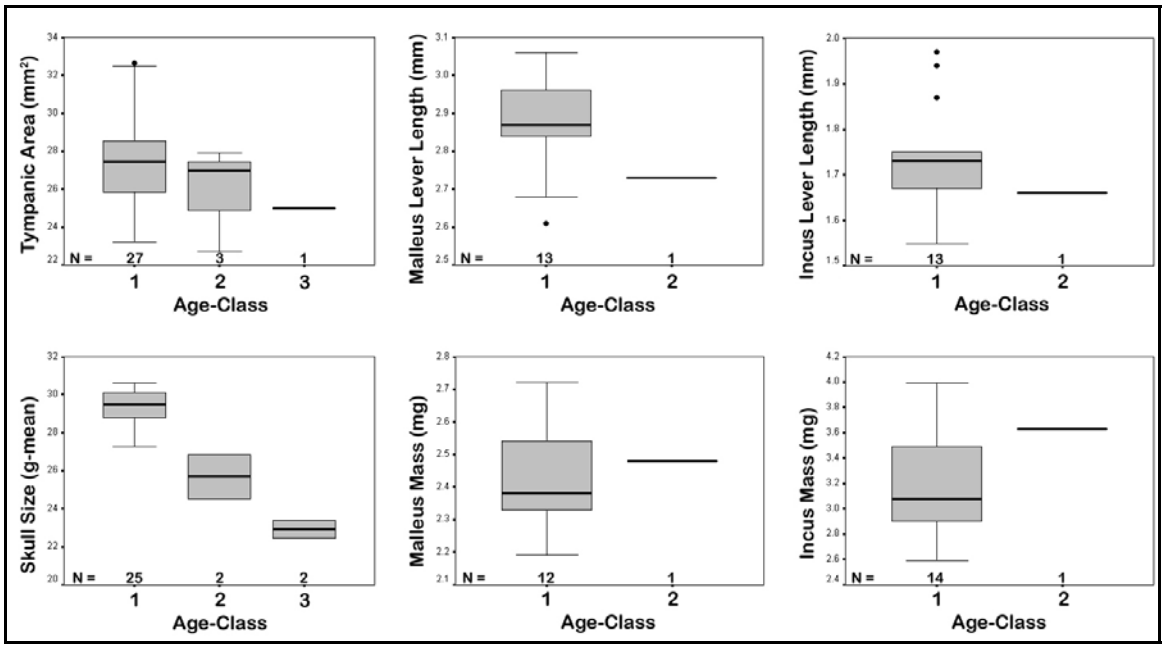

Figure 6.2 – Box-plots of ontogenetic comparisons for *Aotus nancymae*.

overlap in the inter-quartile ranges of these groups. The difference between means for age-class 1 and 3 amounts to around 2.3 mm^2 (4.5%). Lever arm length does not evince a clear ontogenetic pattern, although the means for the specimens in age-class 3 (n = 2 for both the malleus and incus) are actually the highest of any age-class. The strongest trends in auditory measures were found in ossicular mass. There was no overlap in inter-quartile ranges between age-classes 1 and 2 (although there is overlap in the total ranges) and the single specimen in class 3 is completely outside the ranges of the other two groups. Skull size is much smaller in age-class 3 specimens and age-class 2 specimens are slightly smaller than those from age-class 1.

The box-plots for *A. nancymae* are presented in Figure 6.2. The tympanic ring shows a similar trend as in *A. azarae* but again the differences are relatively small (~2.5 mm^2 – 4.9%). There are no age-class 3 representatives for the other auditory variables but

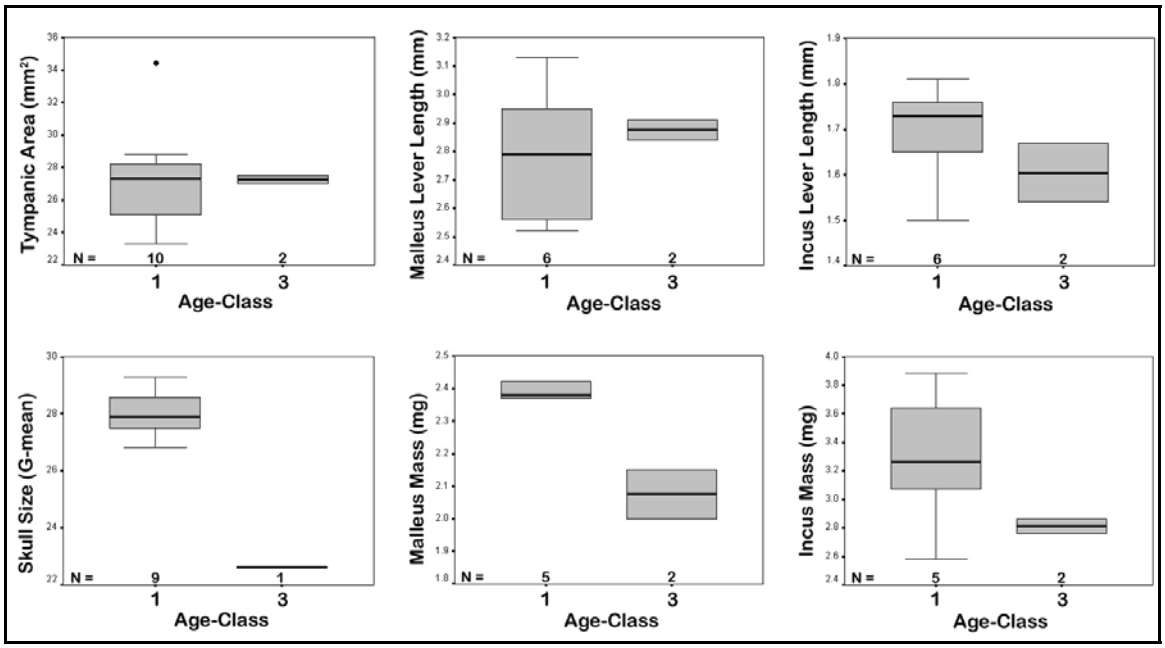

Figure 6.3 – Box-plots of ontogenetic comparisons for *Aotus vociferans*.

the values for the single age-class 2 individual are below the inter-quartile ranges for both mallear and incudal lever arm lengths although still within the overall ranges. Unexpectedly, ossicular mass for this age-class 2 individual is actually above the average for the age-class 1 specimens. The differentiation in skull size between groups is quite evident.

There are no age-class 2 or 3 specimens for *A. trivirgatus*, but *A. vociferans* has three individuals in the age-class 3 category (Figure 6.3). Unlike the previous *Aotus* comparisons there is no ontogenetic pattern in tympanic membrane size. The mean for incudal lever arm length in age-class 3 is lower than that in age-class 1 but there is considerable overlap in the inter-quartile ranges. The strongest trends are evident in the ossicular mass data where there is a clear separation between the means and inter-quartile ranges for both bones between the adult and sub-adult groups. The g-mean of skull size is

Species	Sex		A_{tm}	LA_m	LA_i	M_m	M_i	SS	M_b
A. azarae	Female	Mean	26.89	2.88	1.66	2.29	3.43	29.70	1147.64
		N	23	14	14	12	13	24	7
		SD	3.86	0.15	0.13	0.26	0.35	0.77	190.68
	Male	Mean	27.84	2.75	1.63	2.25	3.50	30.02	1136.25
		N	17	7	7	7	8	16	8
		SD	2.20	0.21	0.17	0.16	0.30	0.89	204.64
A. nancymae	Female	Mean	27.40	2.87	1.75	2.47	3.29	29.37	916.67
		N	13	6	6	6	7	11	9
		SD	2.44	0.12	0.12	0.18	0.36	0.68	109.20
	Male	Mean	27.39	2.88	1.70	2.41	3.07	29.19	803.00
		N	10	5	5	5	5	9	5
		SD	2.21	0.18	0.12	0.14	0.54	1.18	245.91
A. trivirgatus	Female	Mean	28.58	2.87	1.56	2.28	3.13	28.76	
		N	6	3	3	2	2	6	
		SD	3.12	0.21	0.08	0.09	0.04	1.03	
	Male	Mean	29.12	3.30	1.66	2.52	3.05	29.09	
		N	6	1	1	2	3	7	
		SD	2.35			0.07	0.66	0.64	
A. vociferans	Female	Mean	27.72	2.68	1.68	2.15	2.82	27.46	
		N	6	3	3	2	2	5	
		SD	3.49	0.24	0.16	0.37	0.34	0.55	
	Male	Mean	26.78	2.94	1.71	2.40	3.57	28.91	
		N	3	2	2	2	2	2	
		SD	3.00	0.27	0.08	0.03	0.44	0.49	

Table 6.1 – Adult male and female species means for *Aotus*. A_{tm} = tympanic membrane area, LA_m = mallear lever arm length, LA_i = incudal lever arm length, M_m= mallear mass, M_i = incudal mass, SS = g-mean of skull size, M_b = body mass.

also much smaller in the age-class 3 specimen than in the adults. These comparisons suggest that age-related differences in skull size and/or body mass appear to affect ossicular mass although the effects on tympanic membrane size and ossicular lever arm length are not evident. To take a conservative approach, the sub-adult specimens will be excluded from the *Aotus* comparisons of sexual dimorphism and inter-species differences.

Table 6.1 presents the male and female species means and standard deviations for all variables excluding sub-adults. No significant differences were detected in sexual dimorphism for any of the auditory variables in any species of *Aotus*. The only species

that showed hints of sexual dimorphism in overall size was *A. vociferans* with males having skulls that are just over 5% larger than that of females. However, this difference was not significant ($p < 0.10$) by traditional standards, although a larger sample size could prove this difference to be real. When the species were compared after pooling males and females, no significant differences were detected in any of the auditory variables. Therefore, the auditory data for all species of *Aotus* will be pooled for subsequent analyses in the following chapters. Body mass data were available for *A.azarae* and *A. nancymae* specimens and *A. azarae* was found to be significantly heavier ($p \leq 0.001$), agreeing with previous body mass estimates (Smith and Jungers 1997). Differences were also detected in skull size and Bonferroni post-hoc comparisons revealed that *A. azarae* is significantly ($p < 0.01$) larger than *A. trivirgatus* (4%) and *A. vociferans* (7%), and *A. nancymae* is significantly ($p < 0.01$) larger than *A. vociferans* (5%). However, these differences in skull size are relatively slight and not associated with significant differences in auditory parameters. The fact that *A. azarae* is about 9% larger in body mass than *A. nancymae* yet only 2% larger in skull size suggests that head and body size are not tightly linked in this genus. In addition, even relatively large differences in body mass did not result in significant differences in auditory structures.

Saimiri

The *Saimiri* ontogenetic comparison consists of only age-class 1 and 2 specimens and again the sample sizes for age-class 2 are small. Still, the patterns are suggestive of age-related effects on the size of certain auditory structures. Figure 6.4 shows the box-plots for *S. boliviensis* for both age-classes. The means for tympanic membrane area are

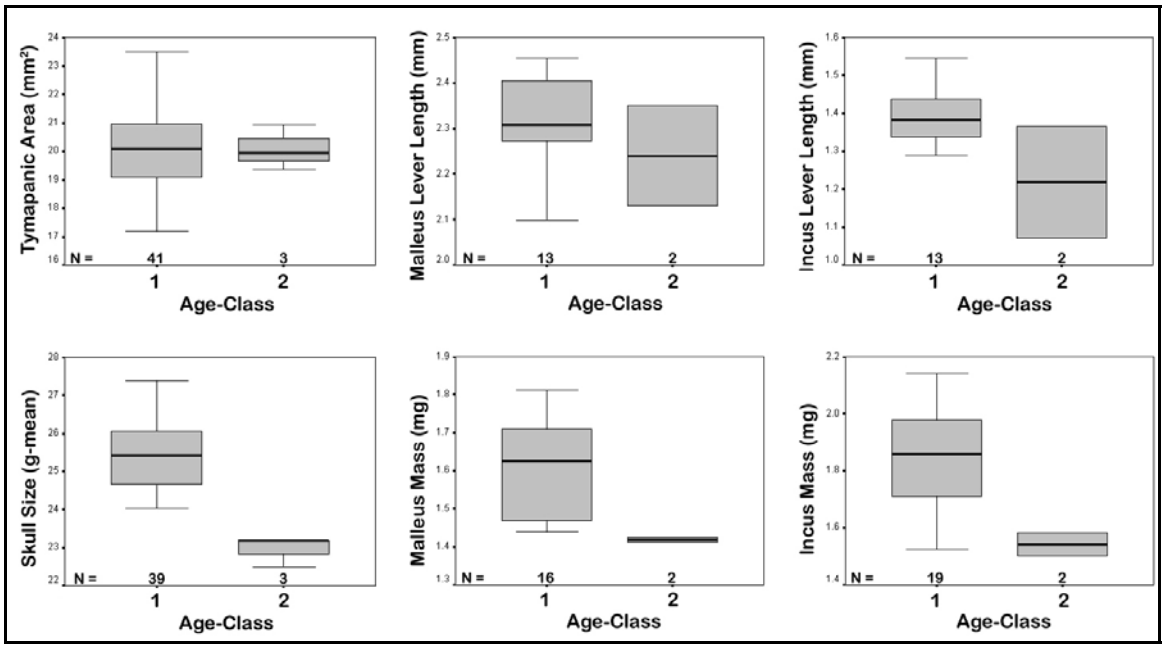

Figure 6.4 – Box-plots of ontogenetic comparisons for *Saimiri boliviensis*.

nearly identical. The means for both mallear and incudal lever arm length are lower in the younger specimens but there is some overlap in the inter-quartile ranges, particularly for the malleus. The masses of the ossicles however, show much broader separation and mallear mass for age-class 2 specimens fall just below the total range for age-class 1. The geometric mean of skull size indicates that age-class 1 individuals are about 11% larger than age-class 2 and there is no overlap in the ranges of the two groups. The ontogentic pattern for skull size is akin to that for incus mass and similar associations can be seen in *Aotus* as well (Figures 6.1 and 6.3).

The box-plots for *S. sciureus* are presented in Figure 6.5. The patterns appear to be virtually identical to those illustrated by *S. boliviensis* although no data were available for ossicular lever arm lengths. As before, there is no apparent difference in tympanic membrane size but the masses of the ossicles show a strong age-related effect. Although these are based on a single individual, the values fall well below the total range of age-

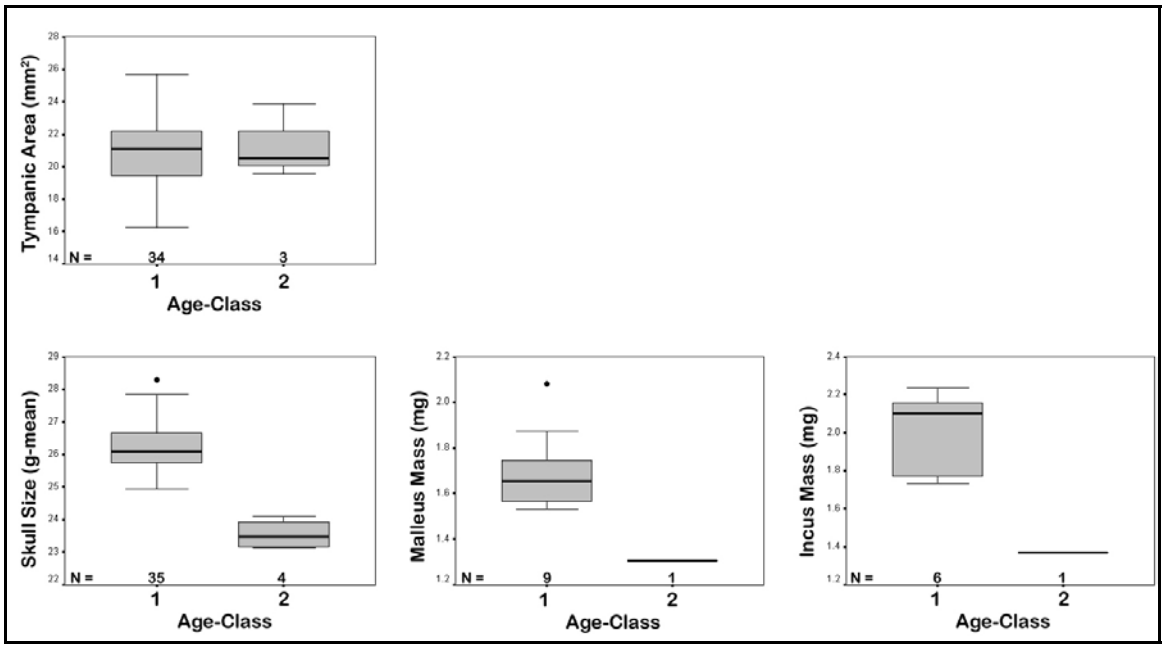

Figure 6.5 – Box-plots of ontogenetic comparisons for *Saimiri sciureus*.

class 1, and in fact, incus mass is over 0.6 mg^3 lighter (13.8%) than the mean for age-class 1. Also similar to *S. boliviensis*, skull size is 12% larger in age-class 1 specimens. Based on the results from the ontogenetic comparison, age-class 2 data will be excluded from the sexual dimorphism and phylogenetic analyses.

Table 6.2 presents the male and female means for *S. boliviensis* and *S. sciureus*. There were no significant differences between the sexes in any of the variables for *S. sciureus*. In contrast, *S. boliviensis* showed significant differences in ossicular mass ($p < 0.05$) and skull size and body mass ($p < 0.01$). Ossicular mass was 3% heavier in males than in females, skull size was 5% larger, and body mass was 8% larger. Tympanic membrane area was also almost 1 mm^2 larger (~2.5%) in males but did not reach statistical significance ($p = 0.063$). Based on these findings, it would seem worthwhile to examine the *Saimiri* data both with and without pooling the sexes.

Species	Sex		A_{tm}	LA_m	LA_i	M_m	M_i	SS	M_b
S. boliviensis	Female	Mean	19.42	2.34	1.38	1.51	1.76	24.87	766.50
		N	18	4	4	5	7	18	12
		SD	1.24	0.06	0.07	0.13	0.18	0.56	141.68
	Male	Mean	20.39	2.31	1.39	1.65	1.93	26.10	957.00
		N	22	9	9	11	11	20	12
		SD	1.78	0.12	0.08	0.10	0.13	0.72	169.68
S. sciureus	Female	Mean	21.19	2.59	1.47	1.70	2.15	26.00	815.54
		N	13	1	1	6	1	12	13
		SD	2.54			0.20		0.46	142.12
	Male	Mean	21.02	2.36	1.38	1.70	2.05	26.50	822.37
		N	19	3	3	3	4	21	19
		SD	2.16	0.13	0.11	0.17	0.20	0.96	125.45

Table 6.2 - Adult male and female species means for *Saimiri*. See Table 6.1 for coding.

When the sexes are pooled for each species the only variable that is significantly different between the species is skull size ($p < 0.05$) with *S. sciureus* being about 4% larger than *S. boliviensis*. If just the males are considered, *S. sciureus* is found to be significantly heavier in body mass ($p < 0.05$) but no other differences were found. When examining just the females, tympanic membrane area and mallear mass were found to be significantly smaller ($p < 0.05$) in *S. boliviensis*, as was skull size ($p < 0.001$). The fact that there is only one *S. sciureus* specimen for ossicular lever arm lengths and incudal mass prevents critically evaluating these variables. If the males and females for both species are considered separately (four groups) there is a significant difference in incudal mass, skull size, and body mass. *S. boliviensis* females are significantly lighter than *S. boliviensis* males (as stated above), and have smaller skulls than the other three groups. Therefore, it appears that it is the smaller skull size of *S. boliviensis* females that may be driving the differences in auditory structures. Considering that *Saimiri* audiograms are only available for males, and the finding that *S. sciureus* females did not differ

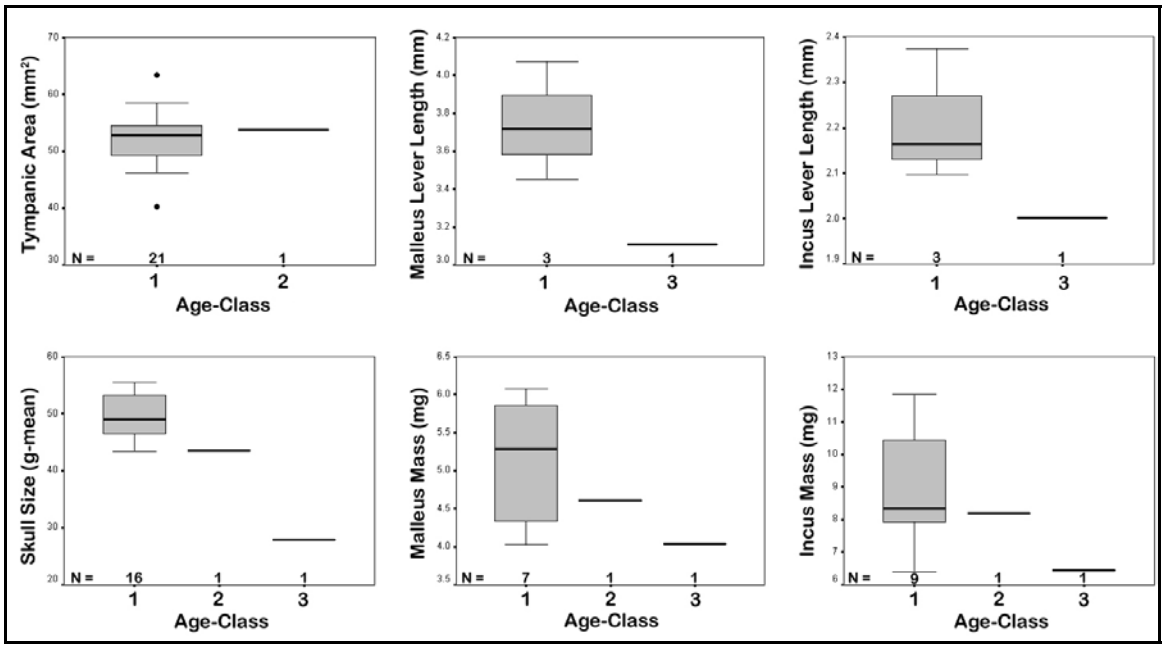

Figure 6.6 – Box-plots of ontogenetic comparisons for *Alouatta seniculus*.

from the males of either species, a conservative approach would be to exclude *S. boliviensis* females from genus mean computations for later comparisons with *Saimiri* audiograms.

Alouatta

Ontogenetic data were available for two species of the genus *Alouatta*, although both species were constrained by having only a single individual representing sub-adult age-classes. The box-plots for *Alouatta seniculus* are presented in Figure 6.6. Tympanic membrane area is the only comparison that does not suggest size-related changes with increasing age: the age-class 2 individual falls within the age-class 1 range, and has in fact, a slightly larger surface area than the adult mean. In contrast, the age-class 3 values for mallear and incudal lever arm length are below the total ranges for the respective age-

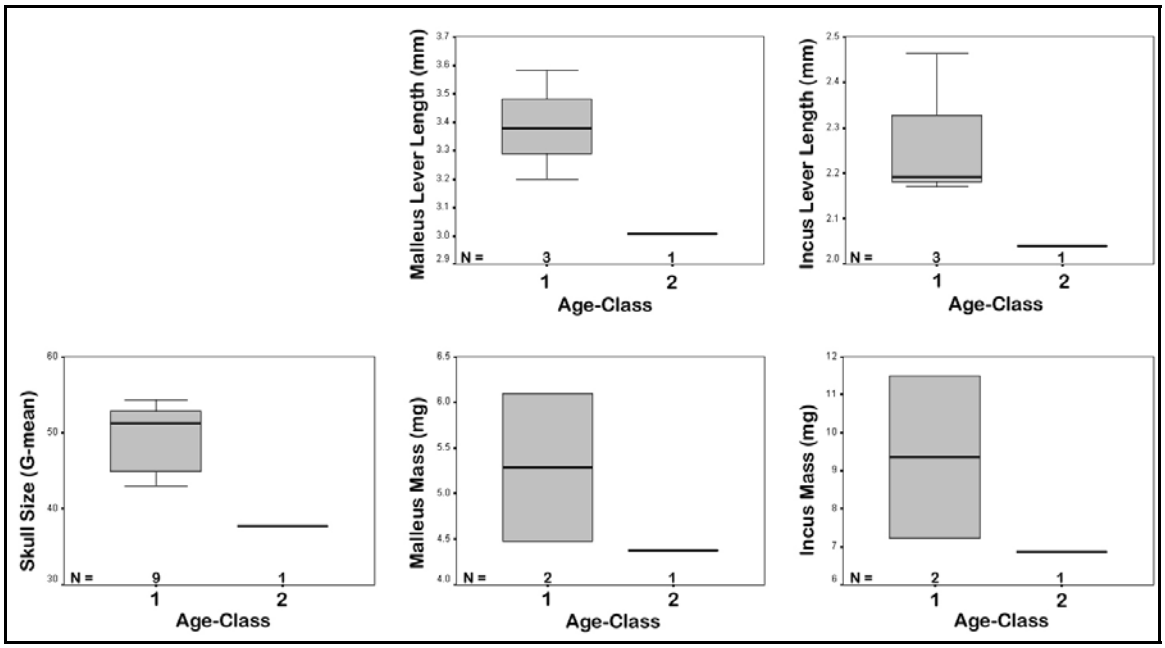

Figure 6.7 – Box-plots of ontogenetic comparisons for *Alouatta caraya*.

class 1 box-plots. Mallear length was about 0.6 mm shorter (19.4%) and incudal length was almost 0.2 mm shorter (8.5%) than the adult means. Ossicular mass follows a pattern that roughly parallels the changes in skull size through ontogeny. The age-class 2 individual falls towards the bottom of the inter-quartile range for age-class 1, and the age-class 3 individual falls just beneath the age-class 1 total range in both mallear and incudal mass comparisons.

The box-plots for *Alouatta caraya* are presented in Figure 6.7 and overall they illustrate comparable patterns as seen in *A. seniculus*, although no data were available for tympanic membrane area. The age-class 2 value for mallear lever arm length is almost 0.4 mm shorter (13.6%) than the mean for age-class 1 and well below the total range. Likewise, incudal lever arm length is also shorter (~0.15 mm – 7.3%) in the age-class 2 individual compared with the three age-class 1 subjects. For ossicular mass, the values for the age-class 2 individual fall just beneath the range (inter-quartile and total) for the

Species	Sex		A_{tm}	LA_m	LA_i	M_m	M_i	SS	M_b
A. caraya	Female	Mean	48.86	3.29	2.18	4.48	7.23	44.46	5559.00
		N	4	2	2	1	1	4	4
		SD	4.41	0.13	0.02			1.31	602.93
	Male	Mean	52.90	3.58	2.46	6.10	11.49	52.64	8020.00
		N	3	1	1	1	1	5	5
		SD	3.68					1.22	870.06
A. seniculus	Female	Mean	51.25	3.58	2.27	4.49	7.46	46.64	5785.00
		N	13	2	2	4	4	9	8
		SD	4.77	0.19	0.15	0.56	0.85	1.85	594.07
	Male	Mean	54.21	4.07	2.10	5.93	10.13	53.06	7827.50
		N	8	1	1	3	5	7	4
		SD	5.38			0.21	1.40	2.20	1004.67

Table 6.3 - Adult male and female species means for *Alouatta*.

two age-class 1 individuals. Although both species comparisons are limited by small sample-sizes, it is interesting how similar the ontogenetic patterns are for each of the auditory variables.

Table 6.3 gives the male and female species means and standard deviations for *A. seniculus* and *A. caraya*. In both species, the males are considerably larger than the females in body mass, skull size and most auditory variables. Male *A. seniculus* were 11% heavier in body mass and had skulls that were 14% larger than females of the same species. This was accompanied by having ossicles that were 10% more massive while the tympanic membrane was only 3% larger. Only one male and two females produced lever arm measurements but these data suggest that males have longer mallear lever arms (14%) while the females show slightly longer incudal lever arms (8%). Ossicular mass was significantly different for both the malleus ($p = 0.011$) and incus ($p = 0.010$) as was body mass ($p = 0.001$) and skull size ($p = 0.001$). The small sample size for lever arm length limits the ability to detect true differences, if they exist. On the other hand, the finding that tympanic membrane area does not significantly differ appears to be a more credible result due to the relatively large sample sizes.

The degree of sexual dimorphism in *A. caraya* was comparable to that of *A. seniculus* with males being 13% larger in body mass than females and having skulls that were 18% bigger. Also similar to *A. seniculus*, mallear mass was 11% greater in males, while incudal mass was 17% greater. The other auditory variables showed lower levels of dimorphism with males having tympanic membranes that were 4% bigger, mallear lever arms that were 9% longer, and incudal lever arms that were 13% longer. Only body mass and skull size were found to be significantly different ($p = 0.014$), although as stated before, the small sample sizes for the ossicles limits the power of the analysis. When the sexes were pooled for each species, no significant intra-generic differences were found. However, when the sexes are compared independently, the females were found to be significantly smaller than the males in body mass and skull size ($p < 0.001$), as well as mallear mass ($p = 0.014$) and incudal mass ($p = 0.010$).

Ateles

The ontogenetic comparisons for *Ateles paniscus* are presented in Figure 6.8. The mean for tympanic membrane area is nearly 7 mm^2 smaller (6.2%) for the age-class 2 specimens and there is no overlap in the inter-quartile ranges. A significant difference was found between age-classes ($p = 0.020$) but it should still be pointed out that several adult specimens (outliers) show values that are lower than those of any sub-adults. Only one age-class 2 specimen was available for the ossicular lever arm comparisons. Mallear lever arm length fell just below the inter-quartile range for adults while incudal lever arm length was actually well above the total adult range. The single sub-adult specimen with mallear mass data had a value just below the adult total range. Very little data was

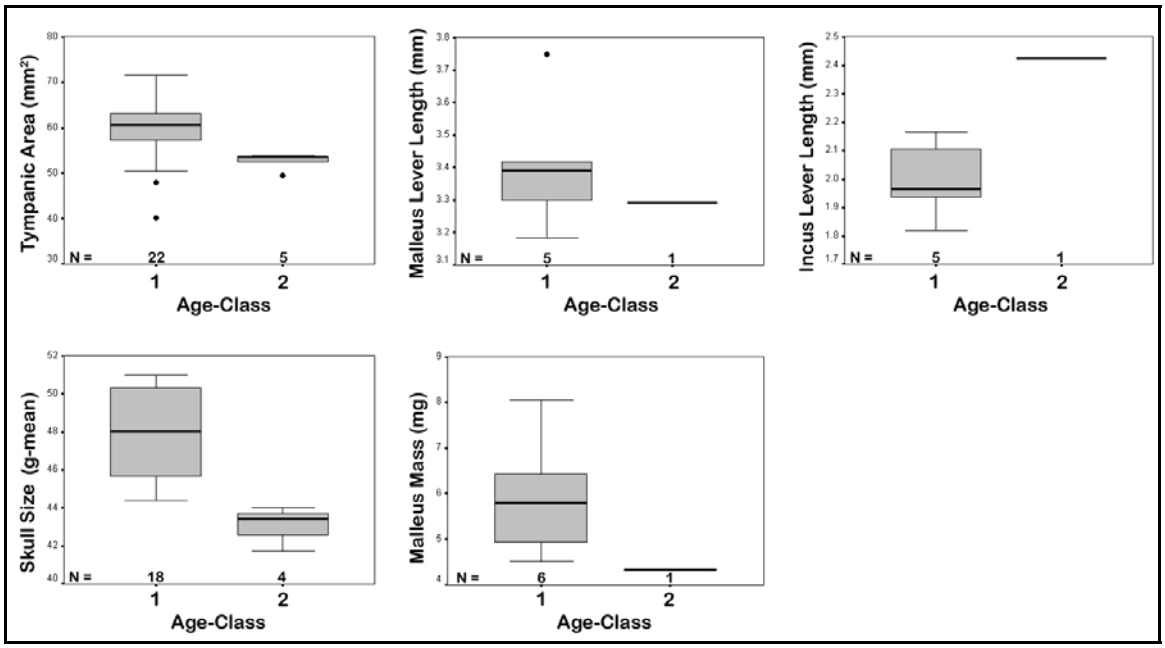

Figure 6.8 – Box-plots of ontogenetic comparisons for *Ateles paniscus*. Significant differences were found for tympanic membrane area (p = 0.020).

available for *A. paniscus* males but the females tended to have slightly higher values for tympanic membrane area (2%) although skull size was approximately equal between the sexes. Because *A. paniscus* represented the preponderance of the *Ateles* auditory data, no intra-generic phylogenetic analyses were performed.

Cacajao

Limited ontogenetic data are available for *Cacajao calvus* and are presented in Figure 6.9. Tympanic membrane size for the two age-class 3 specimens is surprisingly close the upper limit of the total range for the age-class 1 specimens. The single age-class 3 specimen with lever arm data shows mallear length falling towards the bottom of the adult range while incudal length falls towards the top of the adult inter-quartile range. Mallear mass for the age-class 3 specimen fits comfortably within the adult range, while

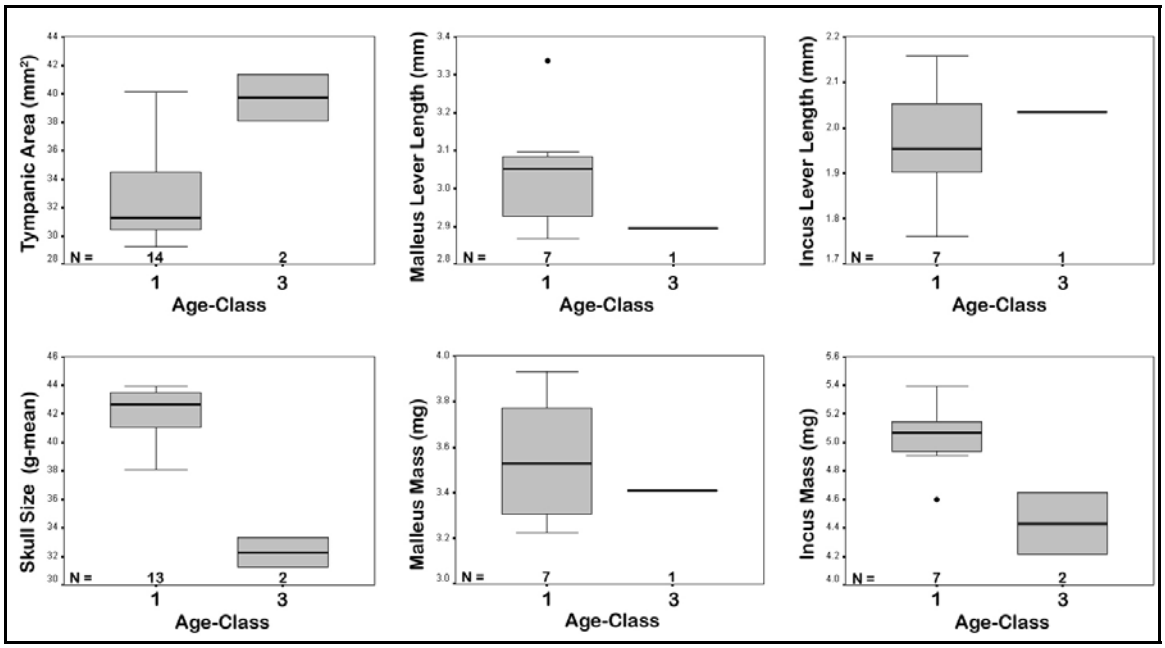

Figure 6.9 – Box-plots of ontogenetic comparisons for *Cacajao calvus*.

the values for incudal mass are well below the adult range. Skull size shows the largest differences between age-classes with the adults being one-third larger than age-class 3 individuals. As in some previous cases, incudal mass and skull size show similar patterns of difference between adult and sub-adult groups.

Table 6.4 presents the male and female species means for *C. calvus* and *C. melanocephalus*. No significant differences were detected in auditory structures between *C. calvus* males and females although mallear lever arm length was nearing significance ($p = 0.057$). Skull size was found to be significantly larger ($p = 0.001$) in males and was about 7% bigger than that of the females. Sexual differences in skull size were similar in *C. melanocephalus* (males almost 8% larger than females; $p = 0.029$) but again this difference was apparently not large enough to result in significant differences in auditory structures. Still, three auditory structures (tympanic membrane area, incudal lever length,

Species	Sex		A_{tm}	LA_m	LA_i	M_m	M_i	SS
C. calvus	Female	Mean	32.25	3.17	2.03	3.48	5.06	40.71
		N	6	3	3	3	3	6
		SD	2.91	0.15	0.11	0.39	0.15	1.36
	Male	Mean	33.51	2.94	1.92	3.60	5.00	43.37
		N	8	4	4	4	4	7
		SD	4.41	0.08	0.14	0.22	0.33	0.40
C. melanocephalus	Female	Mean	29.52	2.56	1.48	2.57	3.91	38.36
		N	4	3	3	3	3	4
		SD	3.47	0.12	0.03	0.28	0.57	1.10
	Male	Mean	32.80	2.91	1.73	2.88	4.19	41.36
		N	5	3	3	3	5	4
		SD	2.56	0.20	0.06	0.05	0.18	0.68

Table 6.4 - Adult male and female species means for *Cacajao*.

and mallear mass) were approaching traditional significance values ($p \leq 0.10$). When the sexes were pooled for each species, skull size was significantly larger (~ 6%; $p = 0.011$) in *C. calvus* than in *C. melanocephalus*. The ossicular variables were all found to be significantly different between the species with mallear lever arms being about 11% longer ($p = 0.046$), incudal lever arms being 23% longer ($p = 0.004$), mallear mass 9% heavier ($p < 0.001$), and incudal mass 7% heavier ($p < 0.001$) in *C. calvus*. This comparison exemplifies the fact that relatively slight differences between species in skull size can be associated with moderately large (and significant) differences in the sizes of certain auditory structures.

Callicebus

The ontogenetic data for *Callicebus moloch* are shown in Figure 6.10. Although based on a low sample size, the patterns are typical of several of the preceding

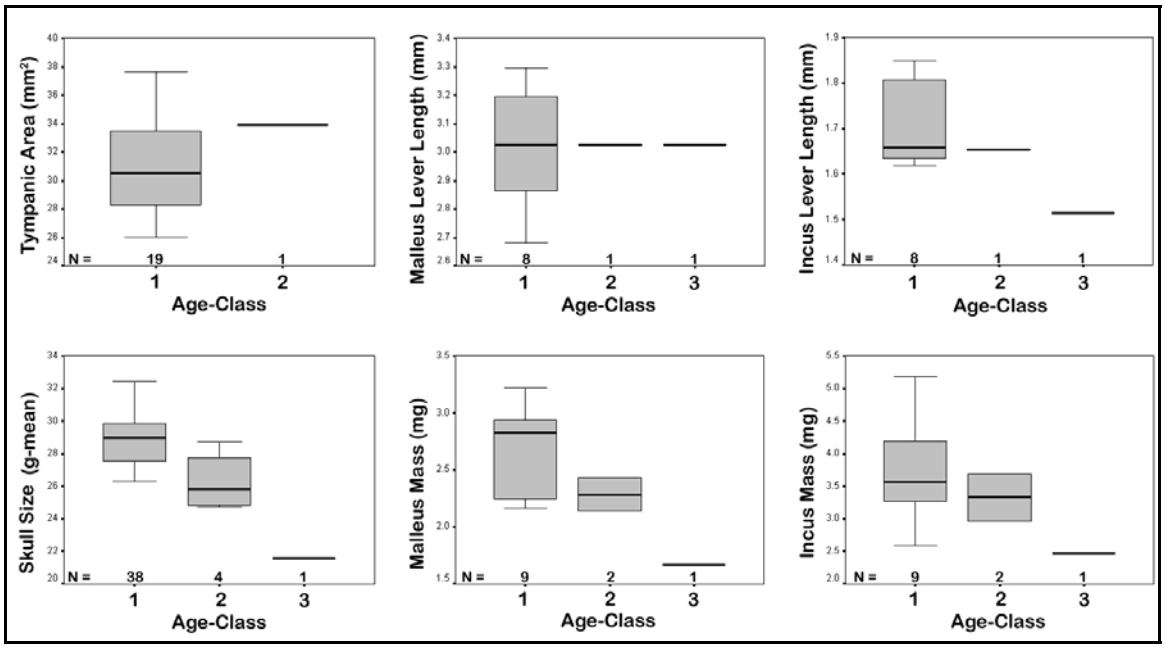

Figure 6.10 – Box-plots of ontogenetic comparisons for *Callicebus moloch*.

comparisons. Tympanic membrane area for the age-class 2 individual falls just above the inter-quartile range for age-class 1 although still within the total range. The mallear lever arm values for age-class 2 and 3 specimens are indistinguishable from the mean for age-class 1. A similar pattern is evident when comparing incudal lever arms except that the age-class 3 subject shows a length that is just over 0.10 mm shorter (6.5%) than that of the other two age-classes. The ontogenetic pattern for ossicular mass closely parallels that of skull size. The age-class 2 values are lower than those of age-class 1, but there is still varying degrees of overlap in the ranges (total and inter-quartile). In all three cases (skull size, mallear mass, incudal mass), the age-class 3 individual illustrates values that are smaller than those of the other two groups. No sexual dimorphism was found in any of the variables for *Callicebus moloch* although body mass was approaching significance ($p = 0.092$). The low sample sizes for other *Callicebus* species prevented critical evaluation.

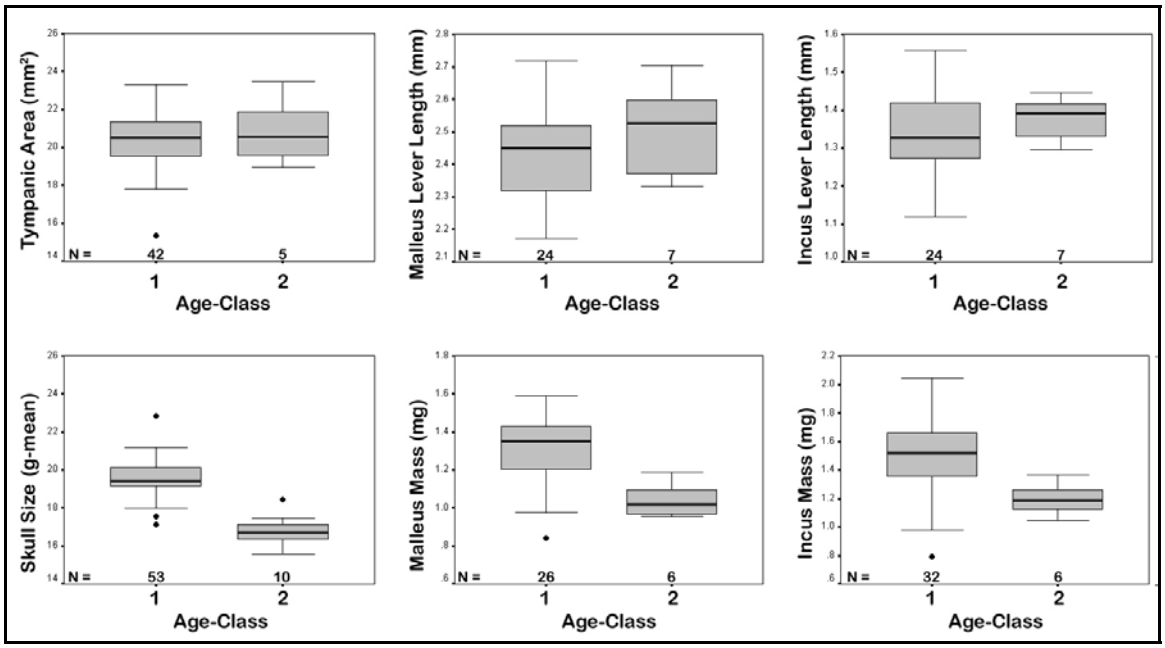

Figure 6.11 – Box-plots of ontogenetic comparisons for *Callithrix jacchus*. Significant differences were found for ossicular mass and skull size ($p < 0.01$).

Callithrix

The species with the largest sample of sub-adult data was *Callithrix jacchus* with 10 individuals in age-class 2. Figure 6.11 shows the box-plots comparing age-class 1 and age-class 2 specimens. The values for tympanic membrane area are practically identical and the age-class 2 means for ossicular lever arm lengths are actually slightly higher than the age-class 1 means. Ossicular mass, on the other hand, is lower in the age-class 2 specimens with no overlap in the inter-quartile ranges. In fact, the means for age-class 2 are around 8% less for both mallear and incudal mass. There is also a clear separation in skull size with the age-class 2 specimens averaging about 17% smaller.

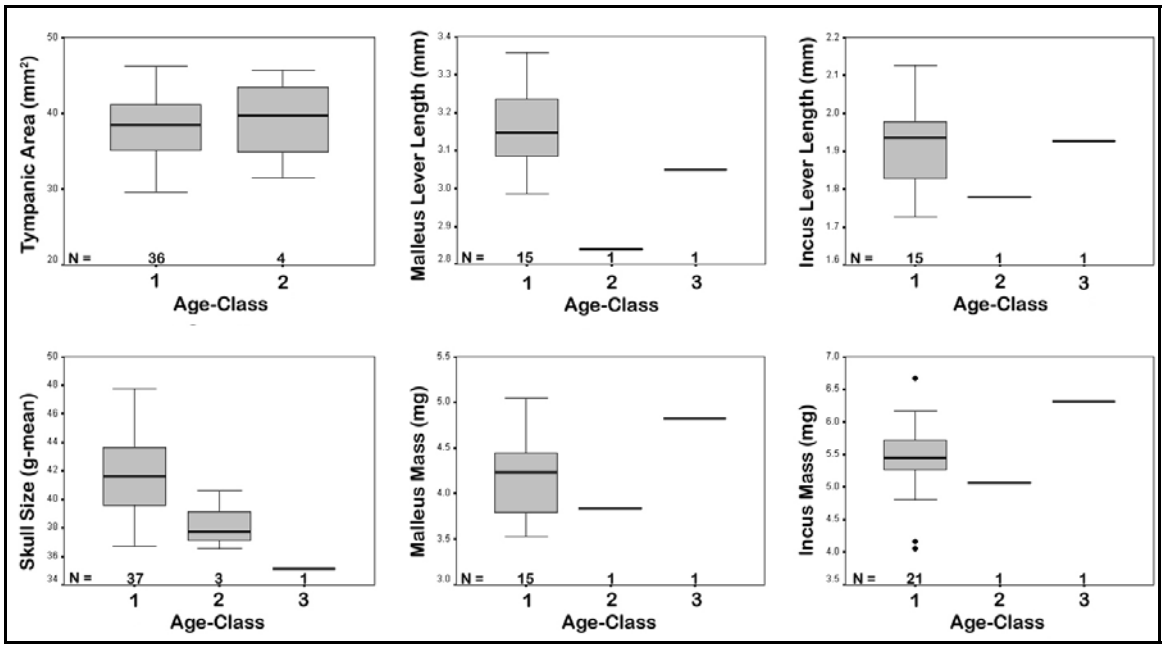

Figure 6.12 – Box-plots of ontogenetic comparisons for *Cebus apella*.

Nonparametric tests revealed that that there were significant differences between the groups for skull size and ossicular mass ($p < 0.01$). No differences were found between the sexes and *C. jacchus* was the only species investigated, so no phylogenetic comparisons were possible.

Cebus

Ontogenetic data were available for two species of capuchin monkeys. The box-plots for *Cebus apella* are presented in Figure 6.12. The tympanic membrane values for age-class 1 and 2 specimens are very similar and skull size shows the typical increase with age pattern. In contrast, the ossicular comparisons illustrate unusual patterns. While the age-class 2 specimen shows lower lever arm and mass values than the means for age-class 1, the age-class 3 values show a reverse in the decreasing size trend. However, all of

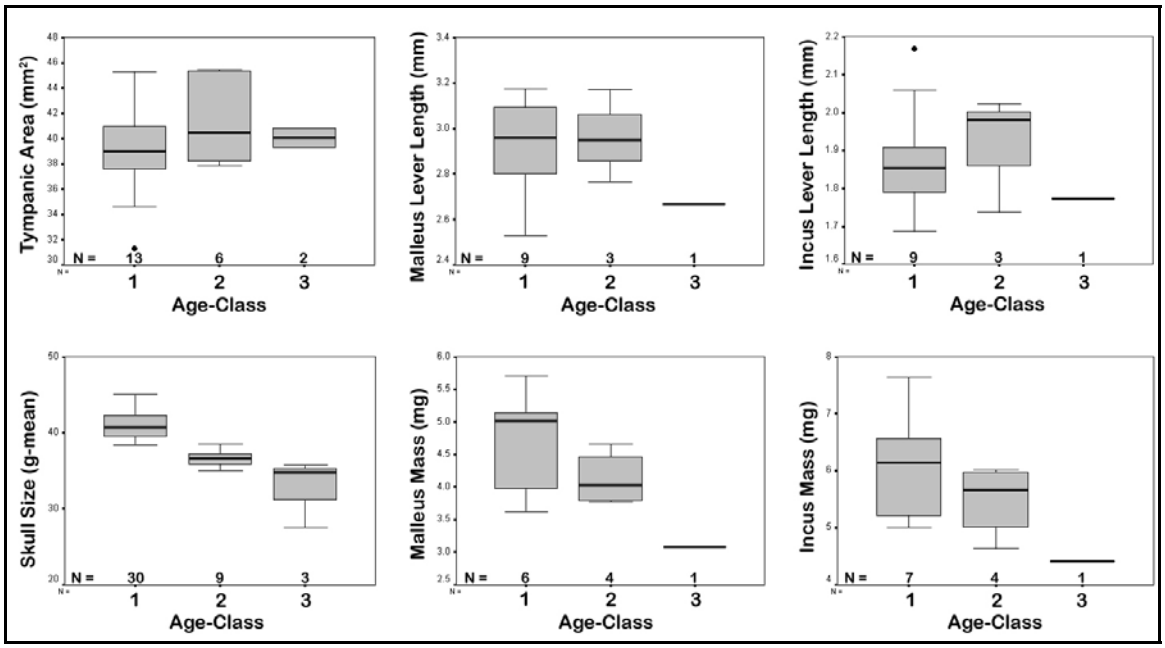

Figure 6.13 – Box-plots of ontogenetic comparisons for *Cebus capucinus*.

the age-class 3 values are based on a single individual and this peculiar pattern should be considered with this reservation in mind.

The ontogenetic comparisons for *Cebus capucinus* are presented in Figure 6.13. Similar to *C. apella*, there was no difference in tympanic membrane size despite considerable growth of the skull. The growth trends in the ossicles on the other hand are different than the patterns illustrated for *C. apella*. The lengths of the lever arms are not considerably smaller in age-class 2 specimens than age-class 1, but the age-class 3 values fall towards the bottom of the other ranges. Ossicular mass shows a stronger decreasing trend with the age-class 3 values outside of the ranges of the other age-groups. Despite the ambiguity in the *C. apella* comparisons and the finding that tympanic membrane size does not show a relationship with skull growth in either *Cebus* species, the sub-adult specimens will be excluded from all further analyses in this chapter.

Species	Sex		A_{tm}	LA_m	LA_i	M_m	M_i	SS	M_b
C. albifrons	Female	Mean	39.58	3.07	1.64	3.91	4.87	38.57	2243.00
		N	4	1	1	1	1	4	4
		SD	1.01					1.41	206.39
	Male	Mean	40.88	3.13	1.96	4.22	5.41	41.58	3453.00
		N	9	6	6	8	8	9	9
		SD	2.15	0.11	0.06	0.34	0.78	1.31	596.91
C. apella	Female	Mean	34.22	3.14	1.86	4.01	5.24	38.98	2183.85
		N	12	6	6	6	8	13	13
		SD	3.16	0.13	0.09	0.38	0.49	1.39	568.00
	Male	Mean	40.24	3.17	1.96	4.28	5.70	43.00	3422.83
		N	23	8	8	8	11	23	23
		SD	3.43	0.10	0.12	0.44	0.49	2.05	1021.10
C. capucinus	Female	Mean	37.58	2.82	1.83	4.22	5.40	40.30	
		N	5	4	4	3	3	15	
		SD	3.70	0.24	0.17	0.74	0.65	1.39	
	Male	Mean	40.40	2.95	1.94	5.27	6.53	41.41	
		N	7	4	4	3	4	15	
		SD	2.76	0.13	0.15	0.38	0.94	1.66	

Table 6.5 - Adult male and female species means for *Cebus*.

Table 6.5 gives the male and female means of each species for all of the parameters. The only significant differences detected between sexes in *Cebus albifrons* were skull size and body mass ($p < 0.001$). However, the male means for auditory structures were consistently higher and there was only one female for the ossicular comparisons, so a larger sample of females may show there to be statistical differences in certain auditory structures as well. *C. apella* showed significant differences in tympanic membrane size, skull size, body mass (all $p = 0.001$) and incudal mass ($p = 0.029$). The females had tympanic membranes that were about 6 mm^2 smaller (8.4%) than the males and incudal mass averaged about 0.6 mg^3 lighter (2.8%). No significant differences in auditory structures were found in *C. capucinus* although skull size and mallear mass were approaching significance ($p \leq 0.10$). Even though body mass dimorphism was about the same in *C. albifrons* and *C. apella*, significant differences in auditory measures were

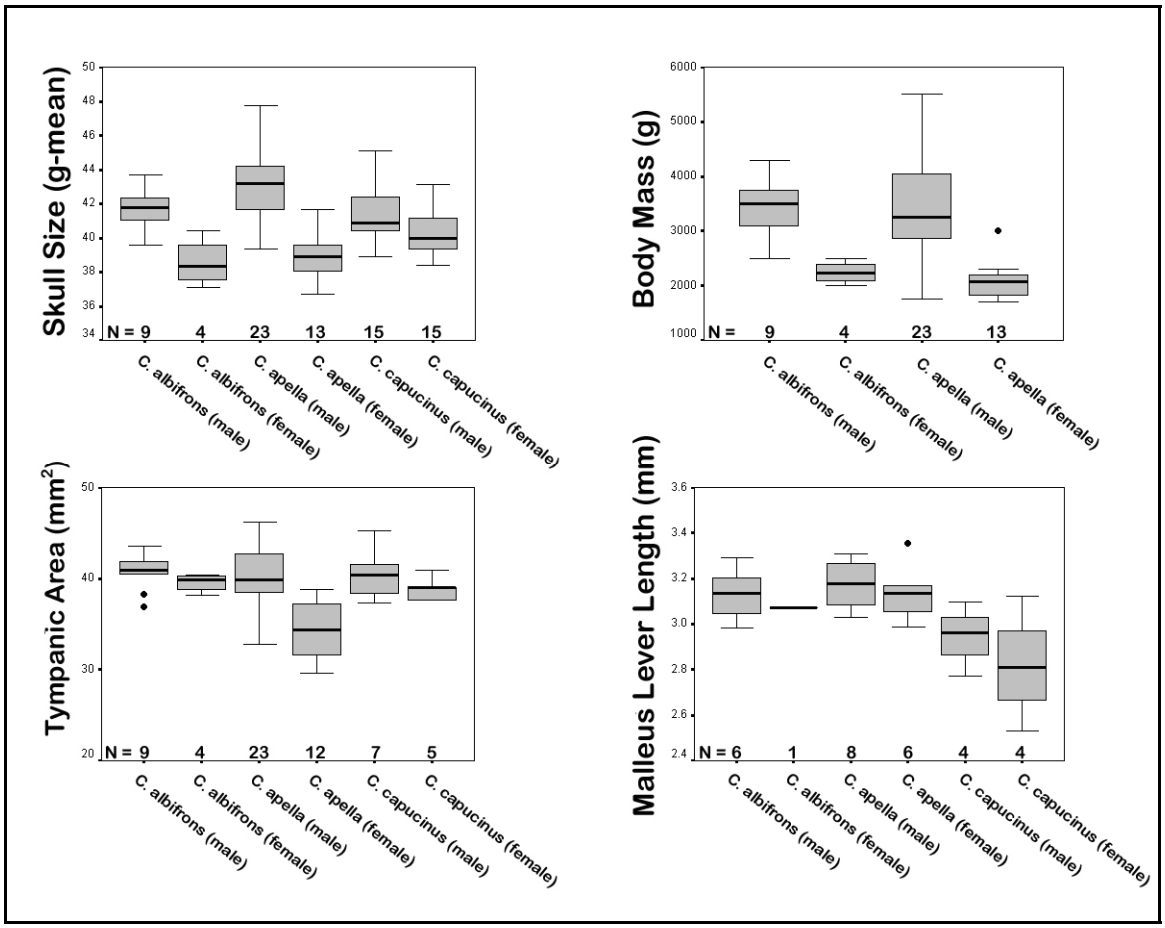

Figure 6.14 – Box-plots of significant variables in three species of *Cebus*.

found only in *C. apella*. This may be related to the larger skull size dimorphism in *C. apella*, with males being about 10% larger than females, compared with 8% in *C. albifrons* and 3% in *C. capucinus*.

When the sexes are pooled for each species, mallear lever arm length was the only variable that was significantly different, with *C. capucinus* showing a smaller length than either *C. albifrons* ($p = 0.021$) or *C. apella* ($p = 0.001$). When the sexes are considered separately for each species (Figure 6.14), significant differences were found in tympanic membrane size ($p < 0.001$), mallear lever arm length ($p = 0.049$), skull size ($p < 0.001$), and body mass ($p < 0.001$). The differences in skull size and body mass resulted from the

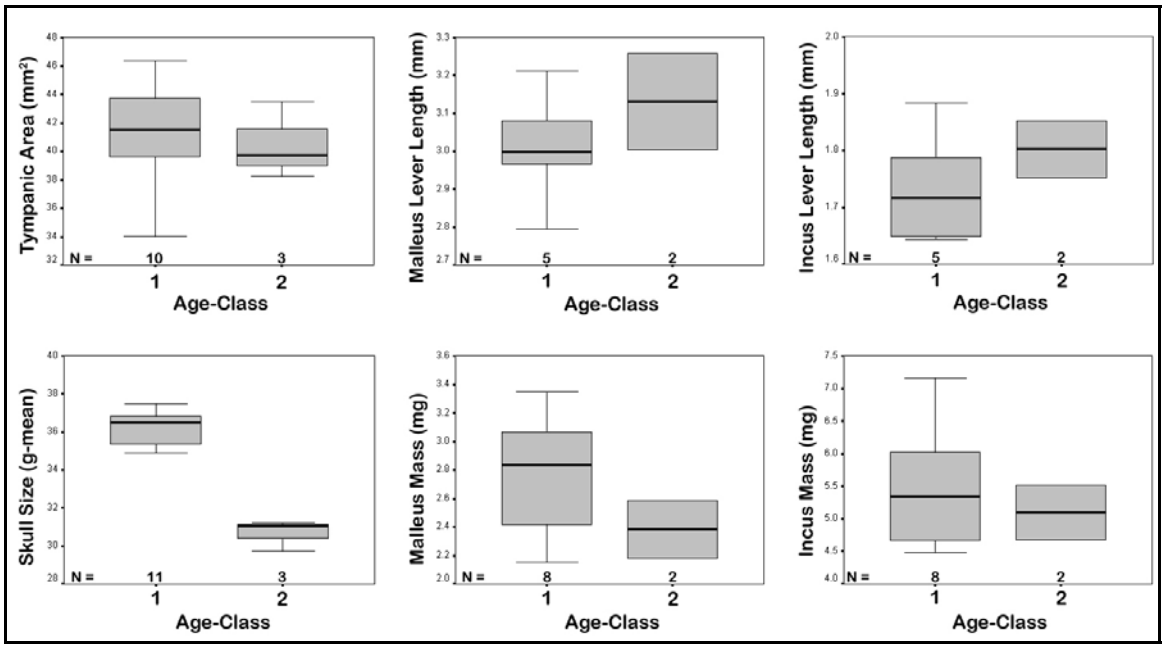

Figure 6.15 – Box-plots of ontogenetic comparisons for *Pithecia monachus*.

smaller values for *C. albifrons* and *C. apella* females described above. The difference in mallear length still appears to be driven by the *C. capucinus* specimens (both male and female). The female *C. apella* was the one group that had a considerably divergent tympanic membrane size. Considering the fact that *C. apella* females have the smallest skull and body size of these species, the smaller membrane is not surprising. What was unexpected was that the *C. albifrons* females did not show a similar degree of difference as the *C. apella* females despite being nearly as small. The shorter mallear lever arm lengths in *C. capucinus* are also unusual considering the size of their skulls. Based on the moderate levels of sexual dimorphism and interspecific differences in various parameters and taxa, it would seem reasonable not to pool these species for deriving genus mean values.

Species	Sex		A_{tm}	LA_m	LA_i	M_m	M_i	SS	M_b
P. monachus	Female	Mean	43.13	3.08	1.79	2.75	4.63	36.16	
		N	3	1	1	3	2	4	
		SD	2.84			0.14	0.22	0.68	
	Male	Mean	40.11	2.99	1.72	2.78	5.74	36.22	2900.00
		N	7	4	4	5	6	7	1
		SD	4.05	0.17	0.11	0.56	0.93	1.13	
P. pithecia	Female	Mean	36.71			3.18	4.96	33.00	1588.00
		N	3			1	2	4	1
		SD	1.37				0.42	1.03	.
	Male	Mean	38.63	3.03	1.80	3.02	5.09	34.69	1202.00
		N	4	2	2	2	2	4	2
		SD	3.57	0.22	0.00	0.19	0.02	1.21	865.50

Table 6.6 - Adult male and female species means for *Pithecia*.

Pithecia

Figure 6.15 shows the box-plots for *Pithecia monachus* comparing age-class 1 and 2 specimens. Despite the fact that skull size is around 18% larger in the age-class 1 specimens, there are only moderate ontogenetic trends in some of the auditory variables. The mean for tympanic membrane size is slightly smaller for age-class 2 although there is considerable overlap in the ranges. The means for lever arm length are actually about 0.1 mm longer (5.9%) in the younger age-class. The trends for ossicular mass are in the expected direction (less mass in younger specimens) with the means for age-class 1 being almost 0.4 mg^3 heavier (5.3%) than the means for age-class 2 for both ear bones. However, there is overlap in the inter-quartile ranges and only the mean for mallear mass is below the inter-quartile ranges for age-class 1.

Table 6.6 gives the adult male and female species means for *P. monachus* and *Pithecia pithecia*. Whether the sub-adult specimens for *P. monachus* were included or not, there was no sexual dimorphism in any of the variables tested. Little data were available for testing differences between the sexes in *P. pithecia* but the available data

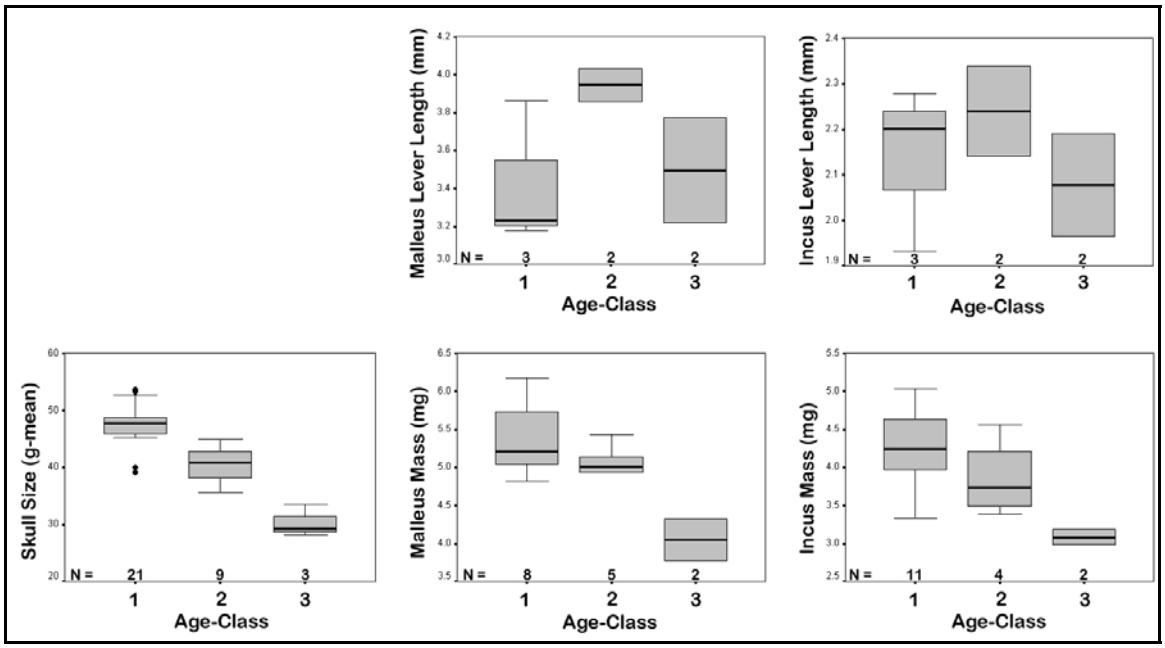

Figure 6.16 – Box-plots of ontogenetic comparisons for *Macaca fascicularis*.

suggest that the differences are no greater than 5% for any parameter. When the sexes are pooled for each species, skull size was about 7% smaller, tympanic membrane size was about 4% smaller, and incudal mass was 3% less in *P. pithecia* compared to *P. monachus*. However, only skull size was found to be significantly different ($p \leq 0.001$) between *P. pithecia* and *P. monachus*.

Macaca

Macaca fascicularis is the only macaque species with an adequate amount of ontogenetic data (Figure 6.16) although no age-class 2 representatives were available for tympanic membrane area. The mean for mallear lever arm length is considerably longer for the age-class 2 specimens than the other two categories and nearly out of the total range for age-class 1. A similar overall pattern can be seen in the incudal lever arm length

Species	Sex		A_{tm}	LA_m	LA_i	M_m	M_i	SS	M_b
M. fasciculuaris	Female	Mean	33.89	3.23	1.93		3.76	43.98	3840.00
		N	2	1	1		4	6	2
		SD	2.24				0.38	3.55	56.57
	Male	Mean	36.20	3.52	2.24	5.33	4.55	49.10	4550.00
		N	4	2	2	6	7	13	1
		SD	4.18	0.48	0.05	0.51	0.29	2.74	
M. nemestrina	Female	Mean		3.96	2.31	7.05	4.68	52.26	
		N		1	1	1	2	2	
		SD					0.72	5.11	
	Male	Mean				5.42	5.59	55.77	
		N				1	1	2	
		SD						2.56	

Table 6.7 - Adult male and female species means for *Macaca*.

comparison (age-class 2 higher than the other groups) although the difference between the means is no greater than 0.20 mm (9.7%) between any age-class. Mallear mass shows a slight decrease from age-class 1 to age-class 2 but the age-class 3 specimens fall well below the ranges of the other two categories and are around 1.0 mg^3 (7.4%) or more lighter. The separation between age-class 1 and 2 is larger in the incudal mass box-plots but their inter-quartile ranges still show overlap. As before, the age-class 3 specimens are the most clearly distinct and show no overlap with the other age categories.

Table 6.7 presents male and female means for adult *M. fascicularis* specimens as well as limited data on *Macaca nemestrina.* Significant differences were detected between male and female adult *M. fascicularis* specimens for skull size ($p = 0.003$) and incudal mass ($p = 0.024$) with males having skulls that were 12% larger and incudes that were 7% more massive. Incudal lever arm length and body mass also showed considerable differences (16% and 6% respectively) but were not found to be significant, likely due to low sample sizes (n = 1 and 2 for both comparisons). Although the low sample sizes for *M. nemestrina* prevent statistical evaluation (for sexually

dimorphic or intra-generic comparisons), the species means are consistently higher than in *M. fascicularis* and show a similar degree of difference as does skull size between the species. For example, skull size is about 14% bigger in *M. nemestrina* than in *M. fascicularis*, mallear lever arm length is 16 % longer, incudal lever arm length is 8% longer, and mallear and incudal mass are 5% heavier. Based on this limited comparison, it would seem unwise to pool data from different macaque species without first considering the differences in overall size.

Results: PROSIMIANS

Eulemur

Moderate amounts of ontogenetic data were available for *Eulemur fulvus* and the box-plots are presented in Figure 6.17. The mean for tympanic membrane area was 5% smaller in the age-class 2 specimens, which is similar to the differences between age-class 1 and 2 specimens for ossicular mass and skull size. However, there is still overlap in the inter-quartile ranges for all of these parameters except skull size, which is clearly separated with no overlap in the ranges. There was little distinction between lever arm lengths, and in fact, the age-class 2 box-plots fall toward the upper range of the age-class 1 values. No significant differences were detected between adult male and female *E. fulvus* specimens. No auditory data for were available for male *Eulemur macaco* specimens. Comparing *E. fulvus* with *E. macaco* (females only), both species have very

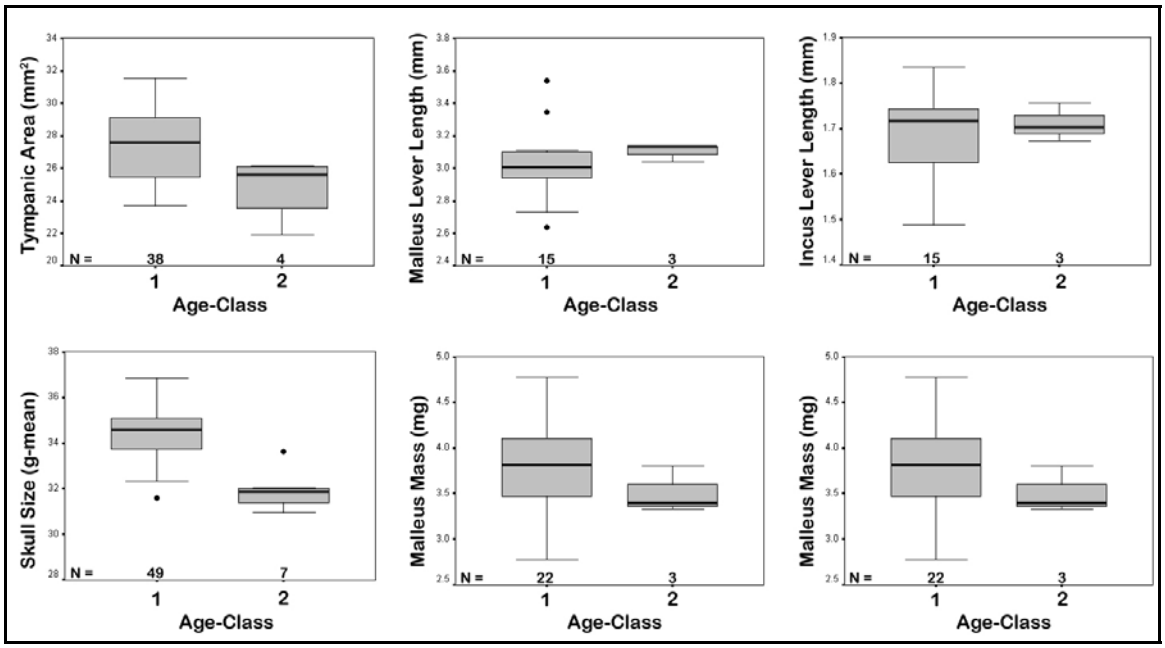

Figure 6.17 – Box-plots of ontogenetic comparisons for *Eulemur fulvus*.

similarly-sized skulls and incudal lever arm lengths (Table 6.8). In spite of this monomorphism in overall skull size, *E. macaco* had a mallear lever arm length that was 5% larger and ossicular mass that was also about 5% larger than the values for *E. fulvus*.

Species	Sex		A_{tm}	LA_m	LA_i	M_m	M_i	SS
E. fulvus	Female	Mean	26.59	2.97	1.69	3.50	3.39	34.36
		N	16	6	6	9	11	22
		SD	1.78	0.06	0.06	0.39	0.27	1.55
	Male	Mean	27.59	3.05	1.68	3.80	3.50	34.53
		N	15	7	7	9	9	19
		SD	2.04	0.32	0.13	0.37	0.42	1.15
E. macaco	Female	Mean	27.94	3.11	1.65	4.29	4.03	34.10
		N	3	1	1	1	1	3
		SD	0.96					1.23
	Male	Mean						35.27
		N						1
		SD						

Table 6.8 - Adult male and female species means for *Eulemur*.

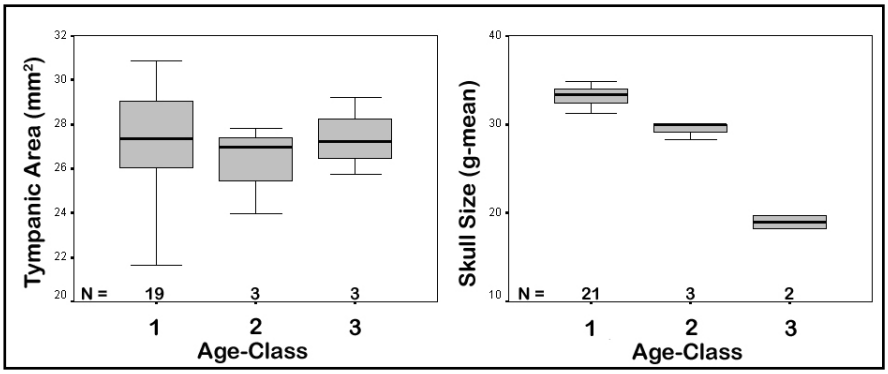

Figure 6.18 – Box-plots of ontogenetic comparisons for *L. catta*.

Lemur

Ontogenetic data for only the tympanic membrane was available for *Lemur catta* but is presented here since there are 3 representatives from both the age-class 2 and age-class 3 categories. Figure 6.18 shows the clear separation of the box-plots for skull size with no overlap between any of the age-class categories. In contrast, the tympanic membrane means and ranges are very similar although the age-class 2 inter-quartile ranges are slightly lower than the other two groups. This example provides persuasive evidence that tympanic membrane size is within the adult range even in the youngest specimens despite considerable differences in skull size. No differences were found between the sexes for any of the variables and *L. catta* was the only species in this genus investigated.

Varecia

Similar to *L. catta*, *Varecia variegata* yielded very limited ontogenetic data (Figure 6.19). The age-class 2 mean for tympanic membrane area is very close to the mean for age-class 1 although the inter-quartile range is a bit higher. The mean for age-

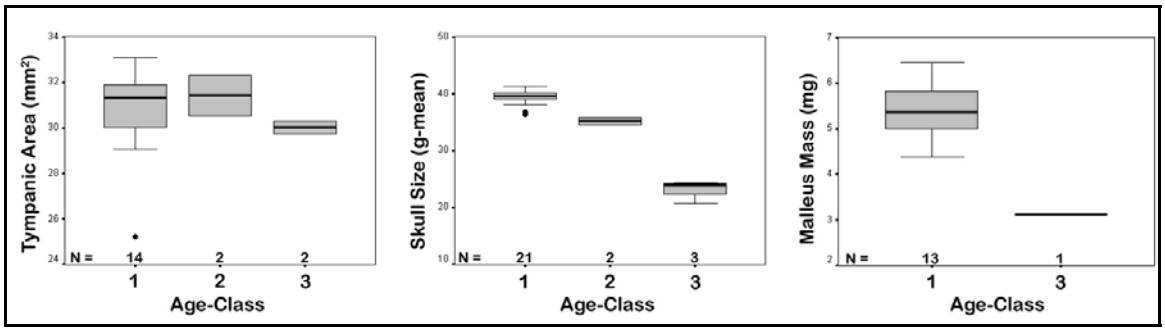

Figure 6.19 – Box-plots of ontogenetic comparisons for *Varecia variegata*.

class 3 is just over 1 mm^2 lower (1.6%) than that of the other groups but still overlaps the ranges. This difference is slight considering the distinct differences in skull size between each age-class. The single age-class 3 specimen has a value for mallear mass that is well below the range and is over 2.0 mg^3 lighter (16.3%) than the mean for age-class 1. No differences were found between adult males and females and *Varecia* is a single-species genus, preventing intra-generic comparisons.

Galago

Only two age-class 2 specimens were available for *Galago senegalensis* and their values are shown along with the age-class 1 box-plots in Figure 6.20. The means and inter-quartile ranges for tympanic membrane area were quite similar between the adults and sub-adults. Similarly, the lever arm lengths for the single age-class 2 specimen were not greatly different from the adult values and fall within their inter-quartile range. In contrast, the sub-adult value for mallear mass is at the edge of the adult range and incudal mass falls below the total adult range. As expected, the age-class 2 specimens have skulls that are considerably smaller than their age-class 1 counterparts. No differences were found between male and female adult values for any of the auditory variables and the

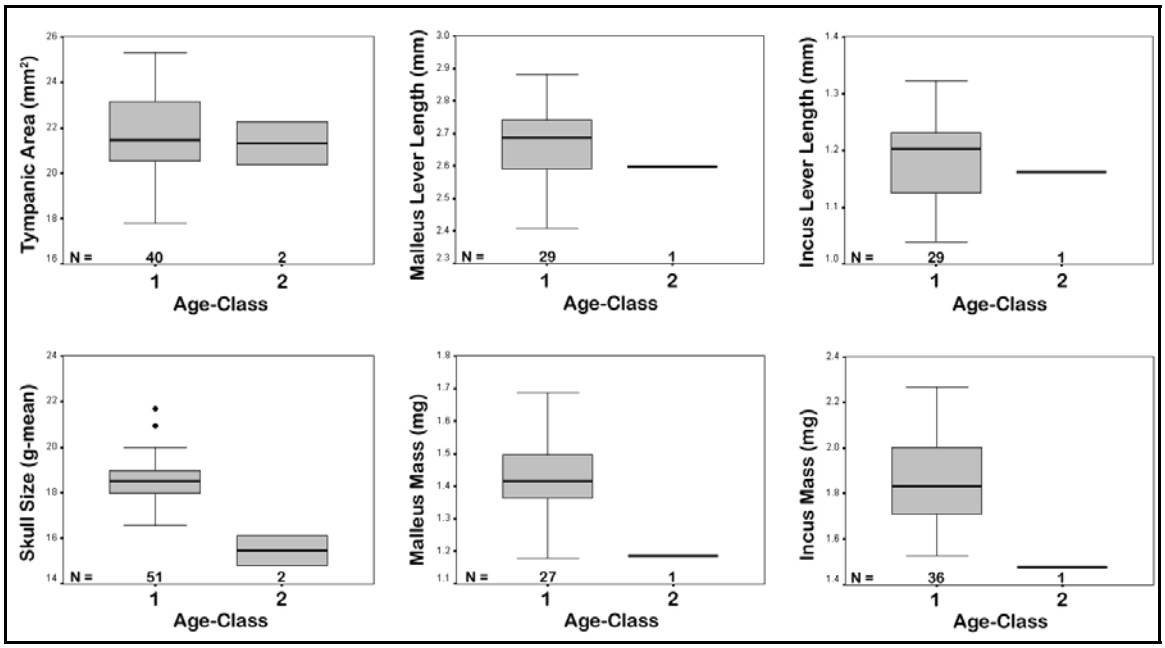

Figure 6.20 – Box-plots of ontogenetic comparisons for *Galago senegalensis*.

difference in skull size was slight (males ~2% larger than females). No other species of *Galago* were examined.

Perodicticus

Perodicticus potto had 2 specimens in the age-class 2 category for each of the variables and the box-plots are presented in Figure 6.21. In this species, the ontogenetic patterns in auditory structures are very subtle considering the fact that skull size is over 20% larger in the adults compared with the sub-adults. Tympanic membrane area shows the opposite trend to skull size with the mean for age-class 2 being a little over 1 mm^2 larger (~2.5%). A similar pattern is found in incudal lever arm length although the difference in length was less than 0.10 mm (7.7%) for the age-class 2 specimens and there is considerable overlap in the ranges. No differences are apparent in mallear lever

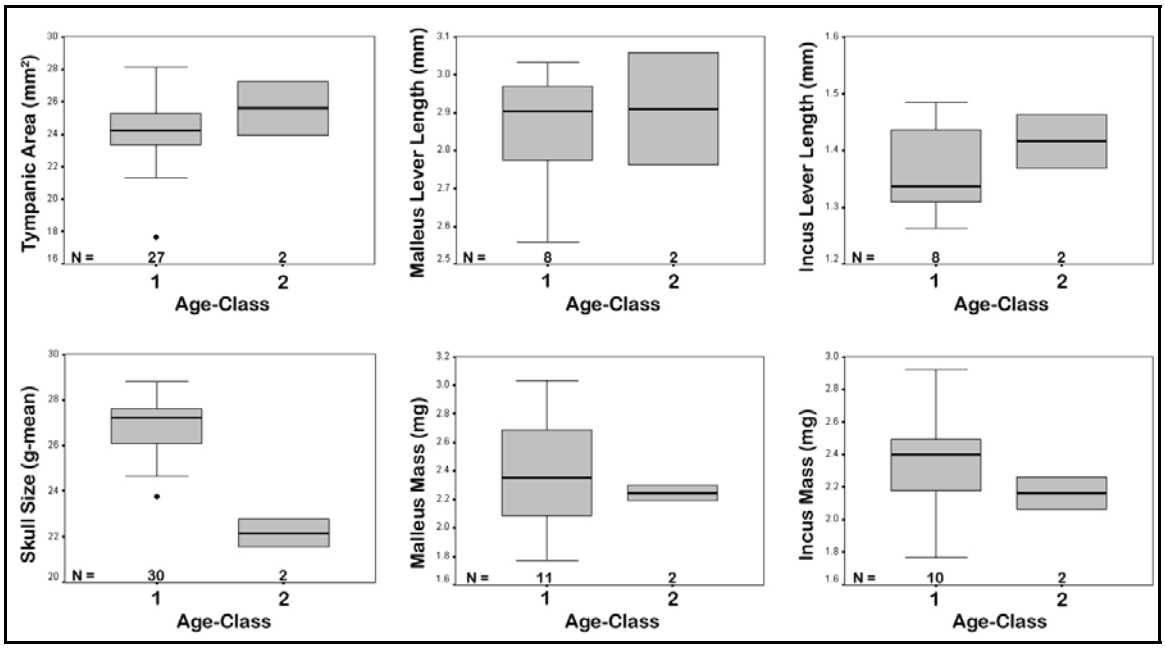

Figure 6.21 – Box-plots of ontogenetic comparisons for *Perodicticus potto*.

arm lengths. The ossicular mass patterns are in the expected direction (smaller skulls correlated with less mass) but are still very slight. The mean value for mallear mass is only ~0.10 mg^3 lighter (1.5%) for age-class 2 and within the range of the age-class 1 specimens. Incudal mass shows more separation between classes (just over 0.20 mg^3 – 2.9%), but again, there is overlap in the inter-quartile ranges. No differences were found between adult male and female specimens and *P. potto* is the only species of this genus.

Discussion

A summary of the results from the ontogenetic comparisons is presented in Table 6.9. The individual cells are coded to indicate overall changes in the size of auditory structures with age: grey signifies an increase in size from sub-adult to adult classes; black denotes a decrease in size from sub-adult to adult classes; and white indicates either

Species	A_{tm}	LA_m	LA_i	M_m	M_i
A. azarae	1 ≈ 2 > 3	1 > 2 ≤ 3	1 > 2 ≤ 3	1 > 2 >> 3	1 > 2 >> 3
A. nancymae	1 ≈ 2 ≥ 3	1 > 2	1 > 2	1 ≈ 2	1 < 2
A. vociferans	1 ≈ 3	1 ≤ 3	1 > 3	1 >> 3	1 > 3
S. boliviensis	1 ≈ 2	1 > 2	1 > 2	1 >> 2	1 > 2
S. sciureus	1 ≈ 2			1 >> 2	1 >> 2
A. seniculus	1 ≈ 2	1 >> 3	1 >> 3	1 ≥ 2 >> 3	1 ≈ 2 >> 3
A. caraya		1 >> 2	1 >> 2	1 > 2	1 > 2
A. paniscus	1 > 2	1 ≥ 2	1 << 3	1 >> 2	
C. calvus	1 < 3	1 > 3	1 ≈ 3	1 ≈ 3	1 > 3
C. moloch	1 < 2	1 ≈ 2 ≈ 3	1 ≈ 2 > 3	1 > 2 >> 3	1 > 2 >> 3
C. jacchus	1 ≈ 2	1 ≤ 2	1 ≤ 2	1 > 2	1 > 2
C. apella	1 ≈ 2	1 >> 2 < 3	1 > 2 < 3	1 ≥ 2 < 3	1 > 2 < 3
C. capucinus	1 ≈ 2 ≈ 3	1 ≈ 2 > 3	1 < 2 > 3	1 > 2 >> 3	1 > 2 >> 3
P. monochus	1 ≥ 2	1 < 2	1 < 2	1 > 2	1 ≥ 2
M. fascicularis		1 < 2 > 3	1 ≤ 2 > 3	1 > 2 >> 3	1 > 2 >> 3
E. fulvus	1 > 2	1 ≤ 2	1 ≈ 2	1 > 2	1 > 2
L. catta	1 ≈ 2 ≈ 3				
V. variegata	1 ≈ 2 < 3			1>>3	
G. senegalensis	1 ≈ 2	1 ≈ 2	1 ≈ 2	1 > 2	1 >> 2
P. potto	1 < 2	1 ≈ 2	1 < 2	1 ≈ 2	1 > 2

Table 6.9 – A summary of the ontogenetic comparisons for all species showing differences between age-classes. White background indicates either no change or a reversal in the size pattern; grey backgrounds indicate an increase in auditory structure size with increasing age; black backgrounds indicate a decrease in size with increasing age.

no change in size or an ambiguous pattern (a reversal in size from age-class 1 to 2 to 3). When the age-class 2 or 3 categories were represented by a single individual, the value had to be outside of the inter-quartile range to qualify as a significant change in size. When the value (or mean) for an age-class was completely outside of the total range for the preceding age-class, the difference was noted with a double "greater or less than" symbol.

One-half of the species (9 of 18) showed no difference (or a reversal) in the size of the tympanic membrane with increasing age-class. Of the remaining nine, five suggested an increase in size with increasing age and four implied a decrease in size with increasing age. The five species that showed an increase in size with increasing age

present rather under-whelming evidence in support of this trend. *A. azarae* indicated a decrease in size in only age-class 3 and this difference amounted to little more than 2 mm^2 (4.5%). A similar case was illustrated by *A. nancymae* except in this example, the value for the age-class 3 individual fell within the inter-quartile range of age-class 2 which had a mean nearly indistinguishable from age-class 1. In both *Aotus* species, the sub-adult values (or ranges) rarely exceeded the total range of age-class 1. Similarly, the difference in means between age-class 1 and age-class 2 for *P. monachus* is less than 1 mm^2 (1.2%) and around 2.5 mm^2 (5%) in *E. fulvus* with considerable overlap with their respective adult inter-quartile ranges. The largest difference was demonstrated by *A. paniscus* with the adults being almost 7 mm^2 larger (6.2%) than the sub-adults. Still, as mentioned previously, there were several adult *A. paniscus* specimens that had values lower than any of the sub-adults (Figure 6.9). The majority of these results suggest that the tympanic membrane grows little, if any, during the post-natal stages investigated here. Consequently, species mean estimates of tympanic membrane area will include specimens from all age-classes for further analyses.

Ontogenetic data on ossicular lever arm length were presented for seventeen species (Table 6.9). The comparisons of mallear lever arm length showed six species with no change, four with a decrease in size with increasing age-class, and seven with an increase in size with increasing age. The incudal lever arm length patterns were comparable with seven species illustrating no change, four with a decrease in size with increasing age-class, and six with an increase in size with increasing age-class. In seven species, there appeared to be a change in the size of one ossicle but not the other which

suggests that mallear and incudal lever arms are not linked, although this observation could also be the product of small sample sizes or simply sampling error.

Four of the species (*A. paniscus*, *A. nancymae*, *C. calvus*, *C. capucinus*) that displayed an increase in size with increasing age had a sample size of 1 for the sub-adult age-classes and these values always fell within the range of the adult specimens. Likewise, the age-class 2 range for incudal lever arm length of *A. vociferans* (n = 2) is also encompassed within the adult range. The mallear data for *S. boliviensis* shows the same pattern as in *A. vociferans* (n = 2 for age-class 2 and both values are within the adult range), but the incudal lever arm length for one of the two specimens placed about 0.2 mm below the adult range. The age-class 3 specimen for *C. moloch* also had an incudal lever arm length that was below the values for the other age-classes. However, the value is based on a single specimen and was only 0.1 mm below the adult range. The two species of *Alouatta* demonstrated the strongest evidence for changes in the size of auditory structures with age. Both the age-class 2 specimen of *A. caraya* and the age-class 3 specimen of *A. seniculus* had mallear and incudal lever arm lengths that fell outside of the adult ranges (between 0.1 mm and 0.3 mm below). Despite the fact that they had a sample size of only one for the sub-adults in each comparison, the consistency (both ossicles) and similarity between species is intriguing and deserves further investigation to explore if this is a unique trait of *Alouatta*.

In summary, over one-third of the comparisons found no difference between adult and sub-adult lever arm lengths and there were approximately the same number of species that displayed a decrease rather than an increase in size with age. The majority of the species that did display an increase in size were plagued by small sample sizes and

rarely had values outside of the adult range. Given that the evidence for post-natal growth of mallear and incudal lever arm lengths is negligible and the reality that ossicular data are difficult to obtain, the adult and sub-adult lever arm lengths will be pooled to derive species means.

The most compelling evidence for growth during ontogeny comes from the ossicular mass comparisons (Table 6.9). Mallear mass was compared in nineteen species and of these, fifteen showed an increase in mass with increasing age while four were suggestive of no changes in mass through ontogeny. Incudal mass was compared in seventeen species, and again, fifteen showed an increase in mass with increasing age but one species presented the opposite pattern (deceasing mass with age) and another species demonstrated no change. Three-of-the-four species (*A. nancymae*, *C. calvus*, and *C. apella*) that suggested no change had a sample size of one and the forth (*P. potto*) had a sample size of two. The trends for two of these species (*C. calvus and P. potto*) were in the right direction (increase in mass) but their values were only slightly below the means for age-class 1. The only unusual patterns were presented by the reversal in size trajectory of the *C. apella* age-class 3 specimen and the relatively massive incudal value for the *A. nancymae* age-class 2 specimen. Even with these few atypical tendencies, the bulk of the comparisons suggest that ossicular mass does increase with increasing age. Therefore, the adult and sub-adult data will not be pooled for succeeding analyses.

Table 6.10 presents a summary of the differences in sexual dimorphism for all of the variables (published values for body mass are also included). As in the previous table, the cells have been coded to help aid in interpretation: a cell that has a white background and contains the symbol "♀ ~ ♂" represents differences that were less than 5%; a black

Species	A_{tm}	LA_m	LA_i	M_m	M_i	SS	M_b1	M_b2
A. azarae	♀ ≈ ♂	♀ 5% > ♂	♀ ≈ ♂	♀ ≈ ♂	♀ ≈ ♂	♀ ≈ ♂	♀ ≈ ♂	♀ ≈ ♂
A. nancymae	♀ ≈ ♂	♀ ≈ ♂	♀ ≈ ♂	♀ ≈ ♂	♀ ≈ ♂	♀ ≈ ♂	♀ 5% > ♂	♀ ≈ ♂
A. trivirgatus	♀ ≈ ♂	♂ 15% > ♀	♂ 6% > ♀	♀ ≈ ♂	♀ ≈ ♂	♀ ≈ ♂		♀ ≈ ♂
A. vociferans	♀ ≈ ♂	♂ 10% > ♀	♀ ≈ ♂	♀ ≈ ♂	♂ 9% > ♀	♂ 5% > ♀		♀ ≈ ♂
S. boliviensis	♀ ≈ ♂	♀ ≈ ♂	♀ ≈ ♂	♀ ≈ ♂	♀ ≈ ♂	♂ **5%** > ♀	♂ **8%** > ♀	♂ 9% > ♀
S. sciureus	♀ ≈ ♂	♀ 10% > ♂	♀ 6% > ♂	♀ ≈ ♂	♀ ≈ ♂	♀ ≈ ♂	♀ ≈ ♂	♂ 6% > ♀
A. caraya	♀ ≈ ♂	♂ 9% > ♀	♂ 13% > ♀	♂ 12% > ♀	♂ 20% > ♀	♂ **18%** > ♀	♂ **15%** > ♀	♂ 16% > ♀
A. seniculus	♀ ≈ ♂	♂ 14% > ♀	♀ 8% > ♂	♂ **11%** > ♀	♂ **11%** > ♀	♂ **14%** > ♀	♂ **12%** > ♀	♂ 9% > ♀
A. paniscus	♀ ≈ ♂					♀ ≈ ♂		♀ ≈ ♂
C. calvus	♀ ≈ ♂	♀ 8% > ♂	♀ 6% > ♂	♀ ≈ ♂	♀ ≈ ♂	♂ **7%** > ♀		♂ 7% > ♀
C. melanocephalus	♂ 6% > ♀	♂ 14% > ♀	♂ 17% > ♀	♀ ≈ ♂	♀ ≈ ♂	♂ **8%** > ♀		♂ 6% > ♀
C. moloch	♀ ≈ ♂	♀ 14% > ♂	♀ 6% > ♂			♀ ≈ ♂	♀ 13% > ♂	♀ ≈ ♂
C. jacchus	♀ ≈ ♂	♀ ≈ ♂	♂ 5% > ♀	♀ ≈ ♂	♀ ≈ ♂	♀ ≈ ♂	♀ ≈ ♂	♀ ≈ ♂
C. albifrons	♀ ≈ ♂	♀ ≈ ♂	♂ 20% > ♀	♀ ≈ ♂	♀ ≈ ♂	♂ **8%** > ♀	♂ **18%** > ♀	♂ 13% > ♀
C. apella	♂ **9%** > ♀	♀ ≈ ♂	♂ 6% > ♀	♀ ≈ ♂	♀ ≈ ♂	♂ **10%** > ♀	♂ **19%** > ♀	♂ 15% > ♀
C. capucinus	♀ ≈ ♂	♂ 5% > ♀	♂ 6% > ♀	♂ 8% > ♀	♂ 7% > ♀	♀ ≈ ♂		♂ 15% > ♀
P. monochus	♀ ≈ ♂	♀ ≈ ♂	♀ ≈ ♂	♀ ≈ ♂	♂ 8% > ♀	♀ ≈ ♂		♂ 8% > ♀
P. pithecia	♀ ≈ ♂			♀ ≈ ♂	♀ ≈ ♂	♂ 5% > ♀	♂ 5% > ♀	♂ 8% > ♀
M. fascicularis	♀ ≈ ♂	♂ 9% > ♀	♂ 15% > ♀		♂ **7%** > ♀	♂ **12%** > ♀	♂ 6% > ♀	♂ 16% > ♀
M. nemestrina				♀ 10% > ♂	♂ 6% > ♀	♂ 7% > ♀		♂ 22% > ♀
E. fulvus	♀ ≈ ♂	♀ ≈ ♂	♀ ≈ ♂	♀ ≈ ♂	♀ ≈ ♂	♀ ≈ ♂		♀ ≈ ♂
E. macaco						♀ ≈ ♂		♀ ≈ ♂
L. catta	♀ ≈ ♂	♀ ≈ ♂	♀ ≈ ♂	♀ ≈ ♂	♀ ≈ ♂	♀ ≈ ♂		♀ ≈ ♂
V. variegata	♀ ≈ ♂	♀ ≈ ♂	♂ 7% > ♀	♀ ≈ ♂	♀ ≈ ♂	♀ ≈ ♂		♀ ≈ ♂
G. senegalensis	♀ ≈ ♂	♀ ≈ ♂	♀ ≈ ♂	♀ ≈ ♂	♀ ≈ ♂	♀ ≈ ♂		♂ 5% > ♀
P. potto	♀ ≈ ♂	♂ 6% > ♀	♀ ≈ ♂	♀ ≈ ♂	♀ ≈ ♂	♀ ≈ ♂		♀ ≈ ♂

Table 6.10 – A summary of the sexual dimorphism comparisons for all species. White background indicates differences that were less than 5%; grey background indicates males were larger than females; black background indicates females were larger than males. Significant differences between sexes are noted in bold. Auditory variables are the same as in previous tables, M_b1 = mass estimates of specimens from museum information, M_b2 = mass estimates based on Smith and Jungers (1997).

background represents differences where females had larger values than males (♀ > ♂); and a grey background represents differences where males had larger values than females (♂ > ♀). The first notable pattern to address is the general similarity in skull size and body mass dimorphism (although body mass appears to show slightly higher levels of sexual dimorphism). Even in the absence of significant levels of dimorphism in skull size or body mass (< 5%), several species show dimorphism in auditory structures with differences up to 15% (*e.g.*, *A. azarae*, *A. trivirgatus*, *C. jacchus*, *P. potto*, *V. variegata*). On the other hand, in most species where skull size or body mass dimorphism is greater

than 5%, there are often auditory structures with comparable levels of dimorphism. Furthermore, when skull size or body size dimorphism is 10% or greater, there is always dimorphism in at least some of the auditory variables. This suggests that species exhibiting high levels of sexual dimorphism in skull or body size, area likely to also show considerable levels of dimorphism in auditory structures.

The patterns of intra-specific differences in auditory structures are not as clearly associated with differences in overall size (skull and body) as in the previous comparisons. For example, significant differences were found in auditory structures in *Saimiri* and *Cacajao* with only 5% to 6% variation in skull size (and similar variation in body mass). However, significant differences in auditory structures were not detected in *Aotus* and *Pithecia* which showed intra-specific diversity in skull size up to 7%. Of course, the absence of differences in these genera could be linked to limitations related to sample sizes. On the other hand, the two species of *Eulumur* investigated (*E. fulvus* and *E. macaco*) had skull sizes that were only about 1% different but showed auditory variables that were about 5% dissimilar. A similar example is presented by capuchin monkeys which show little diversity in skull size (≈ 2%), yet significant distinctions were found in mallear lever arm length. These examples suggest that relatively large differences in skull size are likely to be correlated with differences in auditory structures but that there can still be variation in auditory size in species with similar skull size. Therefore, it should not be assumed that similarly sized species will have similarly sized auditory structures without first examining this potential source of intra-generic diversity. Still, one question remains to be addressed: At what levels do statistically significant

differences in auditory structures result in biologically significant differences in hearing sensitivity?

CHAPTER 7

The primary goals of this chapter are threefold: 1) to investigate correlations between form and function in the primate auditory system[36]; 2) explore the influence of phylogenetic methods on the results; and 3) compare these findings to expectations from auditory theory and previous research. The audiometric variables defined in Chapter 3 were used as measures of auditory "function". These analyses used only the speaker-derived datasets due to the large quantity of comparisons performed and the fact that the headphones-derived datasets typically had low sample sizes. The measures that were used to represent the "form" of the auditory system were the 22 morphometric variables described in Chapter 4. Table 7.1 gives the mean values for geometric mean of skull size, interaural distance and all 22 morphometric variables for the taxa with speaker-derived audiograms.

Treatment of the Data

The first essential step before proceeding with statistical comparisons was to evaluate the distributions of each variable to see if they satisfied the basic assumptions of parametric techniques (*i.e.*, that the variables are normally distributed). To test for the

[36] Preliminary analyses of these data were presented in Coleman and Ross (2004) and Coleman (2004a, 2006).

Taxa	SS	IA	S_p	A_p	A_{tm}	A_{sf}	ACR	LA_m	LA_i	LAR	PTR_{fa}	PTR_{ea}
Ateles spp.	47.9	49.8	1.38	622	58.3	1.60	36.4	3.39	2.07	1.64	59.60	39.30
Aotus spp.	29.3	28.5	1.29	467	27.4	0.75	36.4	2.85	1.67	1.71	62.10	41.00
C. jacchus	19.6	20.1	1.31	357	20.5	0.56	36.9	2.45	1.35	1.82	67.20	44.40
C. torquatus	57.0	45.1	1.26	913	.	.	.	4.31	2.50	1.72	.	.
C. mitis	44.5	38.2	.	.	47.3	1.25	37.8	4.07	2.35	1.74	65.60	43.30
E. fulvus	34.4	30.6	1.29	586	27.1	0.67	40.4	3.03	1.69	1.79	72.40	47.80
G. senegalensis	18.6	18.9	1.55	785	21.5	0.55	38.8	2.67	1.18	2.25	87.60	57.80
L. catta	33.2	30.1	1.39	578	27.1	0.77	35.0	3.41	1.62	2.10	73.70	48.60
L. albigena	51.8	46.2	.	.	56.0	1.38	40.7	4.51	2.99	1.51	61.40	40.50
M. fascicularis	47.4	38.3	1.33	874	35.0	1.11	31.5	3.59	2.15	1.67	52.70	34.80
M. fuscata	52.2	43.1	.	.	.	.	.	.	.	.	.	.
M. mulatta	47.8	40.8	1.15	1164	.	1.14	.	3.28	1.99	1.64	.	.
N. coucang	25.5	24.3	1.70	244	23.5	0.53	44.6	2.86	1.32	2.17	96.90	63.90
P. potto	26.9	26.6	1.57	253	24.4	0.74	33.2	2.87	1.37	2.09	69.20	45.70
P. anubis	70.6	55.4	.	.	.	.	.	.	.	.	.	.
P. cynocephalus	70.5	56.6	.	.	.	.	.	.	.	.	.	.
Saimiri spp.	26.2	27.0	1.08	354	20.7	0.63	32.9	2.33	1.39	1.68	55.10	36.40
T. glis	17.6	16.4	1.19	162	11.0	0.26	41.8	2.30	1.21	1.91	79.80	52.70

Taxa	ITR_{fa}	ITR_{ea}	M_m	M_i	M_{mi}	M_s	M_{mis}	V_{me}	V_{tc}	V_{es}	V_{ac}	L_c
Ateles spp.	0.0102	0.0155	5.92	9.38	15.30	0.85	16.1	.	.	.	.	.
Aotus spp.	0.0094	0.0143	2.33	3.32	5.70	0.19	5.8	0.40	0.07	0.12	0.22	22.4
C. jacchus	0.0082	0.0124	1.32	1.48	2.80	0.14	2.9	0.15	0.05	0.05	0.05	20.3
C. torquatus	.	.	.	.	.	.	.	.	.	.	.	.
C. mitis	0.0088	0.0133	4.90	5.31	10.20	.	.	1.85	0.16	1.17	0.52	30.9
E. fulvus	0.0077	0.0117	3.72	3.46	7.20	.	.	0.39	.	.	.	21.2
G. senegalensis	0.0051	0.0077	1.42	1.85	3.30	0.14	3.4	0.22	0.08	0.10	0.03	17.6
L. catta	0.0064	0.0098	3.48	3.68	7.20	.	.	0.68	.	.	.	20.8
L. albigena	0.0108	0.0164	.	7.35	.	.	.	.	.	.	.	.
M. fascicularis	0.0114	0.0172	5.37	4.26	9.60	0.36	10.0	1.73	0.11	1.17	0.45	28.8
M. fuscata	.	.	.	.	.	.	.	.	.	.	.	.
M. mulatta	.	.	.	.	.	.	.	.	.	.	.	.
N. coucang	0.0048	0.0072	2.24	2.72	5.00	.	.	0.37	0.06	0.23	0.07	18.6
P. potto	0.0069	0.0105	2.37	2.37	4.70	0.23	5.0	0.37	0.06	0.21	0.09	21.0
P. anubis	.	.	8.55	.	.	.	.	.	.	.	.	.
P. cynocephalus	.	.	.	9.65	.	.	.	.	.	.	.	.
Saimiri spp.	0.0108	0.0164	1.65	1.92	3.60	0.19	3.8	0.28	0.04	0.09	0.16	25.7
T. glis	0.0066	0.0099	0.77	1.20	2.00	.	.	0.06	.	.	.	15.0

Table 7.1 - Mean morphometric variables[37] for all taxa with speaker derived audiograms. Linear measurements are in millimeters, areal measurements are in mm^2, weight measurements are in milligrams and volume measurements are in milliliters. See chapter 4 for more details.

[37] SS = g-mean of skull size; IA = interaural distance; S_p = pinna shape index; A_p = pinna area; A_{tm} = tympanic membrane area; A_{sf} = stapedial footplate area; ACR = areal convergence ratio; LA_m = malleus lever arm length; LA_i = incus lever arm length; LAR = lever arm ratio; PTR = pressure transformer ratio; ITR = impedance transformer ratio; M_m = malleus mass; M_i = incus mass; M_{mi} = malleus + incus mass; M_s = stapes mass; $M_{mis} = M_{mi} + M_s$; V_{me} = total middle-ear volume; V_{tc} = tympanic cavity volume; V_{es} = epitympanic sinus volume; V_{ac} = accessory cavity volume; L_c = cochlear length.

goodness-of-fit between the actual distributions and a normal distribution, the Shapiro-Wilk W test for normality was employed. The null hypothesis for this test is that the sample is taken from a normal distribution so that a p-value of > 0.05 suggests that the null hypothesis can not be rejected. The morphometric and audiometric data were tested for normality by considering both the absolute and log-transformed values.

Table 7.2 shows the results from the Shapiro-Wilk W test for the morphometric variables. The columns with a superscript of "1" represent the results from the raw data and those with a "2" represent the results from the log-transformed data. When testing the raw data (using only the species from the optimal speaker dataset), six variables failed the test of normality: ITR_{fa}, ITR_{ea}, incus mass, total middle ear volume, tympanic cavity volume, and epitympanic sinus volume. However, once the data were log-transformed,

MORPHOMETRIC VARIABLE	Optimal Speaker Dataset					Full Speaker Dataset				
	n	W^1	*P* value[1]	W^2	*P* value[2]	*n*	W^1	*P* value[1]	W^2	*P* value[2]
Skull Size (G-Mean)	12	0.8839	0.0985	0.9427	0.5337	18	0.9251	0.1592	0.9542	0.4953
Interaural Distance	12	0.9263	0.3427	0.9756	0.9598	18	0.9584	0.5708	0.9702	0.8022
Pinna Ratio	8	0.9564	0.7754	0.9512	0.7239	11	0.9483	0.6219	0.9509	0.6551
Pinna Area	8	0.8925	0.2471	0.9392	0.6028	11	0.9542	0.6978	0.9445	0.5745
Tympanic Membrane Area	9	0.9499	0.6899	0.8812	0.1615	13	0.8625	0.0416	0.9329	0.3720
Stapedial Footplate Area	10	0.9236	0.3879	0.9145	0.3132	14	0.9341	0.3478	0.9463	0.5051
Areal Convergence Ratio	9	0.9382	0.5627	0.9447	0.6320	13	0.9704	0.8994	0.9667	0.8521
Malleus Lever Arm Length	10	0.9359	0.5094	0.9458	0.6188	15	0.938	0.3577	0.9581	0.6588
Incus Lever Arm Length	10	0.8693	0.0981	0.9072	0.2626	15	0.9117	0.1440	0.9445	0.4423
Ossicular Lever Arm Ratio	10	0.8956	0.1958	0.8956	0.1957	15	0.9063	0.1186	0.9187	0.1839
PTR (full area)	9	0.9662	0.8604	0.9556	0.7514	13	0.9587	0.7338	0.9769	0.9612
PTR (effective area)	9	0.9722	0.9125	0.9864	0.9890	13	0.9493	0.5876	0.9766	0.9589
ITR (full area)	9	0.3898	<0.0001	0.9501	0.6909	13	0.3110	<0.0001	0.9365	0.4136
ITR (effective area)	9	0.5358	<0.0001	0.9415	0.5973	13	0.5918	<0.0001	0.9333	0.3762
Malleus Mass	9	0.8702	0.1235	0.9859	0.9875	14	0.9072	0.1437	0.9872	0.9978
Incus Mass	10	0.7370	0.0025	0.9515	0.6860	15	0.8764	0.0419	0.9671	0.8133
Malleus+Incus Mass	9	0.9414	0.5972	0.9921	0.9983	13	0.8925	0.1055	0.9873	0.9983
Stapes Mass	6	0.8278	0.1030	0.9027	0.3900	7	0.6854	0.0026	0.8425	0.1048
Ossicular Mass	6	0.8363	0.1215	0.9300	0.5801	7	0.8043	0.0452	0.9149	0.4312
Total Middle Ear Volume	9	0.7099	0.0019	0.9735	0.9226	11	0.7172	0.0008	0.9429	0.5549
Tympanic Cavity Volume	9	0.4760	<0.0001	0.7046	0.0016	11	0.6332	<0.0001	0.8409	0.0324
Epitympanic Sinus Volume	7	0.6036	0.0003	0.8971	0.3136	8	0.6697	0.0010	0.8756	0.1708
Accessory Cavity Volume	7	0.8213	0.0660	0.9845	0.9783	8	0.8307	0.0603	0.9562	0.7729
Cochlea Length	9	0.9748	0.9325	0.9844	0.9831	11	0.9493	0.6648	0.9726	0.9118

Table 7.2 - Results for normality tests (Shapiro-Wilk) of morphometric variables. Significant variables (non-normally distributed) highlighted in grey. Superscript of 1 = raw data, superscript of 2 = log-transformed data.

only tympanic cavity volume appeared to be non-normally distributed. Somewhat similar results were found when testing the full speaker (including the suboptimal species) morphometric dataset. These results are also given in Table 7.2 and show that the same six variables, as well as tympanic membrane area, stapes mass, and ossicular mass, appear to be non-normally distributed using the raw data. But as before, after log-transformation only tympanic cavity volume showed indications of being non-normally distributed.

Table 7.3 presents the results from the Shapiro-Wilk W test for normality for the audiometric variables. Testing the optimal speaker raw data, middle audible area, SPL of the first peak, frequency of first peak, and frequency of the second peak all showed significant results rejecting the null hypothesis of normality. Even after these data were log-transformed, these same four variables appeared to have non-normal distributions. Using the full speaker dataset (raw data), SPL and frequency of the first peak, frequency of the second peak, and frequency of the mid-range dip all showed *P*-values of < 0.05. Using the logged values, low audible area, high audible area, and frequency of the first peak, second peak and mid-range dip were all significant indicating non-normal distributions. In some cases logging the data resulted in a normal distribution, in other cases it had no discernable effect, and in two cases it appeared to transform the data into non-normal distributions (low and high audible area).

Taken as a whole, it was impossible to compare the audiometric data with the morphometric data (using either raw or log-transformed data) without violating the assumption of normality for at least some of the variables. One possible solution to this

AUDIOMETRIC VARIABLE	Optimal Speaker Dataset					Full Speaker Dataset				
	n	W[1]	*P* value[1]	W[2]	*P* value[2]	*n*	W[1]	*P* value[1]	W[2]	*P* value[2]
SPL @ 250 Hz	12	0.9475	0.6007	0.9537	0.6915	18	0.9579	0.5622	0.9463	0.3704
Low-Frequency Cutoff	5	0.9628	0.8270	0.9724	0.8907	8	0.9058	0.3257	0.9812	0.9684
High-Frequency Cutoff	10	0.9367	0.5170	0.9449	0.6092	12	0.9467	0.5892	0.9517	0.6617
Low Audible Area	12	0.9169	0.2609	0.9017	0.1669	16	0.9188	0.1612	0.8638	0.0219
Middle Audible Area	12	0.8414	0.0288	0.8173	0.0148	18	0.9366	0.2528	0.9000	0.0577
High Audible Area	10	0.9826	0.9775	0.9522	0.6943	12	0.9521	0.6678	0.8501	0.0368
Total Audible Area	10	0.9628	0.8171	0.9469	0.6315	12	0.9506	0.6463	0.9360	0.4485
Total Range	10	0.9319	0.4670	0.9028	0.2351	12	0.9475	0.6003	0.9147	0.2452
SPL Peak 1	10	0.7314	0.0021	0.8197	0.0251	16	0.7991	0.0026	0.9183	0.1582
Frequency Peak 1	10	0.7612	0.0049	0.7809	0.0085	16	0.7461	0.0006	0.7784	0.0014
SPL Peak 2	12	0.9515	0.6583	0.9580	0.7550	17	0.9722	0.8560	0.9351	0.2648
Frequency Peak 2	12	0.8391	0.0270	0.8445	0.0314	18	0.8265	0.0037	0.8538	0.0097
SPL Mid-Range Dip	10	0.9184	0.3441	0.8917	0.1770	15	0.9367	0.3430	0.8890	0.0647
Frequency Mid-Range Dip	10	0.8830	0.1413	0.8963	0.1995	15	0.8436	0.0141	0.8717	0.0358

Table 7.3 - Results for normality tests (Shapiro-Wilk) of audiometric variables. Same results coding as table 7.2.

problem is to simply use non-parametric statistical methods that do not rely on the assumption of normal distributions. However, non-parametric techniques are not currently available in the phylogenetic statistical software used here (see below) and also preclude the use of regression analyses which are useful for developing predictive equations. Thus, in order to use a uniform methodology in all of the comparisons to be presented next, raw data were used and most of the comparisons employed parametric techniques. The determination to use raw data was made in part because it is easier to interpret the association between two variables using raw data and it avoids the bias introduced when transforming variables from logged values back to raw values (which is beneficial when used for predictive equations-such as in this dissertation). Still, to evaluate the effect of logging the data on the results, both logged and unlogged data were initially analyzed. Since the results were virtually identical, and for the reasons presented above, only the results produced using raw values will be reported.

MORPHOMETRIC – AUDIOMETRIC COMPARISONS USING TIPS[38]

In this section each morphometric variable was tested to evaluate its correlation with individual audiometric variables using traditional statistical approaches (*i.e.*, using non-phylogenetically adjusted data). The first results to be reported will be based on correlations using the optimal speaker dataset. These data are preferable since there is an increased confidence in the audiograms used to derive the audiometric values (see Chapter 3) and rarely does any comparison use more than one species from a single genus. However, since this dataset has a maximum sample size of only 12, a relaxed significance criterion was adopted and correlations producing a p-value of < 0.100 will be reported. The results will be followed by the same analyses utilizing the full speaker dataset. The last results reported for each variable present comparisons between the *relative* morphometric values and the audiometric data (both optimal and full speaker datasets). In all comparisons, the high-frequency sensitivity analyses were performed both with and without *Callithrix jacchus*. This selective omitting of data was performed since the high-frequency thresholds for *C. jacchus* are suspect based on the considerations in Chapter 3 and the low relative values evident in Figure 7.2 (see below).

EXTRA-EAR

Skull size

The next step before examining the correlations between morphometric and audiometric variables was to investigate how these parameters are related to changes in skull size. As defined and used in previous chapters, skull size was approximated by

[38] TIPS refers to using data at the tips of a phylogenetic tree (*i.e.*, actual species values without employing any phyogenetic corrective techniques).

taking the geometric mean of 14 cranial measurements. The relationships between skull size and each morphometric variable are shown graphically as scatterplots in Figure 7.1 along with the significance values (p) and Pearson's correlation coefficients (r). Examining these plots, it can be seen that every variable except pinna ratio and areal convergence ratio was significantly correlated with skull size. These data also show that there are generally positive correlations between skull size and individual morphological structures. However, several of the derivative variables, in particular the ones that are posited to induce a mechanical advantage (*i.e.*, ACR, LAR, PTR, ITR[39]), show a negative relationship so that as skull size increases there is a decrease in mechanical advantage.

There is also a general pattern whereby related groups of variables often show similar correlations with skull size. Ossicular mass, interaural distance, tympanic membrane area and stapedial footplate area produced high correlation coefficients (> 0.900). Individual ossicular lever arm lengths (r = 0.895 – 0.924) and cochlear length (r = 0.851) fell towards the middle of the correlation values while transformer ratios (PTR and ITR), areal convergence and lever arm ratios, and pinna variables showed the weakest correlations. Middle ear volumes illustrate the widest range of correlation values with accessory cavity volume (r = 0.966), epitympanic sinus volume (r = 0.951), and total middle ear volume (r = 0.918) showing high coefficients while tympanic cavity volume (r = 0.790) had a substantially lower coefficient. Considering the fact that all but two of the morphometric variables were significantly correlated with skull size the following morphometric-audiometric correlation analyses will use both absolute and relative (morphometric variable / g-mean of skull size) values.

[39] Although note that the smaller the ITR value the higher the theoretical impedance matching ability as contrasted with PTR values where a larger value indicates higher theoretical pressure transfer.

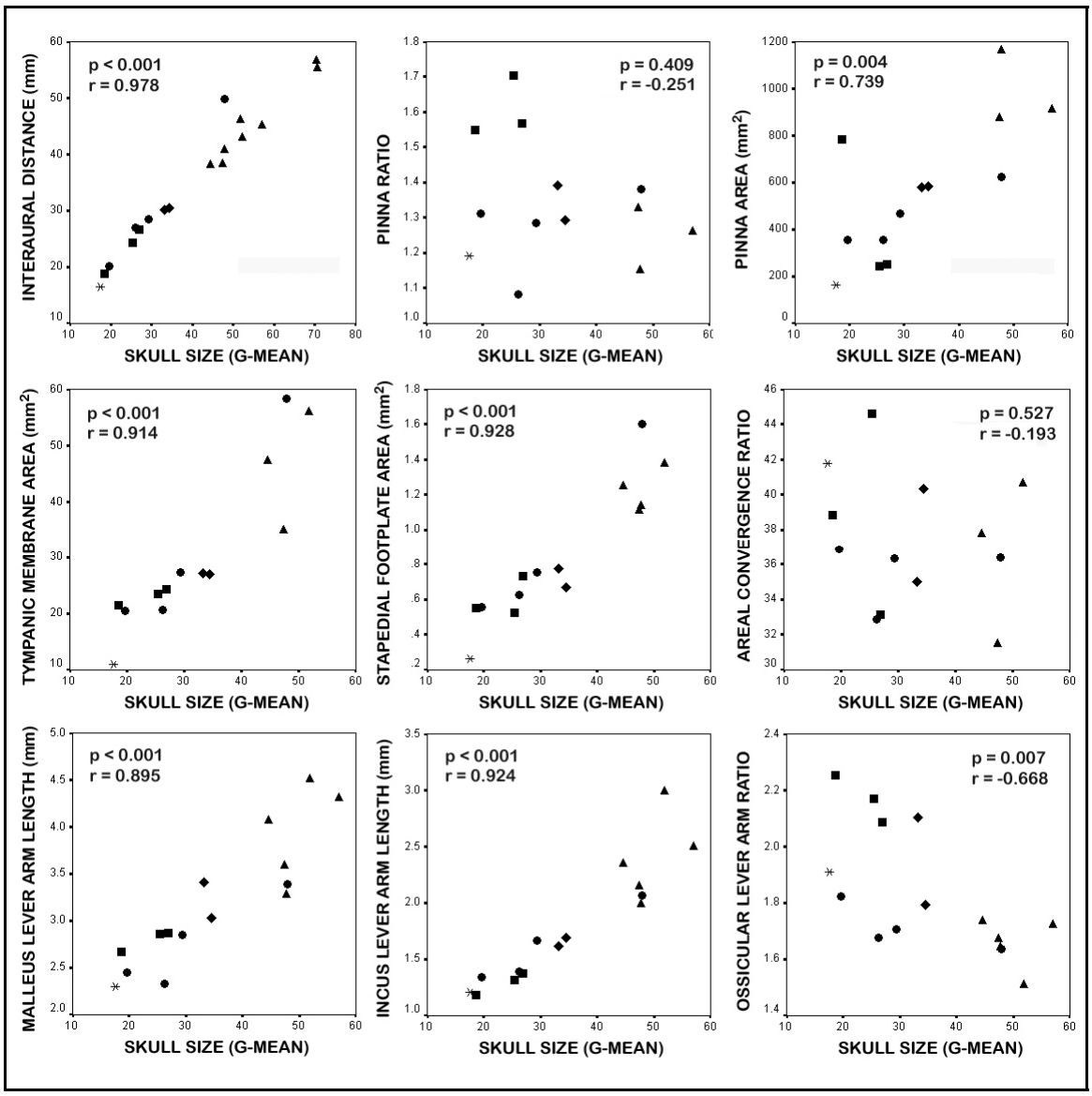

Figure 7.1 - Scatterplots showing relationships between morphometric variables and geometric mean of skull size. Statistics computed using Pearson's correlation coefficient. Coding for taxonomic groups given in last panel.

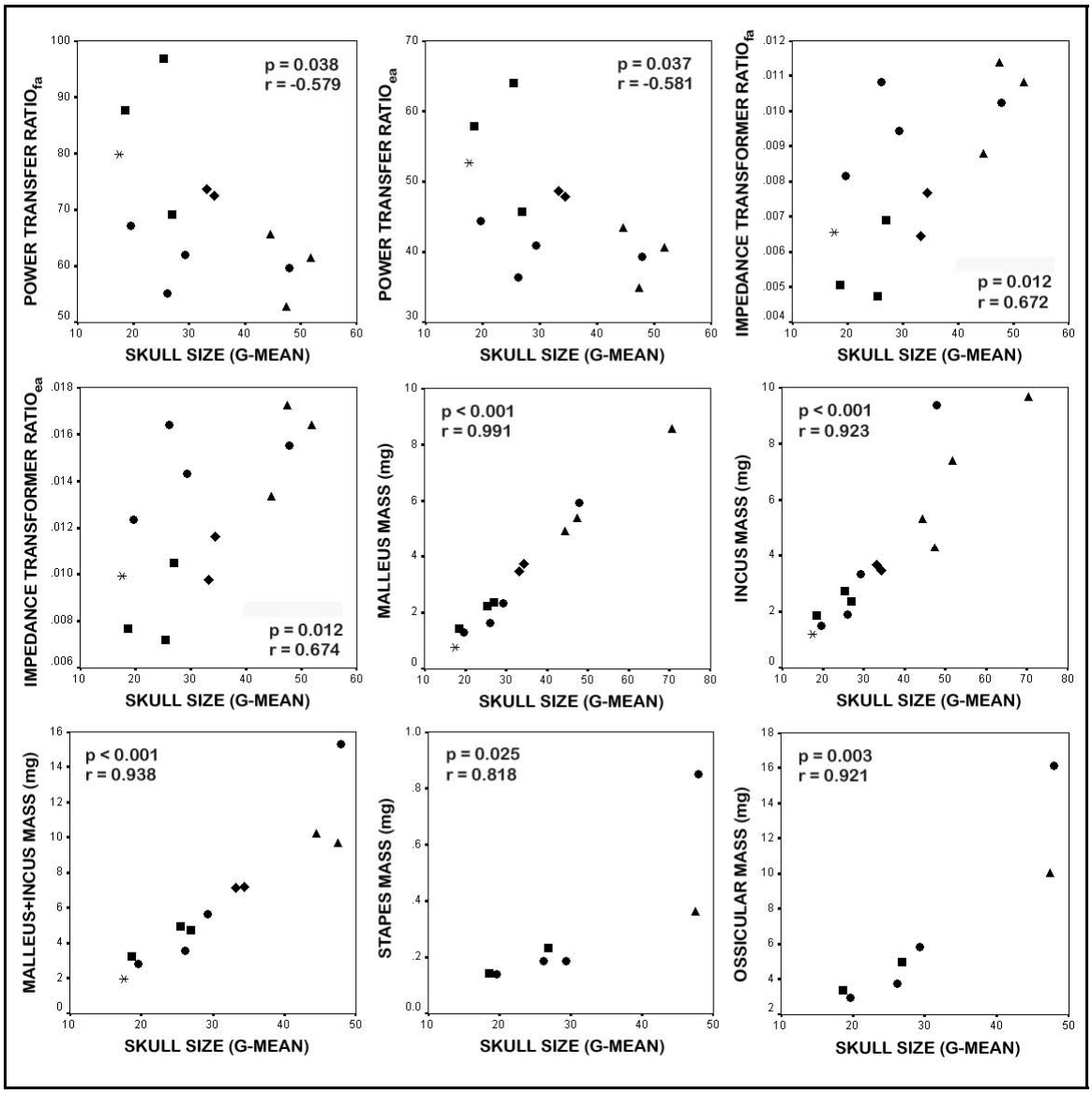

Figure 7.1 cont.

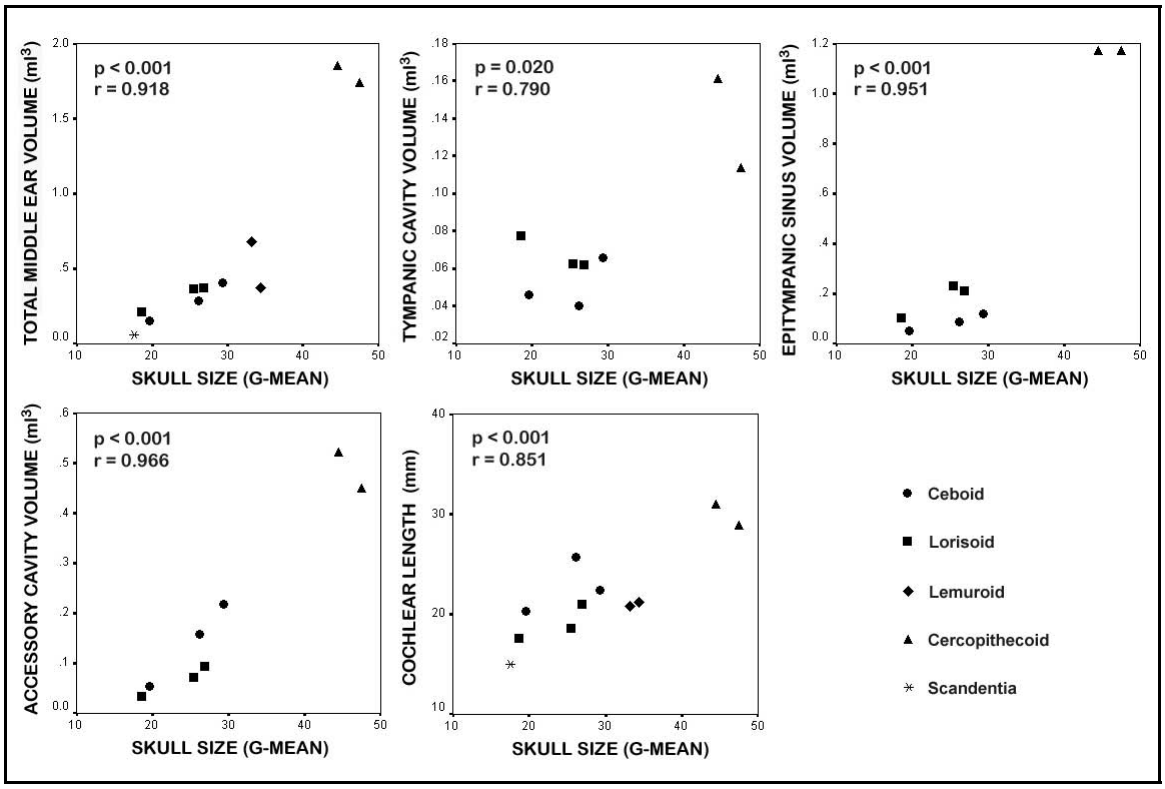

Figure 7.1 cont.

The final preliminary step was to examine the relationships between skull size and measures of auditory sensitivity. The associations between skull size and all audiometric variables (full speaker dataset) are shown as scatterplots in Figure 7.2. Evaluating first the full speaker dataset, five audiometric variables showed significant correlations[40] with skull size: **low audible area**, **SPL @ 250 Hz**, **middle audible area**, **SPL of the first peak**, and **SPL of the mid-range dip**. In addition, low-frequency cutoff, total audible area, and range in octaves were approaching significant levels ($p < 0.100$). Removing *C. jacchus* from the analyses caused both high-frequency cutoff ($p = 0.072$, $r = -0.563$, $n =$

[40] Throughout this chapter variables that are statistically correlated ($p \leq 0.050$) with another variable will be presented in bold, and those that are nearing significance ($p = 0.100 - 0.051$) will be underlined.

11) and high audible area ($p = 0.072$, $r = -0.562$, $n = 11$) to also approach statistical significance.

Essentially the same pattern was found using the optimal speaker dataset with five audiometric variables significantly correlated with skull size: **low audible area** ($p = 0.002$, $r = 0.787$, $n = 12$, **SPL @ 250 Hz** ($p = 0.006$, $r = -0.744$, $n = 12$), **middle audible area** ($p = 0.049$, $r = 0.578$, $n = 12$), **total audible area** ($p = 0.033$, $r = 0.672$, $n = 10$), and **SPL of the mid-range dip** ($p = 0.022$, $r = -0.709$, $n = 10$). When *C. jacchus* was removed from the high-frequency comparisons, as before high audible area ($p = 0.094$, $r = -0.591$, $n = 9$) and high-frequency cutoff ($p = 0.091$, $r = -0.596$, $n = 9$) were nearing significance.

Although the audiometric variables were not as strongly correlated with skull size as were the morphometric variables (*i.e.*, number of significant variables and correlation coefficients) a few noteworthy trends are evident. First, several of the audiometric variables suggest that as skull size increases there is an increase in low-frequency sensitivity but a trend towards a decrease in high-frequency sensitivity. There was also a decrease in the threshold of mid-range dip as the skull gets bigger. One potential shortcoming with the frequency of the first peak data is that only a few species have a value that is not either 1 or 2 kHz. The final point to make is that many of the scatterplots illustrate the tendency for closely related taxa to group together. This observation strengthens the interest in using both traditional statistical techniques and phylogenetic corrective methods to analyze these data.

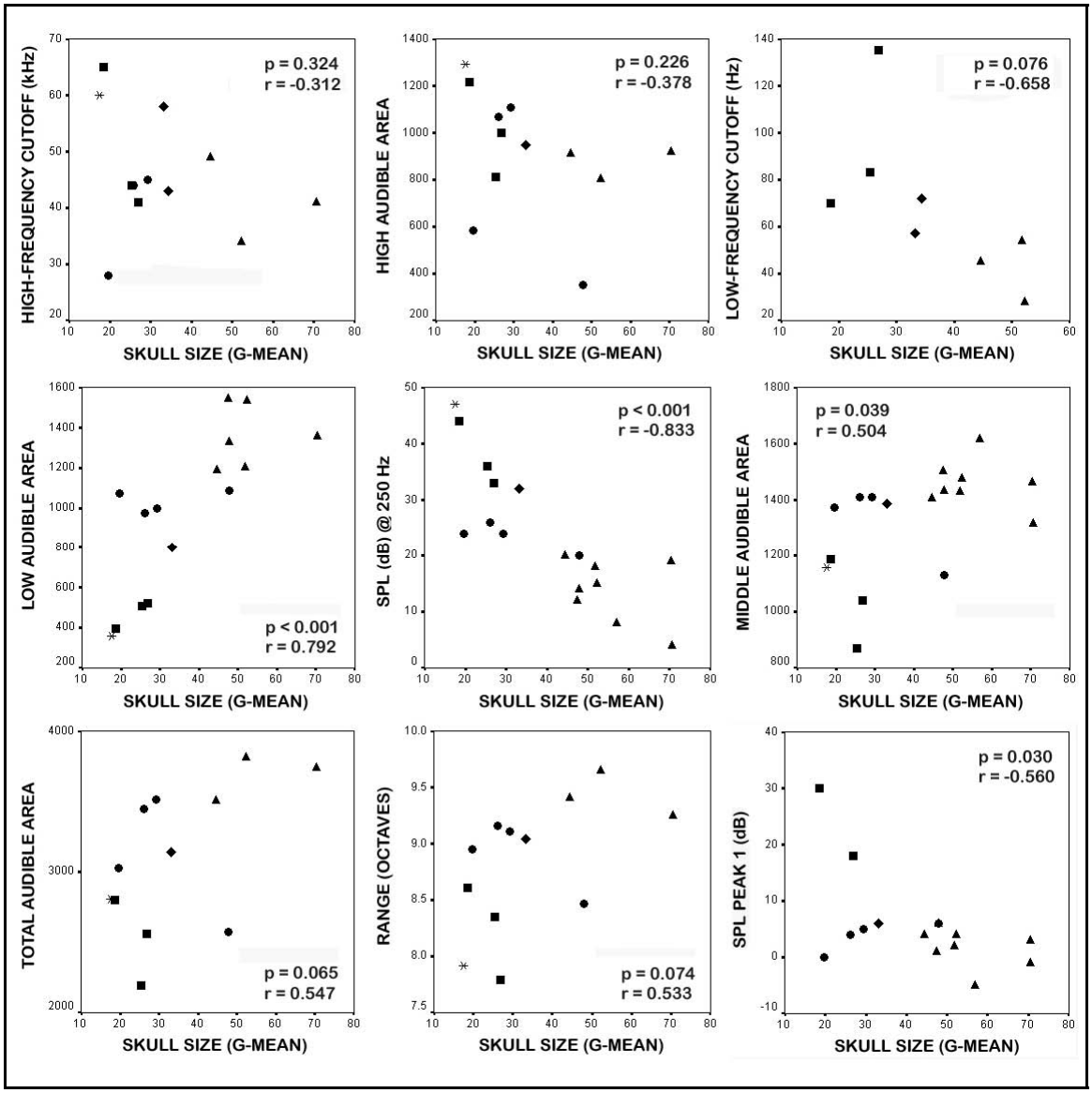

Figure 7.2 - Scatterplots showing relationships between audiometric variables and geometric mean of skull size. Statistics computed using Pearson's correlation coefficient. Coding for taxonomic groups given in last panel.

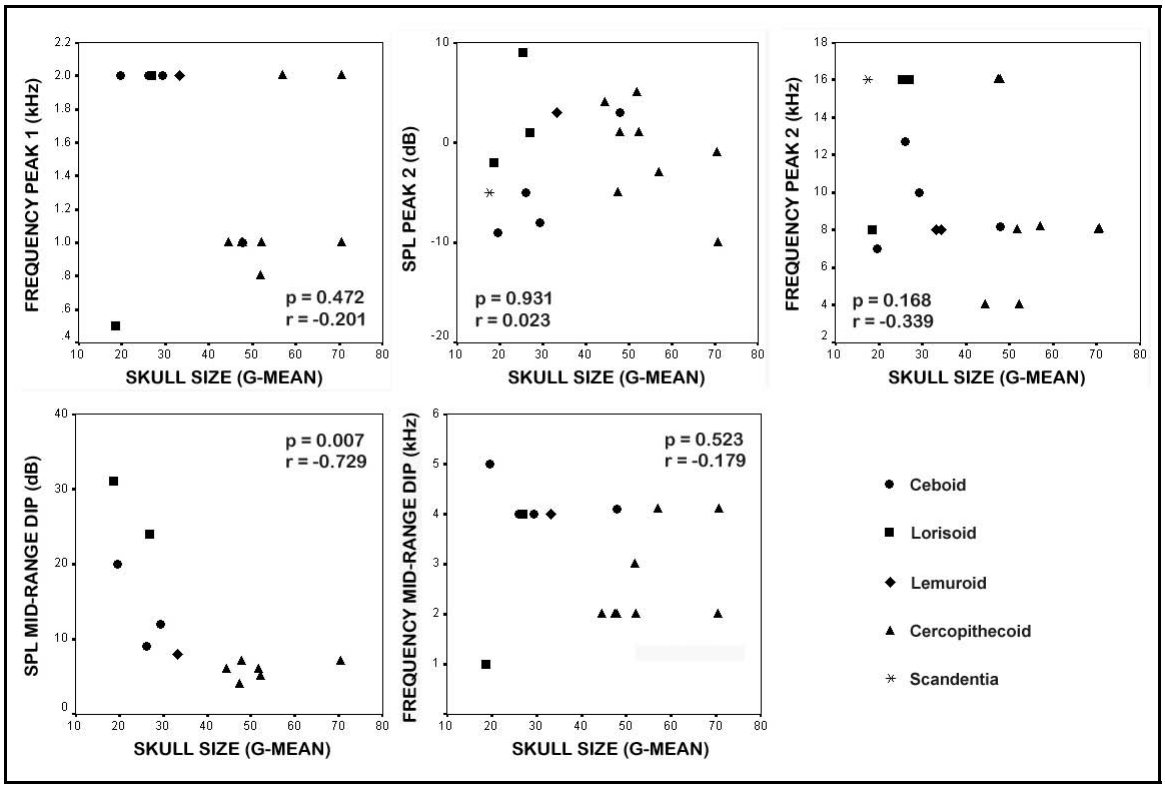

Figure 7.2 cont.

Interaural Distance

The first morphometric variable to discuss is interaural distance. This variable serves as a proxy for the distance between the ears which has been suggested to be a strong selective factor on high-frequency hearing (Masterson *et al*. 1969; Heffner 2004). Using the optimal speaker dataset, significant correlations were found between interaural distance (absolute values) and numerous audiometric variables including **low audible area** ($p = 0.002$, $r = 0.789$, $n = 12$), **SPL @ 250 Hz** ($p = 0.004$, $r = -0.762$, $n = 12$), **middle audible area** ($p = 0.047$, $r = 0.582$, $n = 12$), **total audible area** ($p = 0.028$, $r = 0.687$, $n = 10$), range in octaves ($p = 0.063$, $r = 0.607$, $n = 10$), and **SPL of the mid-range dip** ($p = 0.019$, $r = -0.719$, $n = 10$). High-frequency cutoff ($p = 0.067$, $r = -0.633$, $n = 9$)

and high audible area ($p = 0.077$, $r = -0.616$, $n = 9$) were nearing significance once *C. jacchus* was purged from the dataset.

Employing the full speaker dataset, significant correlations were found with **low audible area** ($p = 0.001$, $r = 0.758$, $n = 15$), **SPL @ 250 Hz** ($p < 0.001$, $r = -0.818$, $n = 17$), **SPL of the first peak** ($p = 0.039$, $r = -0.537$, $n = 15$), and **SPL of the mid-range dip** ($p = 0.006$, $r = -0.737$, $n = 12$). In addition, middle audible area ($p = 0.077$, $r = 0.439$, $n = 17$) and high audible area ($p = 0.099$, $r = -0.499$, $n = 12$) were getting close to significant levels. **High-frequency cutoff** ($p = 0.050$, $r = -0.602$, $n = 11$), **high audible area** ($p = 0.017$, $r = -0.700$, $n = 11$) became significant when *C. jacchus* was removed. The relationship between interaural distance and each variable[41] that showed a notable correlation ($p < 0.100$) are shown in Figure 7.3.

Both datasets reflect similar patterns: there is a clear signal showing that as interaural distance increases there is an increase in low-frequency sensitivity. In contrast, SPL of the mid-range dip shows negative correlations with interaural distance. Although not as strongly supported, increases in interaural distance appear associated with decreases in high-frequency sensitivity (and of course the converse is true as well – increased high-frequency sensitivity is correlated with decreased interaural distance).

When relative interaural distance was evaluated several of the significant correlations using the optimal speaker data disappeared. **Low audible area** ($p = 0.013$, $r = -0.691$, $n = 12$), **SPL @ 250 Hz** ($p = 0.033$, $r = 0.614$, $n = 12$), and **SPL of the mid-range dip** ($p = 0.015$, $r = 0.739$, $n = 10$) were significant using the optimal speaker dataset. When the full speaker dataset was utilized, **low-frequency cutoff** ($p = 0.034$, $r =$

[41] If a variable was significant using both the optimal and full speaker datasets, the one that had the highest correlation coefficient is displayed.

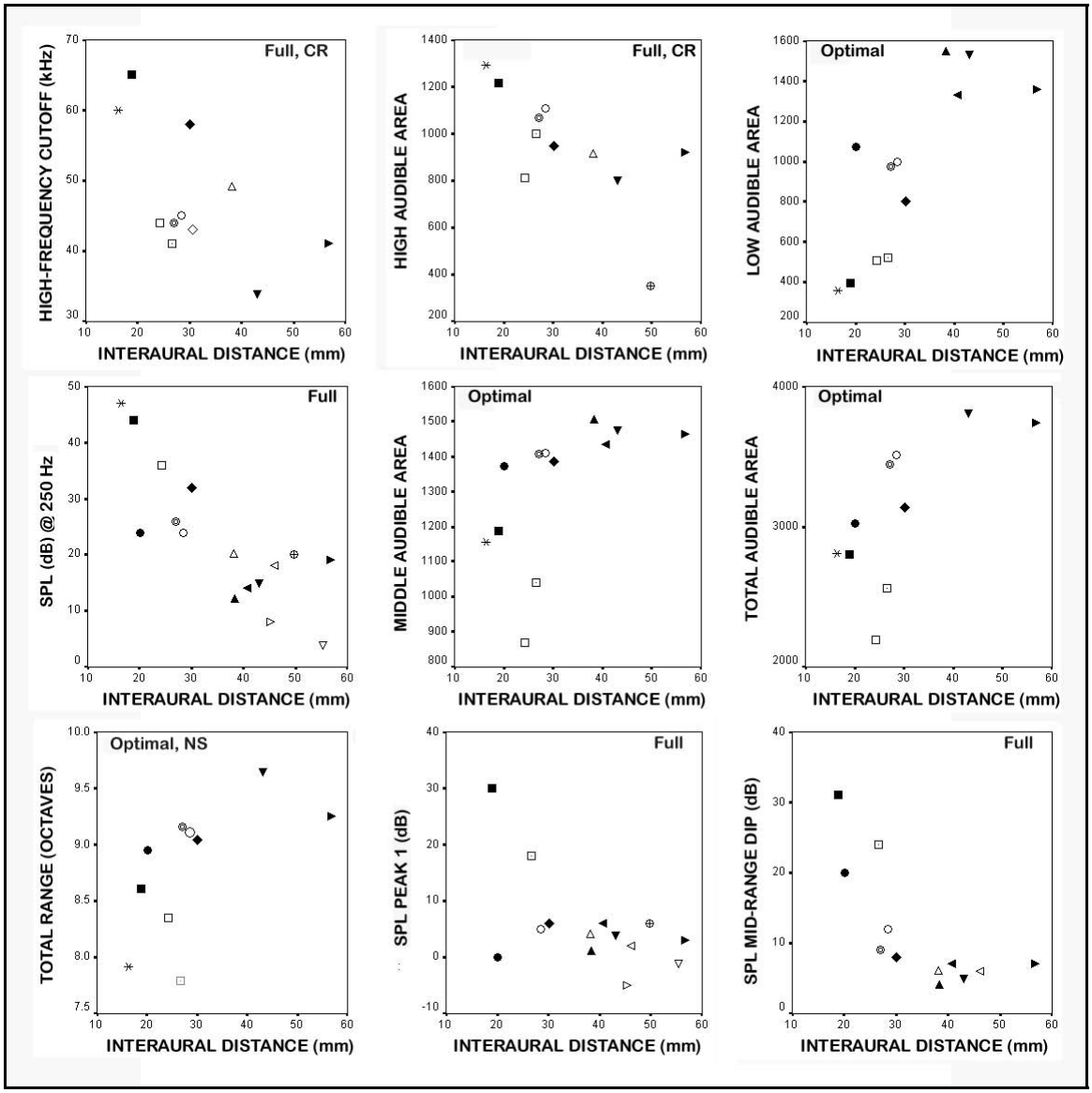

Figure 7.3 - Notable correlations between interaural distance and audiometric variables. Full = full-speaker dataset; Optimal = optimal-speaker dataset; CR = *C. jacchus* removed from analysis; NS = nearing significance (p = 0.100 - 0.050). See next figure for taxonomic coding.

0.744, n = 8), **low audible area** (p = 0.012, r = -0.627, n = 15), **SPL @ 250 Hz** (p < 0.004, r = 0.657, n = 17), **middle audible area** (p = 0.019, r = -0.561, n = 17), **total audible area** (p = 0.042, r = -0.593, n = 12), **SPL of the first peak** (p = 0.044, r = 0.526, n = 15), and **SPL of the mid-range dip** (p = 0.005, r = 0.750, n = 12) were all significant. These relationships are shown in Figure 7.4. High-frequency sensitivity measures were not significant whether *C. jacchus* was included or not.

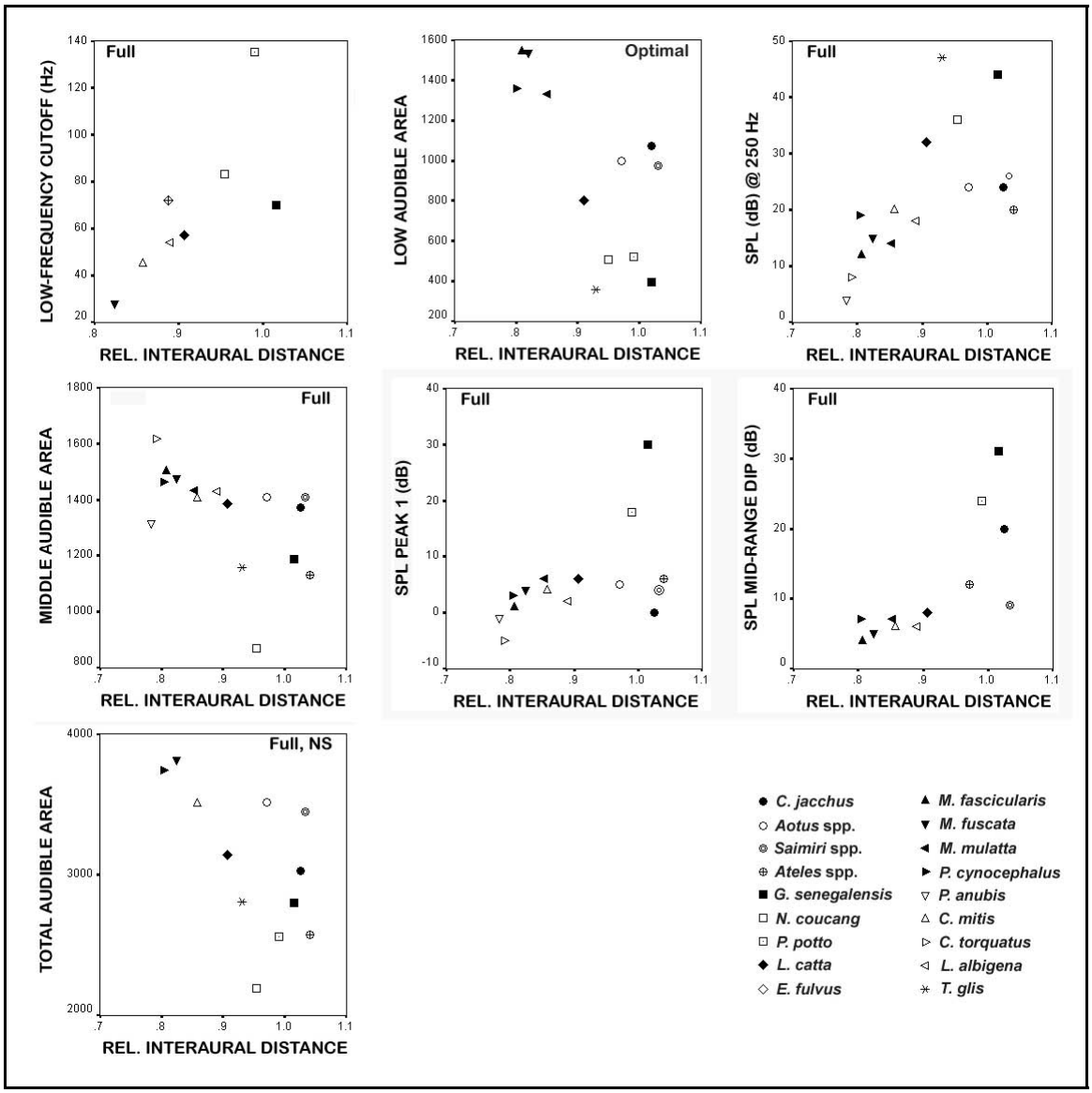

Figure 7.4 - Notable correlations with relative interaural distance.

OUTER EAR

Pinna Shape Ratio

Significant correlations were found between pinna ratio and **total audible area** (p = 0.018, r = -0.798, n = 8), **middle audible area** (p = 0.014, r = -0.744, n = 10), **SPL of the first peak** (p = 0.047, r = 0.714, n = 8), **SPL of the dip** (p = 0.045, r = 0.718, n = 8), and SPL of the second peak (p = 0.058, r = 0.615, n = 10) using the optimal speaker dataset. When considering the full speaker dataset, the results were very similar. In this case, **total audible area** (p = 0.017, r = -0.763, n = 9), **middle audible area** (p = 0.009, r = -0.713, n = 12), **SPL of the first peak** (p = 0.026, r = 0.692, n = 10), **SPL of the dip** (p = 0.045, r = 0.718, n = 8), and **SPL of the second peak** (p = 0.037, r = 0.605, n = 12) were significant. These results are displayed graphically in Figure 7.5. The exclusion of

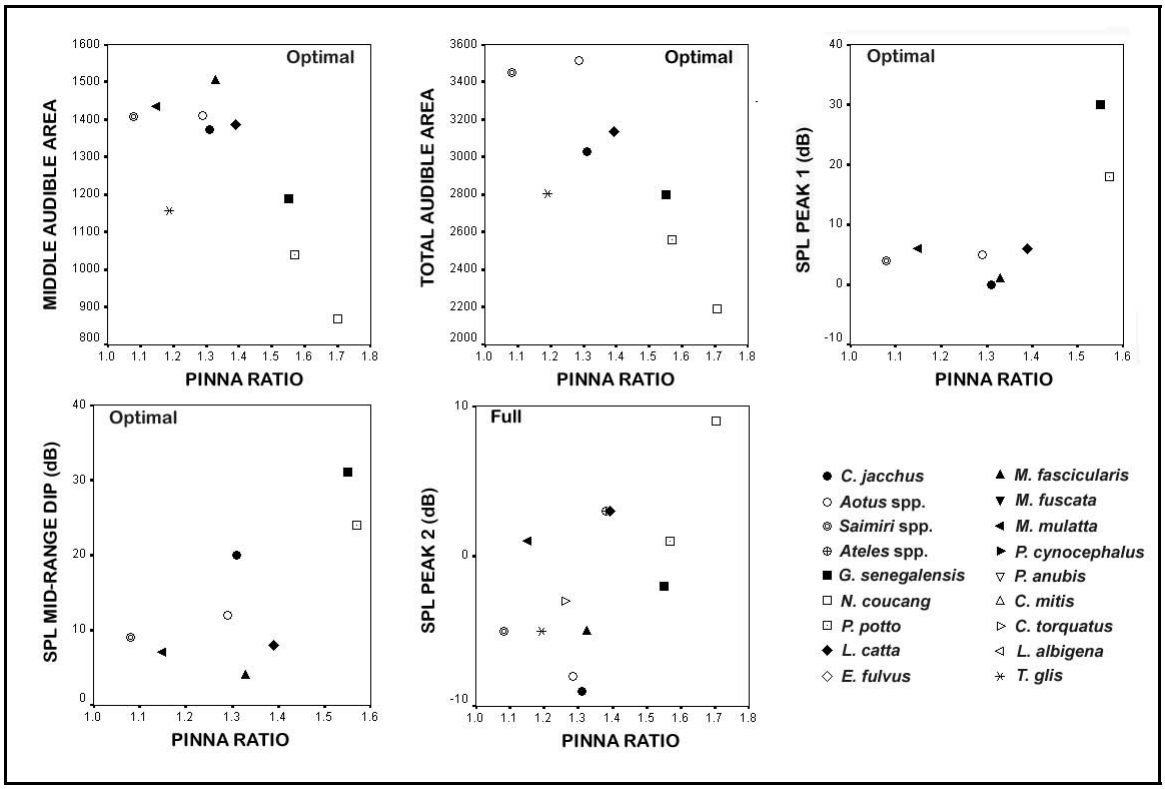

Figure 7.5 - Notable correlations with pinna shape ratio.

C. jacchus from the high frequency sensitivity comparisons had no affect on the results. In general, as the pinna ratio increases (the outer ear becomes taller and narrower), the taxa become less sensitive overall (total audible area), particularly in the mid-frequency range (middle audible area). This is also associated with an increase (less sensitivity) in the SPL of first peak and suggestions of an increase in the SPL of second peak in sensitivity.

Pinna Area

Using the optimal speaker dataset, five audiometric variables were correlated with absolute pinna area including low audible area ($p = 0.059$, $r = 0.614$, $n = 10$), SPL @ 250 Hz ($p = 0.081$, $r = -0.577$, $n = 10$), middle audible area ($p = 0.088$, $r = 0.567$, $n = 10$), **frequency of the first peak** ($p = 0.015$, $r = -0.807$, $n = 8$), and **frequency of the mid-range dip** ($p = 0.016$, $r = -0.805$, $n = 8$). Using the full speaker dataset produced similar results except the p-values and correlation coefficients shifted slightly. The significant variables were **low audible area** ($p = 0.042$, $r = 0.619$, $n = 11$), **SPL @ 250 Hz** ($p = 0.024$, $r = -0.645$, $n = 12$), **middle audible area** ($p = 0.039$, $r = 0.602$, $n = 12$), frequency of the first peak ($p = 0.057$, $r = -0.617$, $n = 10$) and **frequency of the dip** ($p = 0.037$, $r = -0.663$, $n = 10$). The significant variables are illustrated in Figure 7.6 and show that as the absolute area of the pinna increases there is an increase in low and mid-range sensitivity with a decrease in the frequency of the first peak and possibly the frequency of the mid-range dip.

Exploring relative pinna area (optimal data), SPL of the first peak ($p = 0.098$, $r = 0.624$, $n = 8$), **frequency of the first peak** ($p = 0.010$, $r = -0.835$, $n = 8$) and **frequency**

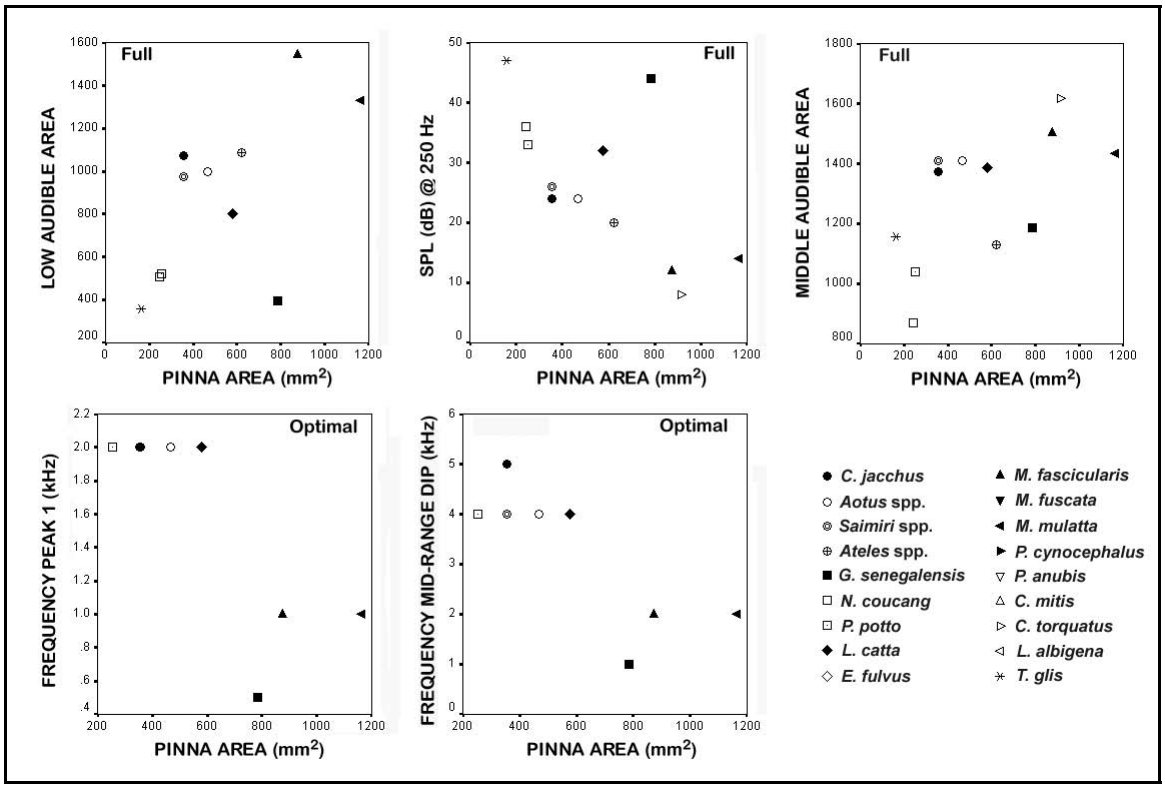

Figure 7.6 - Notable correlations with pinna area.

of the mid-range dip ($p = 0.026$, $r = -0.767$, $n = 8$) showed p-values below 0.100. These variables illustrated the same relationships with relative pinna area when the full speaker dataset was used: SPL of the first peak ($p = 0.061$, $r = 0.610$, $n = 10$), **frequency of the first peak** ($p = 0.025$, $r = -0.698$, $n = 10$) and **frequency of the mid-range dip** ($p = 0.008$, $r = -0.781$, $n = 10$). In addition, high-frequency cutoff ($p = 0.099$, $r = 0.621$, $n = 8$) was nearing traditional significance after omitting *C. jacchus*. These variables are shown in Figure 7.7. Examining these graphs it can be seen that *G. senegalensis* is driving many of the patterns. These results suggest that an increase in the relative pinna area is correlated with a decrease in the frequency of the first peak in sensitivity and frequency of the mid-range dip (and possibly a decrease in SPL of the first peak).

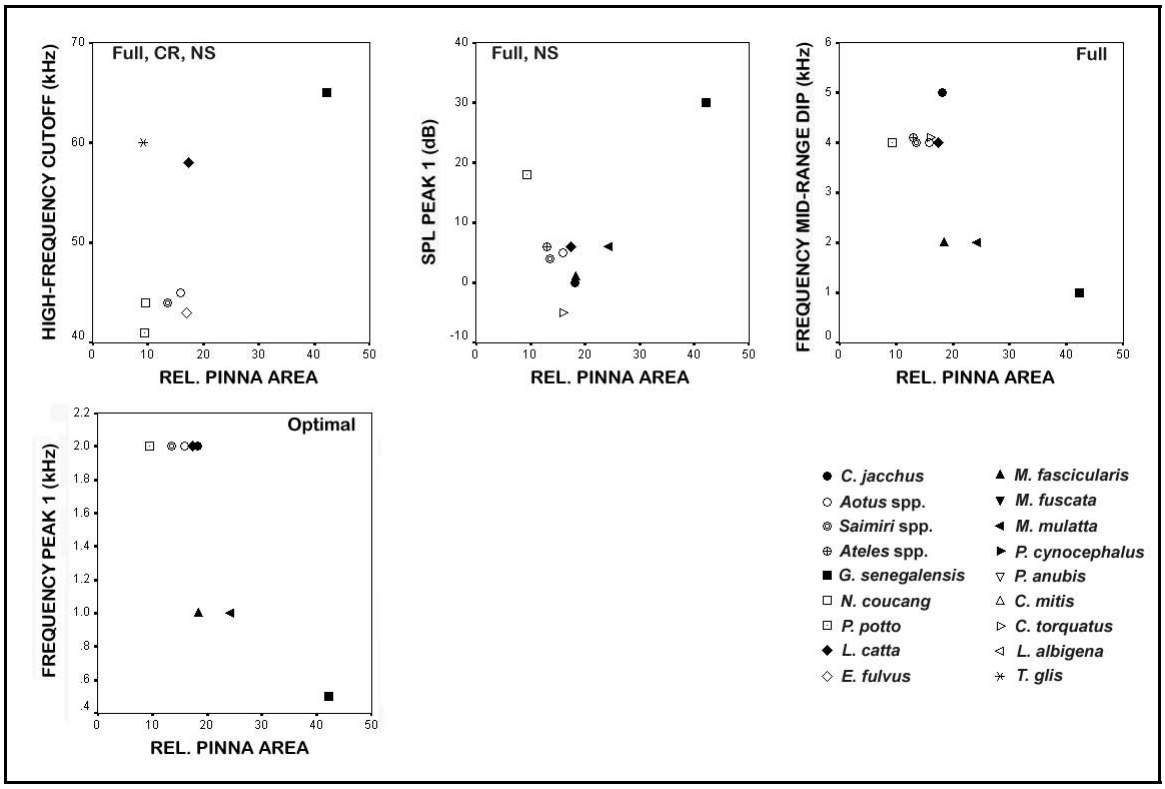

Figure 7.7 - Notable correlations with relative pinna area. *G. senegalensis* is an outlier in most graphs and appears to be partially driving the patterns.

MIDDLE EAR

Tympanic Membrane Area

Tympanic membrane area was significantly correlated with **SPL @ 250 Hz** ($p = 0.016$, $r = -0.766$, $n = 9$) and **low audible area** ($p = 0.037$, $r = 0.696$, $n = 9$) using the optimal speaker dataset. Using the full speaker dataset, five audiometric variables showed notable correlations with tympanic membrane area: **SPL @ 250 Hz** ($p = 0.012$, $r = -.0698$, $n = 12$), **low audible area** ($p = 0.029$, $r = 0.627$, $n = 12$), **high audible area** ($p = 0.035$, $r = -0.669$, $n = 10$), frequency of the first peak ($p = 0.081$, $r = -0.577$, $n = 10$), and SPL of the mid-range dip ($p = 0.085$, $r = -0.604$, $n = 9$). Removing *C. jacchus* from the

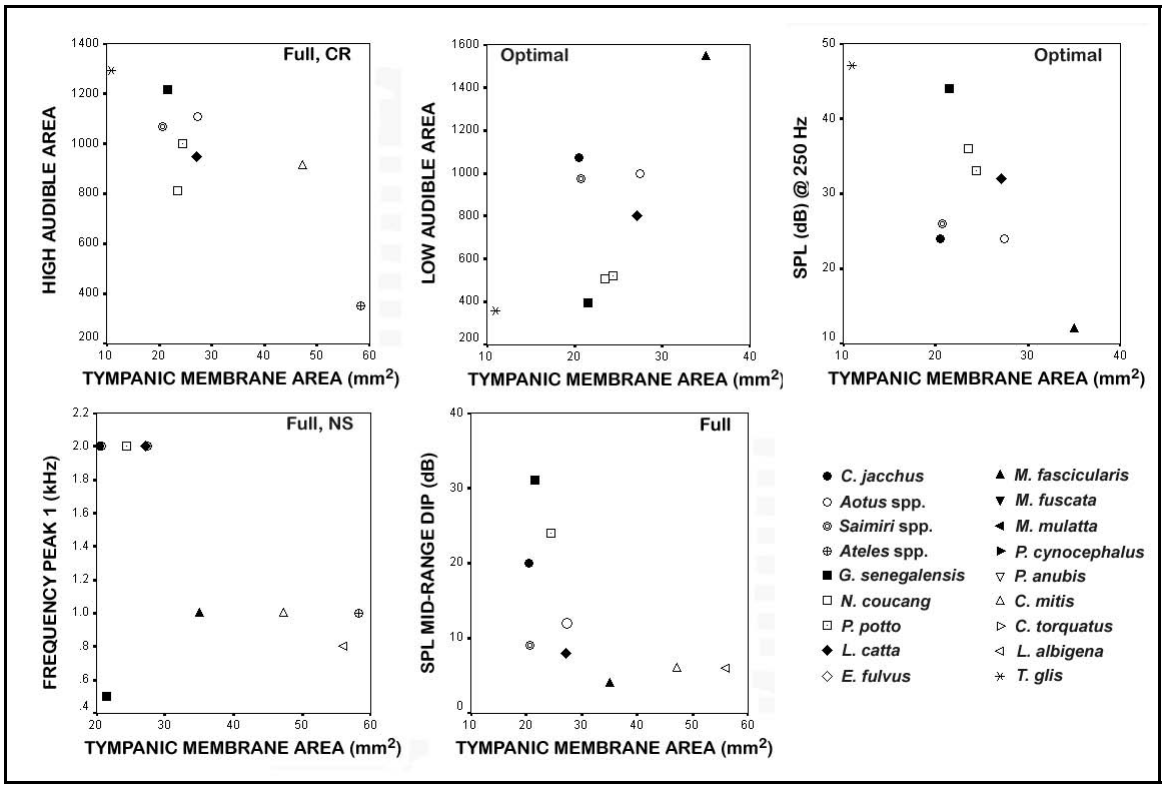

Figure 7.8 - Notable correlations with tympanic membrane area.

analysis caused a slight increase in the correlation coefficient with **high audible area** ($p = 0.004$, $r = -0.844$, $n = 9$). Scatterplots of these variables are given in Figure 7.8. These results suggest that as tympanic membrane size increases there is an increase in low frequency sensitivity and a decrease in high-frequency sensitivity. Additionally, there are weaker associations showing that the magnitude of the mid-range dip and the frequency of the first peak get lower with increasing tympanic membrane size.

When the relative size of the tympanic membrane was examined, it showed a significant correlation with **SPL of the mid-range dip** ($p = 0.006$, $r = 0.898$, $n = 7$) using the optimal speaker dataset and frequency of the second peak ($p = 0.053$, $r = -0.660$, $n = 9$) was approaching significance. When the full speaker dataset was used, SPL of the

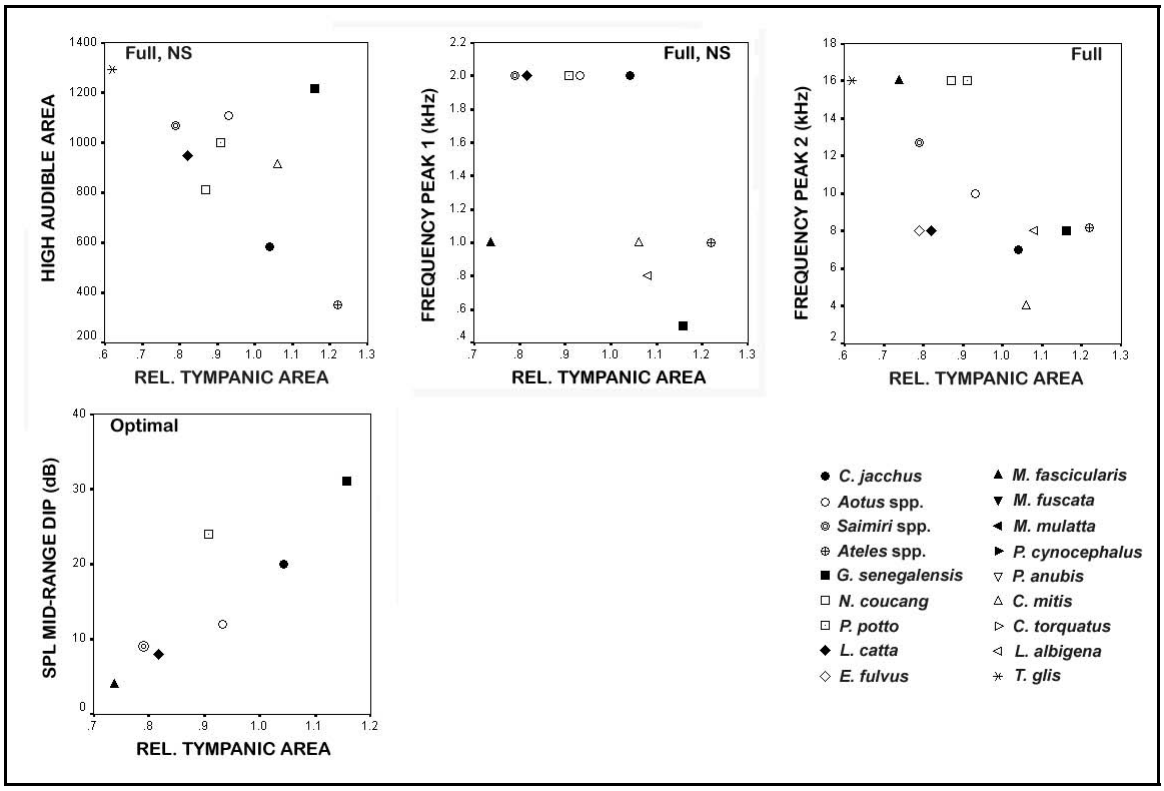

Figure 7.9 - Notable correlations with relative tympanic membrane area.

mid-range dip became non-significant while **frequency of the second peak** ($p = 0.018$, $r = -0.642$, $n = 13$) reached traditional significance levels. In addition, high audible area ($p = 0.081$, $r = -0.576$, $n = 10$) and frequency of the first peak ($p = 0.098$, $r = -0.553$, $n = 10$) illustrated relatively low significance values. Somewhat unexpectedly, high audible area became non-significant once *C. jacchus* was removed. These scatterplots are also given in Figure 7.9.

Stapedial Footplate Area

The relationships between stapedial footplate area and hearing sensitivity were similar to those for tympanic membrane area. Four audiometric variables (optimal

dataset) were significantly correlated with the surface area of the stapedial footplate: **SPL @ 250 Hz** (p = 0.001, r = -0.864, n = 10), **low audible area** (p = 0.004, r = 0.813, n = 10), middle audible area (p = 0.086, r = 0.569, n = 10), and SPL of the mid-range dip (p = 0.056, r = -0.694, n = 8). Three of these variables remained significant using the full speaker dataset, **SPL @ 250 Hz** (p = 0.002, r = -0.778, n = 13), **low audible area** (p = 0.006, r = 0.718, n = 13), and **SPL of the mid-range dip** (p = 0.021, r = -0.711, n = 10). **High audible area** (p = 0.037, r = -0.662, n = 10) and frequency of the first peak (p = 0.076, r = -0.555, n = 11) also showed relatively strong correlations with stapedial footplate area. **High audible area** (p = 0.005, r = -0.831, n = 9) showed an even higher correlation when *C. jacchus* was removed from the comparison. The significant variables are shown in Figure 7.10. Similar to the tympanic membrane results, as stapedial

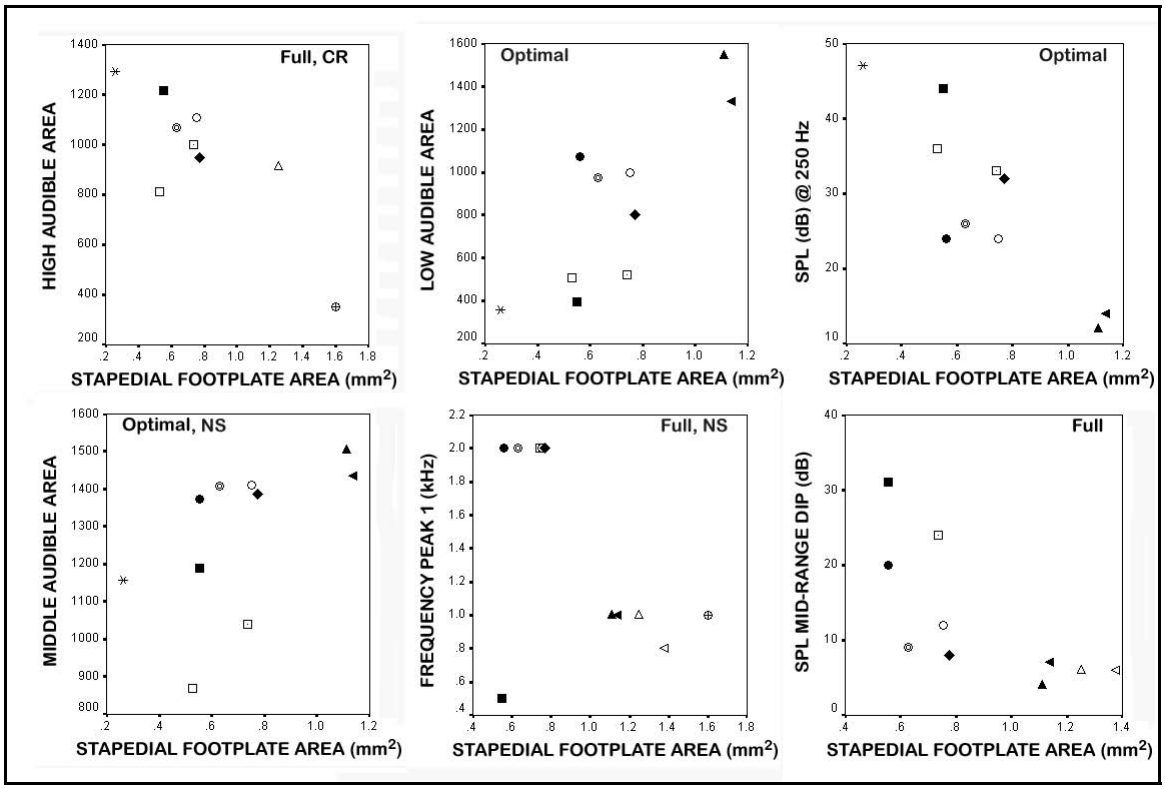

Figure 7.10 - Notable correlations with stapedial footplate area.

footplate area increases there is an increase in low-frequency sensitivity (and possibly mid-frequency sensitivity), a decrease in the SPL of the mid-frequency dip, and a trend towards decreased high-frequency sensitivity.

The relative stapedial footplate comparisons found **SPL of the mid-range dip** ($p < 0.001$, $r = 0.964$, $n = 8$) to be highly significant using the optimal speaker dataset and SPL of the first peak ($p = 0.075$, $r = 0.659$, $n = 8$) and frequency of the second peak ($p = 0.078$, $r = -0.551$, $n = 10$) showed weaker correlations. Using the full speaker dataset, the correlations with **SPL of the mid-range dip** ($p = 0.018$, $r = 0.725$, $n = 10$) and frequency of the second peak ($p = 0.055$, $r = -0.523$, $n = 14$) were only slightly altered but SPL of the first peak became non-significant and high audible area ($p = 0.095$, $r = -0.556$, $n = 10$) was nearing traditional significance levels. As with the high-frequency results from

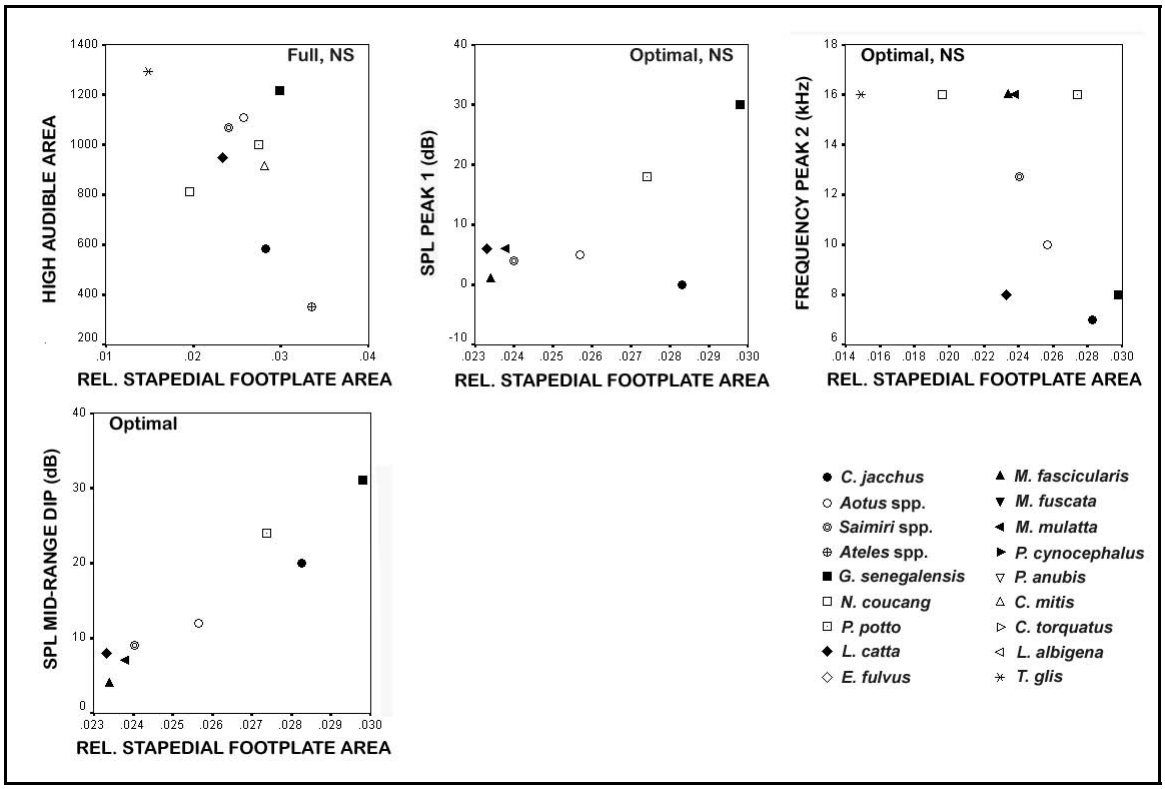

Figure 7.11 - Notable correlations with relative stapedial footplate area.

relative tympanic membrane area, high audible area produced a p-value above 0.100 after *C. jacchus* was excluded. Scatterplots of these patterns are given in Figure 7.11. The results suggest that increases in the relative area of the stapedial footplate are associated with an increase in the SPL of the mid-range dip and possibly a downward shift in the frequency of the second peak

Areal Convergence Ratio

Four audiometric variables were correlated with the areal convergence ratio using the optimal speaker dataset: low audible area ($p = 0.051$, $r = -0.665$, $n = 9$), **SPL @ 250 Hz** ($p = 0.040$, $r = 0.689$, $n = 9$), total audible area ($p = 0.098$, $r = -0.624$, $n = 8$), and **middle audible area** ($p = 0.036$, $r = -0.699$, $n = 9$). Using the full speaker dataset, only

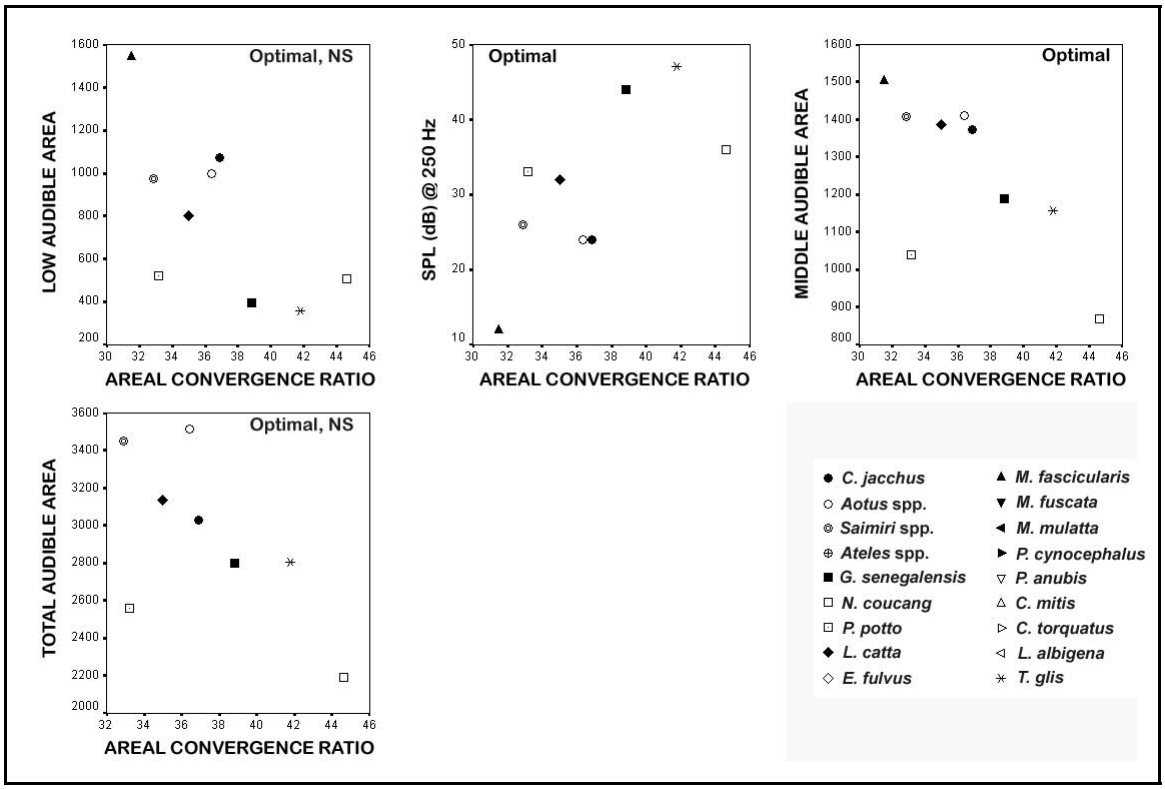

Figure 7.12 - Notable correlations with areal convergence ratio.

middle audible area (p = 0.085, r = -0.517, n = 12) illustrated a correlation (albeit weak) with areal convergence ratio. These relationships are displayed in Figure 7.12. Removing *C. jacchus* had no affect on the high-frequency comparisons for either dataset.

Malleus Lever Arm Length

Using the optimal speaker dataset, SPL @ 250 Hz (p = 0.089, r = -0.564, n = 10) showed a weak correlation with the lever arm length of the malleus. In contrast, when the full speaker dataset was used, four variables produced notable correlations: **low audible area** (p = 0.038, r = 0.581, n = 13), **SPL @ 250 Hz** (p = 0.007, r = -0.681, n = 14), middle audible area (p = 0.079, r = 0.485, n = 14), and SPL of the mid-range dip (p = 0.067, r = -0.599, n = 10). *C. jacchus* had no significant impact on the high-frequency

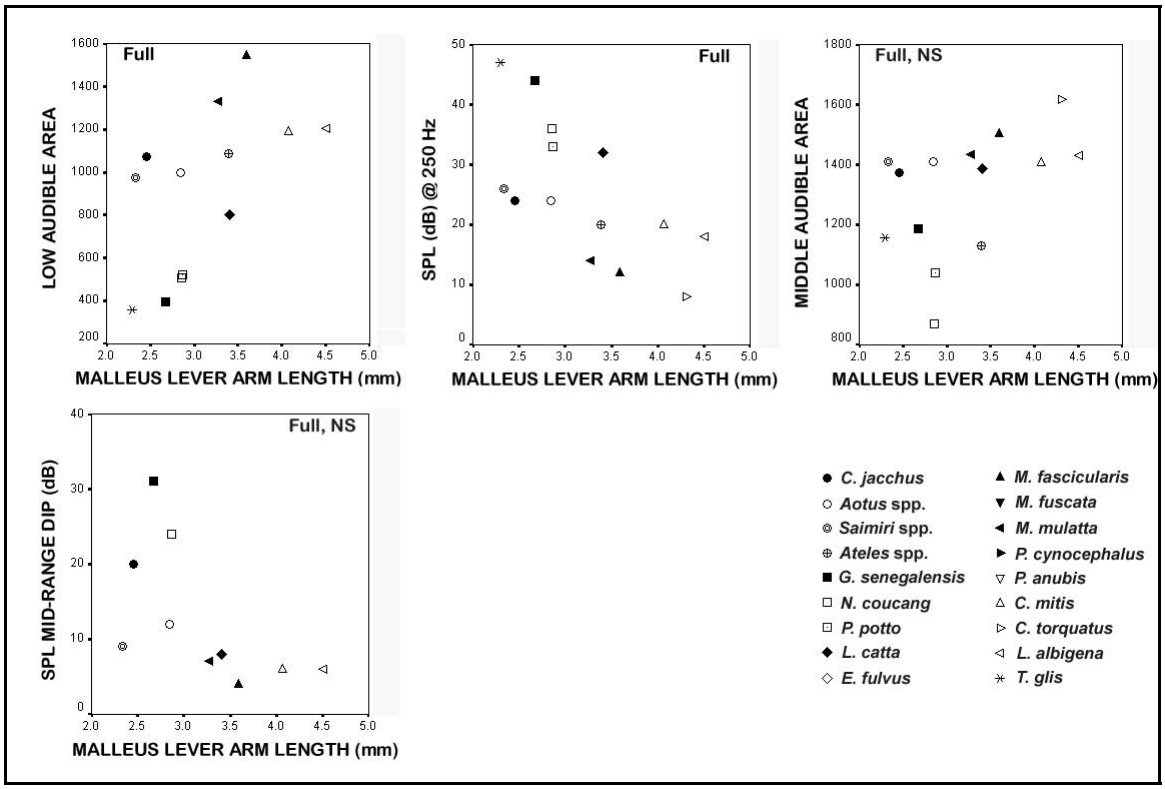

Figure 7.13 - Notable correlations with malleus lever arm length.

results. Scatterplots of these variables are presented in Figure 7.13. These results show a relationship between increased mallear lever arm length and an increase in low frequency sensitivity and a decrease in the SPL of the mid-range dip.

Examining the relative length of the malleus, three audiometric variables were significantly correlated with mallear lever arm length using the optimal dataset: **low audible area** ($p = 0.007$, $r = -0.783$, $n = 10$), **SPL @ 250 Hz** ($p = 0.002$, $r = 0.848$, $n = 10$), and **SPL of the mid-range dip** ($p = 0.004$, $r = 0.883$, $n = 8$). **High-frequency cutoff** ($p = 0.034$, $r = 0.791$, $n = 7$) became significant with *C. jacchus* excluded. The results for the full speaker dataset were similar with a few additional correlations detected: **low audible area** ($p = 0.002$, $r = -0.784$, $n = 13$); **SPL @ 250 Hz** ($p < 0.001$, $r = 0.858$, $n = 14$); **SPL of the first peak** ($p = 0.022$, $r = 0.649$, $n = 12$), and **SPL of the mid-range dip** ($p < 0.001$, $r = 878$, $n = 10$). In this case, when *C. jacchus* was removed, both **high-frequency cutoff** ($p = 0.012$, $r = 0.787$, $n = 9$) and **high audible area** ($p = 0.015$, $r = 0.769$, $n = 9$) became significant. These relationships are shown in Figure 7.14.

The interesting aspect of these results is that the association with low-frequency sensitivity is in the opposite direction of that using the absolute length of the malleus. The trend for SPL of the mid-range dip was also reversed. This is likely related to the fact that larger primates have absolutely longer lever arms and better low-frequency hearing but smaller primates have relatively longer lever arms coupled with worse low-frequency hearing.

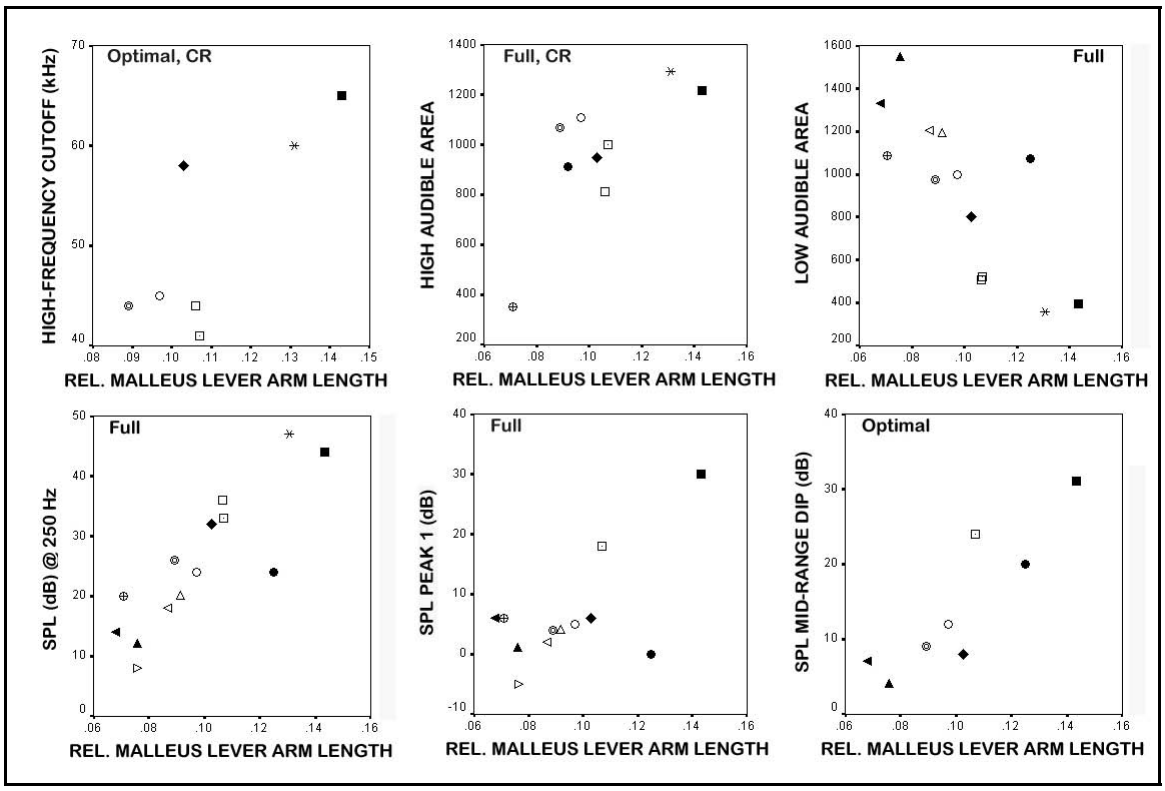

Figure 7.14 - Notable correlations with relative malleus lever arm length.

Incus Lever Arm Length

The significant audiometric variables from the incudal lever arm comparison (optimal dataset) were **low audible area** ($p < 0.001$, $r = 0.879$, $n = 10$), **SPL @ 250 Hz** ($p = 0.001$, $r = -0.871$, $n = 10$), **middle audible area** ($p = 0.038$, $r = 0.659$, $n = 10$), and **SPL of the mid-range dip** ($p = 0.014$, $r = -0.815$, $n = 8$). Essentially the same results were found using the full speaker dataset: **low audible area** ($p = 0.005$, $r = 0.730$, $n = 13$); **SPL @ 250 Hz** ($p < 0.001$, $r = -0.781$, $n = 14$), **middle audible area** ($p = 0.030$, $r = 0.579$, $n = 14$), **SPL of the first peak** ($p = 0.049$, $r = -0.578$, $n = 12$), and **SPL of the mid-range dip** ($p < 0.022$, $r = -0.708$, $n = 10$). Removing *C. jacchus* from the

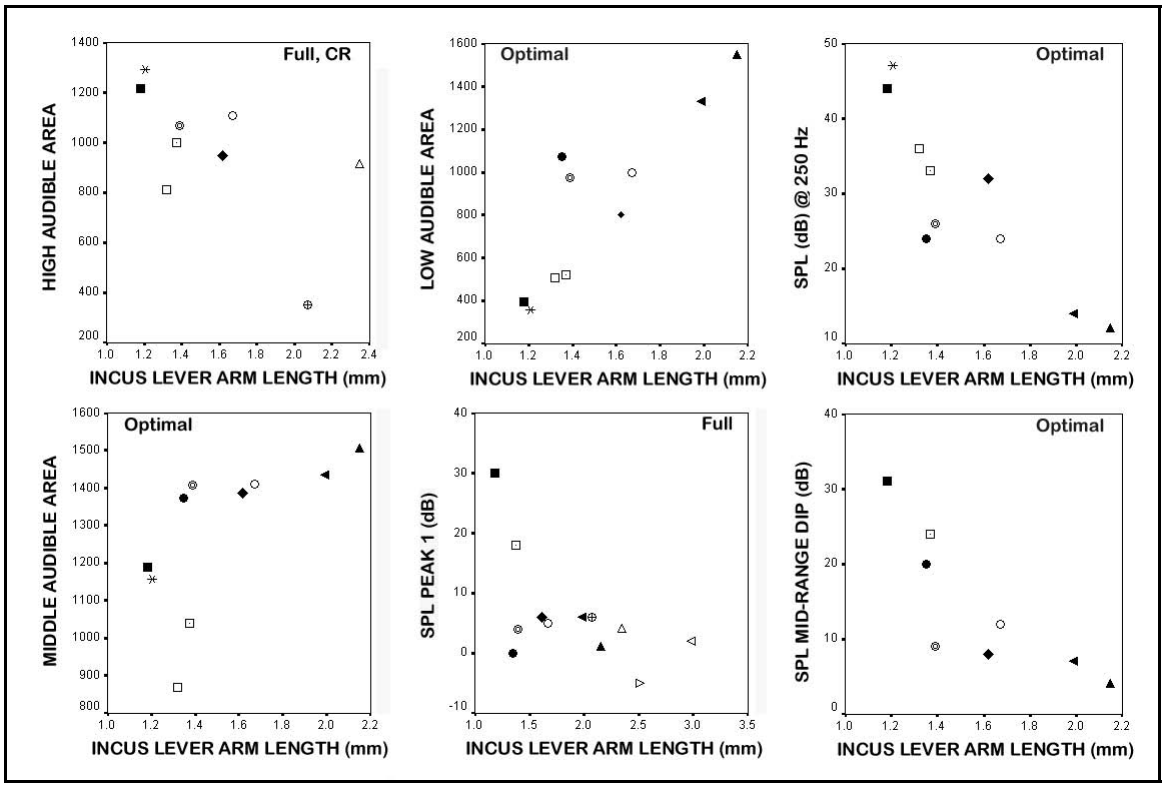

Figure 7.15 - Notable correlations with incus lever arm length.

comparison resulted in high audible area ($p = 0.082$, $r = -0.609$, $n = 9$) nearing significance. These patterns are illustrated in Figure 7.15. Similar to the mallear lever arm results, increases in incudal lever arm lengths are linked with an increase in low and mid-frequency sensitivity and a decrease in the SPL of the mid-range dip. There was also a hint of decreased high-frequency sensitivity.

Considering the relative length of the incus lever arm, SPL @ 250 Hz ($p = 0.066$, $r = 0.600$, $n = 10$), **SPL of the mid-range dip** ($p = 0.050$, $r = 0.706$, $n = 8$), and SPL of the second peak ($p = 0.098$, $r = -0.553$, $n = 10$) showed notable correlations using the optimal speaker dataset. Taking *C. jacchus* out of the equation, **high audible area** also became significant ($p = 0.002$, $r = 0.938$, $n = 7$). Using the full speaker dataset, **SPL @**

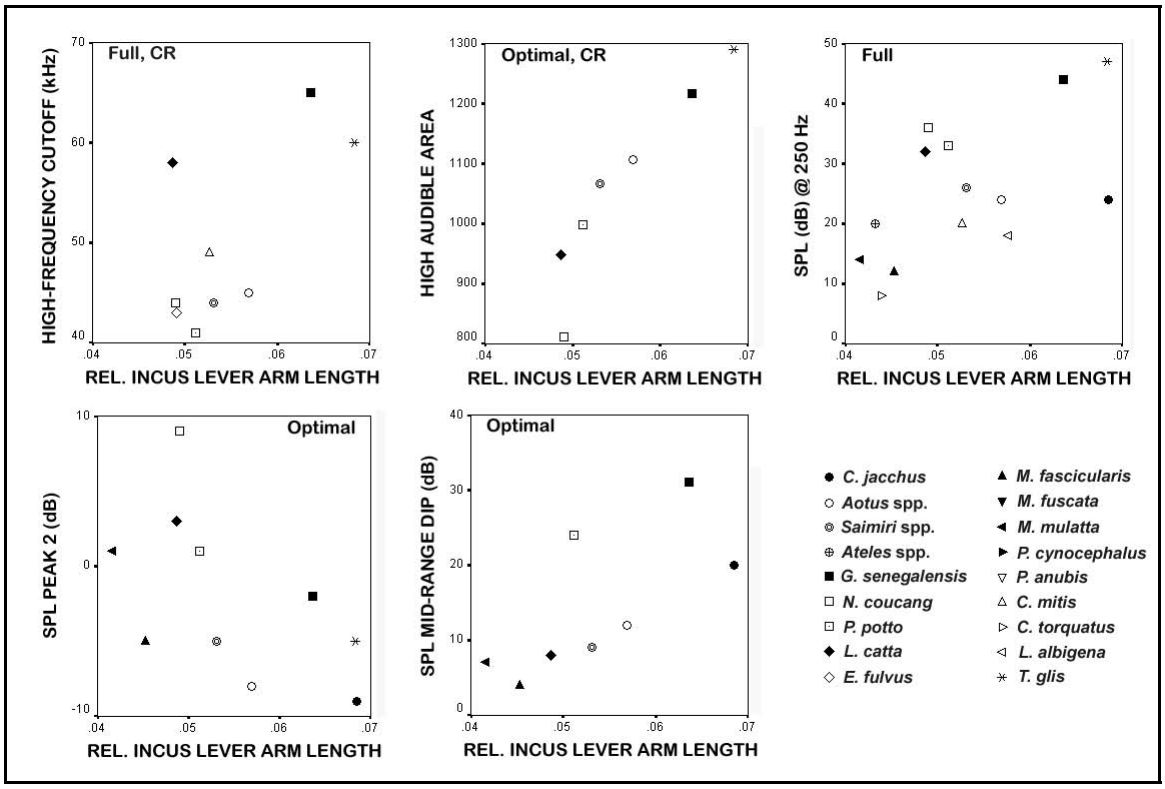

Figure 7.16 - Notable correlations with relative incus lever arm length.

250 Hz ($p = 0.019$, $r = 0.616$, $n = 14$) and SPL of the mid-range dip ($p = 0.061$, $r = 0.610$, $n = 10$) were again found to be significantly correlated with relative incus lever arm length. Furthermore, **high audible area** ($p < 0.001$, $r = 0.917$, $n = 9$) and **high-frequency cutoff** ($p = 0.049$, $r = 0.668$, $n = 9$) were both significant once *C. jacchus* was removed. These results are shown in Figure 7.16 and suggest that as the relative length of the incudal lever arm increases, high-frequency sensitivity increases (as does the SPL of the dip), and low-frequency sensitivity decreases.

Ossicular Lever Arm Ratio

When the lever arm ratio of the malleus and incus was analyzed numerous audiometric variables produced relatively high correlations including **low audible area** ($p = 0.004$, $r = -0.813$, $n = 10$), **SPL @ 250 Hz** ($p = 0.009$, $r = 0.870$, $n = 10$), **middle audible area** ($p = 0.012$, $r = -0.752$, $n = 10$), **SPL of the first peak** ($p = 0.018$, $r = 0.796$, $n = 8$), **SPL of the mid-range dip** ($p = 0.036$, $r = 0.740$, $n = 8$), and SPL of the second

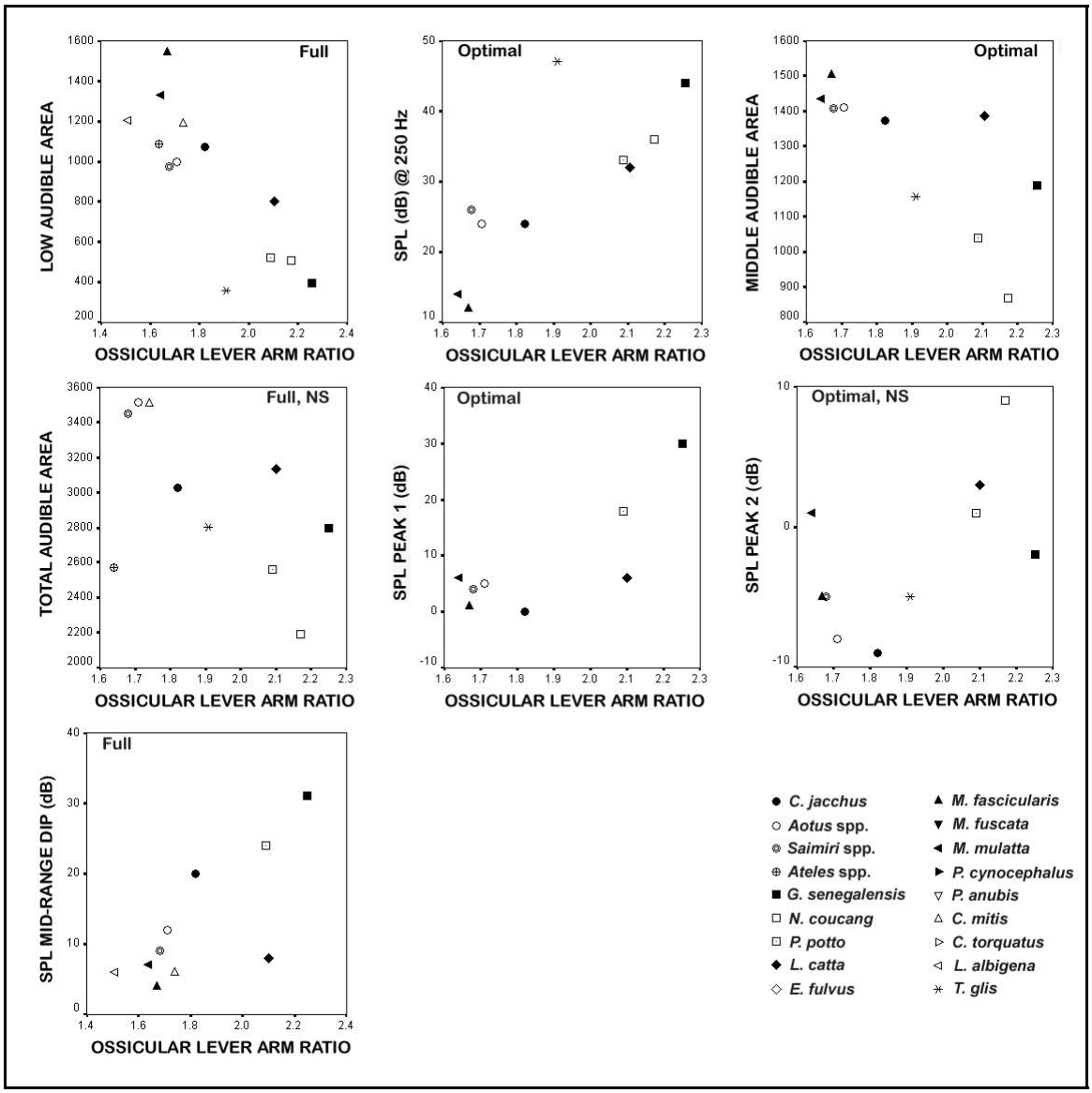

Figure 7.17 - Notable correlations with ossicular lever arm ratio.

peak ($p = 0.074$, $r = 0.587$, $n = 10$). The significant variables using the full speaker dataset were similar and included **low audible area** ($p < 0.001$, $r = -0.820$, $n = 13$), **SPL @ 250 Hz** ($p = 0.001$, $r = 0.775$, $n = 14$), **middle audible area** ($p = 0.014$, $r = -0.641$, $n = 14$), total audible area ($p = 0.093$, $r = -0.559$, $n = 10$), **SPL of the first peak** ($p = 0.004$, $r = 0.760$, $n = 12$), and **SPL of the mid-range dip** ($p = 0.010$, $r = 0.763$, $n = 10$). *C. jacchus* had no impact on the high-frequency correlations. These results are shown in Figure 7.17 and show somewhat unexpectedly, that a higher ossicular lever arm ratio is correlated with higher thresholds for the mid-range dip and peaks in sensitivity but lower sensitivity in the lower and middle ranges.

Pressure Transformer Ratio

The results for the pressure transformer ratio comparison[42] follow similar lines as described above for the ossicular lever arm ratio. The significant variables using the optimal dataset included **low audible area** ($p = 0.009$, $r = -0.806$, $n = 9$), **SPL @ 250 Hz** ($p = 0.011$, $r = 0.790$, $n = 9$), **middle audible area** ($p = 0.007$, $r = -0.820$, $n = 9$), **total audible area** ($p = 0.012$, $r = -0.826$, $n = 8$), **SPL of the first peak** ($p = 0.030$, $r = 0.803$, $n = 7$), **SPL of the mid-range dip** ($p = 0.036$, $r = 0.785$, $n = 7$), and **SPL of the second peak** ($p = 0.049$, $r = 0.668$, $n = 9$). Using the full speaker dataset produced only marginally different results: **low audible area** ($p = 0.001$, $r = -0.816$, $n = 12$), **SPL @ 250 Hz** ($p = 0.002$, $r = 0.806$, $n = 12$), **middle audible area** ($p = 0.007$, $r = -0.732$, $n = 12$), **total audible area** ($p = 0.044$, $r = -0.644$, $n = 10$), **SPL of the first peak** ($p = 0.006$,

[42] The results for PTR_{fa} and PTR_{ea} were qualitatively identical with only slight variations in p-values and correlation coefficients. Therefore only the results for PTR_{fa} are presented.

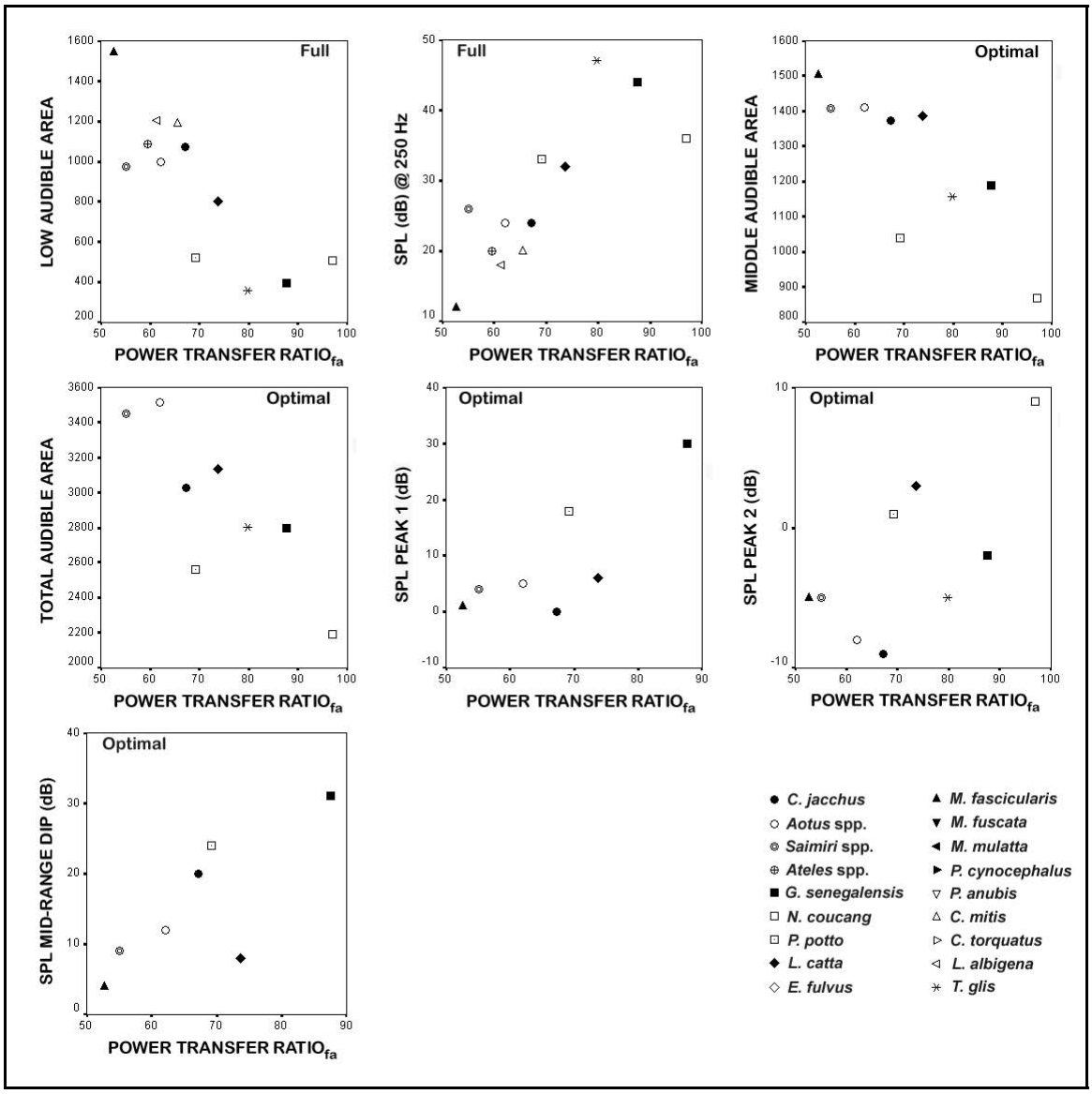

Figure 7.18 - Notable correlations with power transfer ratio.

r = 0.797, n = 10), and **SPL of the mid-range dip** (p = 0.018, r = 0.756, n = 10). There was no alteration in the high frequency results by removing *C. jacchus*. Scatterplots of these associations are shown in Figure 7.18. Comparable to the lever arm results, as the PTR increases there is a decrease in low- and mid-frequency sensitivity (which likely

produces the concomitant decrease in total audible area) and an increase in the thresholds of the mid-range dip and peaks in sensitivity.

Impedance Transformer Ratio

The results from the impedance transformer ratio (ITR) comparisons (using absolute values) did not differ greatly from the PTR comparisons. The significant audiometric variables for the ITR[43] correlations using the optimal speaker dataset were the ever common **low audible area** ($p = 0.003$, $r = 0.859$, $n = 9$), **SPL @ 250 Hz** ($p = 0.006$, $r = -0.826$, $n = 9$), **middle audible area** ($p = 0.012$, $r = 0.786$, $n = 9$), **total audible area** ($p = 0.012$, $r = 0.826$, $n = 8$), SPL of the first peak ($p = 0.053$, -0.748, $n= 7$), SPL of the mid-range dip ($p = 0.051$, $r = -0.752$, $n = 7$), and **SPL of the second peak** ($p = 0.057$, $r = -0.653$, $n = 9$). The results using the full dataset were similar and included **low audible area** ($p < 0.001$, $r = 0.866$, $n = 12$), **SPL @ 250 Hz** ($p < 0.001$, $r = -0.852$, $n = 12$), **middle audible area** ($p = 0.013$, $r = 0.689$, $n = 12$), total audible area ($p = 0.070$, $r = 0.595$, $n = 10$), **SPL of the first peak** ($p = 0.012$, $r = -0.751$, $n = 10$), and **SPL of the mid-range dip** ($p = 0.018$, $r = -0.757$, $n = 9$). *C. jacchus* had no affect on the high-frequency results. These relations are shown in Figure 7.19. As before, the relationship between ITR and low-frequency sensitivity (and mid-frequency as well) is in the reverse direction of what one might predict.

[43] As with the PTR comparisons, the ITR_{fa} and ITR_{ea} results were vertically identical so only the ITR_{fa} results are presented.

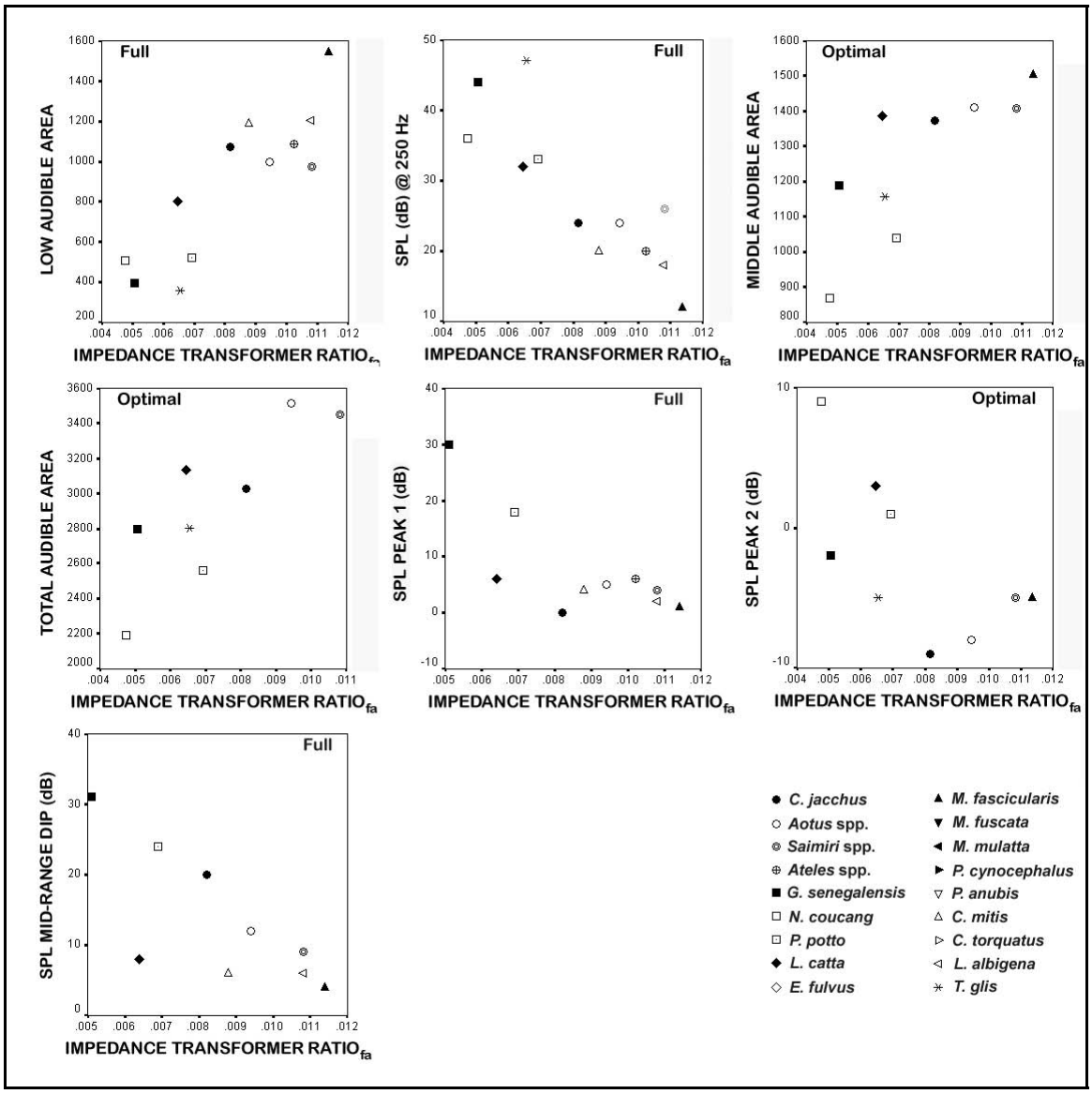

Figure 7.19 - Notable correlations with impedance transformer ratio.

Malleus Mass

Next, the influence of ossicular mass on auditory sensitivity was investigated. Using the optimal speaker dataset, **low audible area** ($p = 0.043$, $r = 0.681$, $n = 9$), **SPL @ 250 Hz** ($p = 0.038$, $r = -0.695$, $n = 9$), SPL of the mid-range dip ($p = 0.095$, $r = -0.676$, $n = 7$) showed notable correlations with malleus mass as did high audible area ($p = 0.064$,

r = -0.727, n = 7) after *C. jacchus* was removed from the comparison. When the full speaker dataset was employed, **low audible area** (p = 0.018, r = 0.693, n = 11), **SPL @ 250 Hz** (p < 0.001, r = -0.832, n = 12), high audible area (p = 0.054, r = -0.623, n = 10), and **SPL of the mid-range dip** (p = 0.043, 5 = -0.721, n = 8) achieved significant values. **High audible area** (p = 0.003, r = -0.853, n = 9) became highly significant when *C .jacchus* was omitted. Figure 7.20 displays these correlations. These results suggest that as malleus mass increases there is an increase in low-frequency sensitivity and a decrease in high-frequency sensitivity and the threshold of the dip. Turning next to the relative mass of the malleus, only high audible area (p = 0.084, r = -0.694, n = 7) was nearing significance using the optimal speaker data (*C. jacchus* excluded). When the full dataset was used, low audible area (p = 0.063, r = 0.577, n =11), **SPL @ 250 Hz**

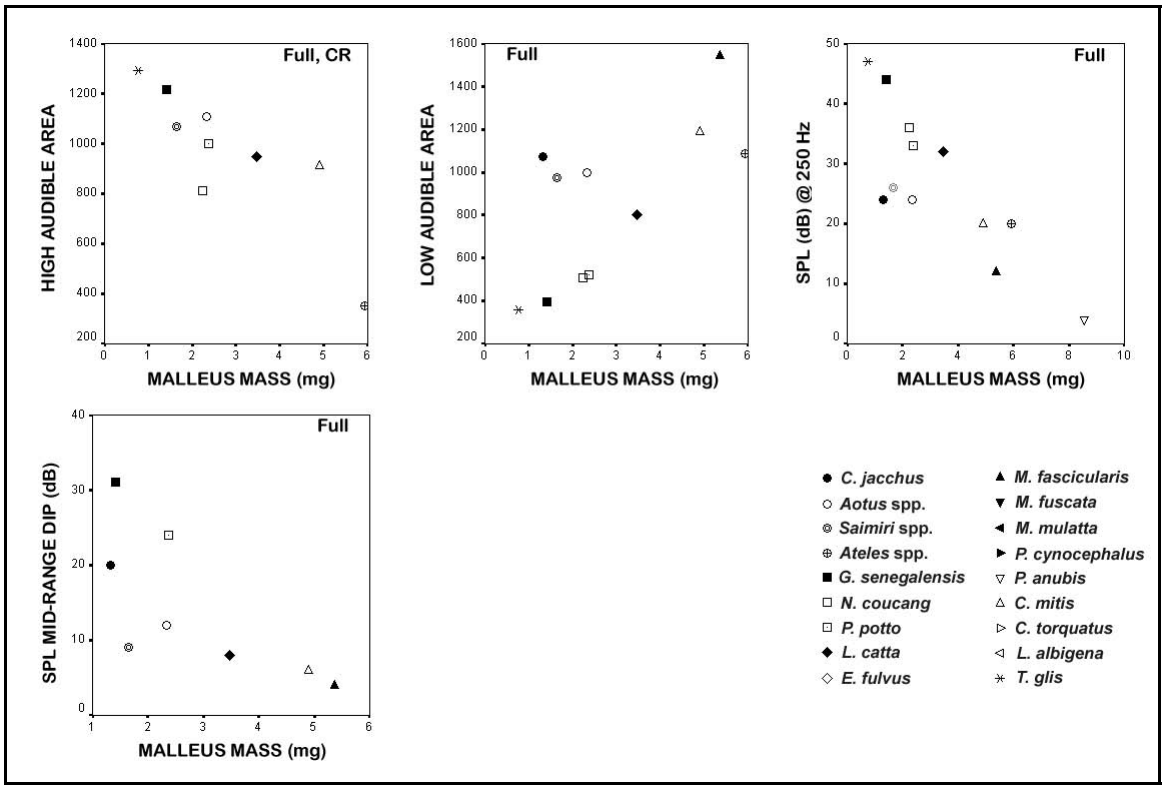

Figure 7.20 - Notable correlations with malleus mass.

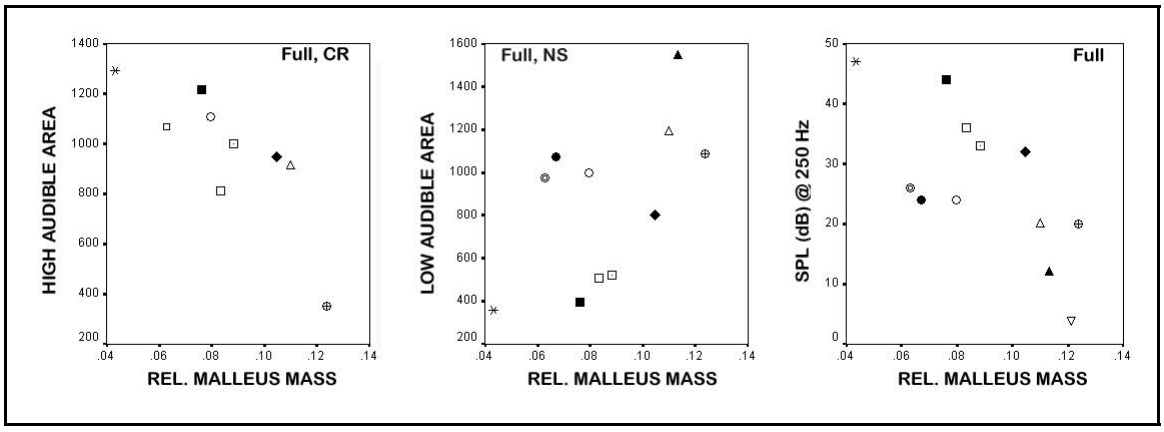

Figure 7.21 - Notable correlations with relative malleus mass.

(p = 0.009, r = -0.717, n = 12) and high audible area (p = 0.063, r = -0.606, n = 10) all showed relatively strong relationships with relative malleus mass. As before, **high audible area** (p = 0.008, r = -0.810, n = 9) became highly significant once *C. jacchus* was taken out of the full dataset analysis. These patterns are shown in Figure 7.21. Similar to the absolute values, these results suggest an association between increasing malleus mass and low frequency sensitivity accompanied by a decrease in high frequency sensitivity.

Incus Mass

Using the optimal speaker dataset, only two variables showed weak correlations with incus mass: low audible area (p = 0.062, r = 0.608, n = 10) and SPL @ 250 Hz (p = 0.099, r = -0.551, n = 10) Expunging *C. jacchus* had no influence on the results. When the full speaker dataset was employed, **low audible area** (p = 0.024, r = 0.619, n = 13), **SPL @ 250 Hz** (p = 0.021, r = -0.631, n = 13), high audible area (p = 0.094, r = -0.528, n = 11), frequency of the first peak (p = 0.097, r = -0.527, n = 11), and SPL of the mid-

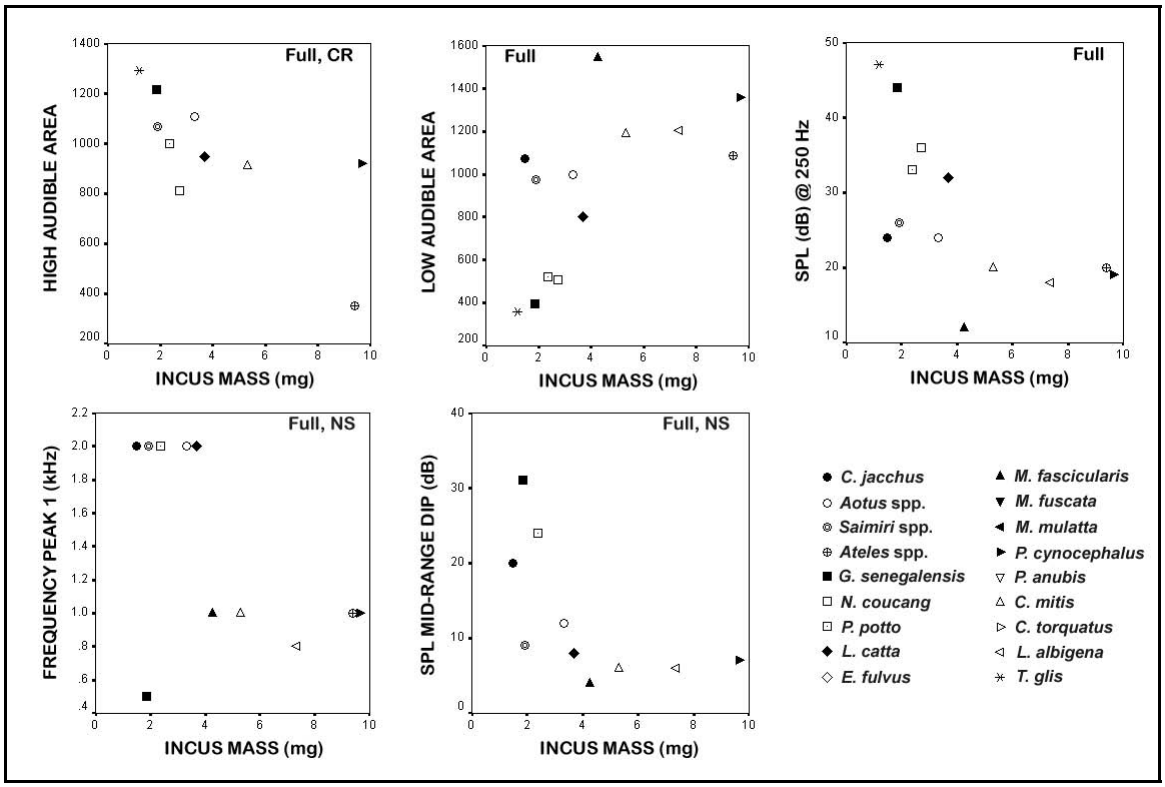

Figure 7.22 - Notable correlations with incus mass.

range dip ($p = 0.063$, $r = -0.607$, $n = 10$) were significantly associated with incus mass. As usual, H**igh audible area** ($p = 0.016$, $r = -0.733$, $n = 10$) illustrated a higher correlation once *C. jacchus* was removed. Figure 7.22 shows these significant relationships. These findings suggest that as incus mass increases there is an increase in low-frequency sensitivity (and possibly in the SPL level of the second peak) and a decrease in high-frequency sensitivity and the SPL of the mid-range dip.

Looking at the relative mass of the incus, only low-frequency cutoff ($p = 0.076$, $r = -0.924$, $n = 4$) showed a notable correlation using the optimal speaker dataset. However, when the full speaker dataset was used, low-frequency cutoff ($p = 0.066$, $r = -0.723$, $n = 7$), **high audible area** ($p = 0.039$, $r = -0.628$, $n = 11$), SPL of the second peak

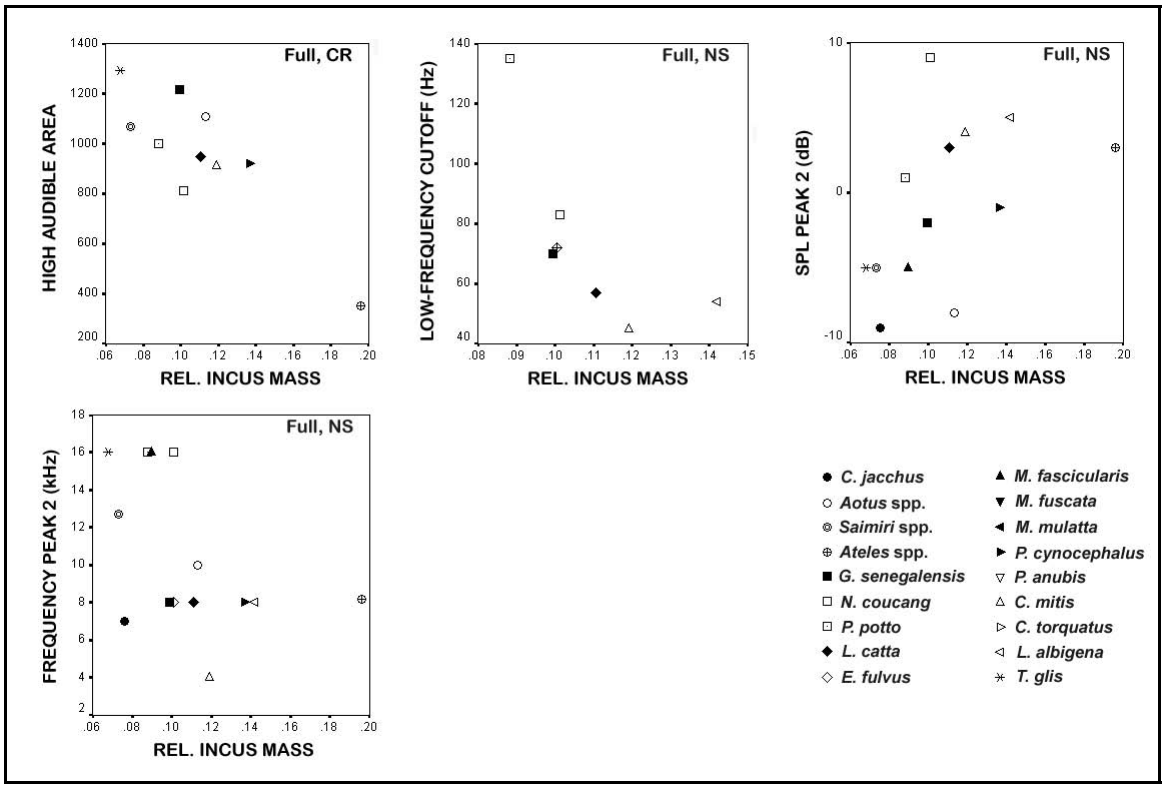

Figure 7.23 - Notable correlations with relative incus mass.

(p = 0.092, r = 0.487, n = 13), and frequency of the second peak (p = 0.092, r = -0.486, n = 14) showed significant correlations with relative incus mass. **High audible area** (p = 0.001, r = -0.861, n = 10) showed higher correlations after omitting *C. jacchus.* These associations are shown in figure 7.23. Even factoring in skull size, there still appears to be a consistent trend towards increased low-frequency sensitivity and decreased high-frequency sensitivity as incus mass increases.

Combined Malleus-Incus Mass

When the combined mass of the malleus and incus was evaluated (optimal data), significant relationships were found with low audible area (p = 0.058, r = 0.650, n = 9),

SPL @ 250 Hz (p = 0.047, r = -0.673, n =9, and SPL of the mid-range dip (p = 0.076, r = -0.707, n = 7) and with high audible area (p = 0.084, r = -0.693, n = 7) when *C. jacchus* was excluded. The full dataset produced very similar results: **low audible area** (p = 0.053, r = 0.597, n = 11), **SPL @ 250 Hz** (p = 0.028, r -0.656, n = 11), **high audible area** (p = 0.037, r = -0.661, n = 10), and **SPL of the mid-range dip** (p = 0.037, r = -0.736, n = 8). As expected, the correlation coefficient was dramatically increased for **high audible area** (p = 0.001, r = -0.894, n = 9) once *C. jacchus* was excluded. These relationships are shown in figure 7.24. No real surprises here, as the general patterns between combined malleus-incus mass and high and low-frequency sensitivity are essentially the same as for the individual bones.

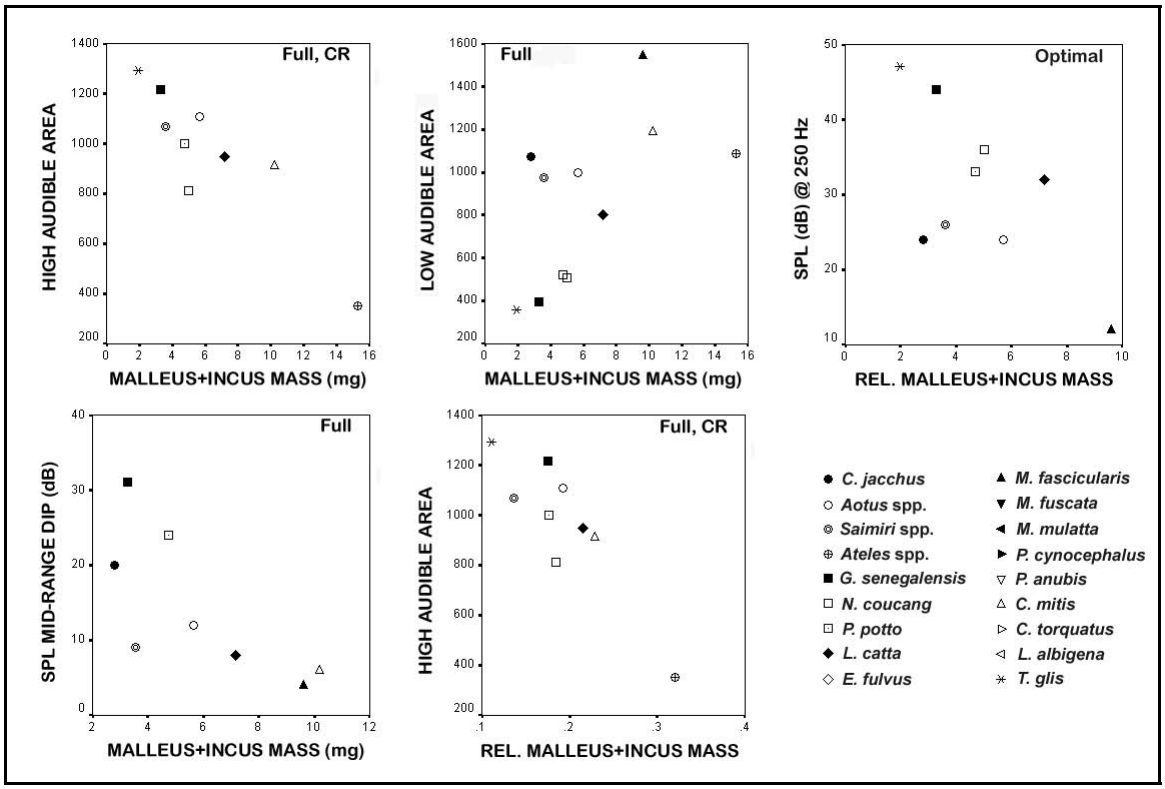

Figure 7.24 - Notable correlations with absolute and relative combined malleus and incus mass.

No variables were significantly correlated with relative malleus-incus mass using the optimal dataset. When the full speaker dataset was used, **high audible area** was significant whether *C. jacchus* was included in the analysis ($p = 0.040$, $r = -0.656$, $n = 10$) or omitted ($p = 0.001$, $r = -0.894$, $n = 9$). This relationship is also illustrated in Figure 7.24 and shows that increases in ossicular mass are related to decreases in high-frequency sensitivity regardless of whether changes in overall size are considered or not.

Stapes Mass

Using the optimal speaker dataset, **frequency of the second peak** ($p = 0.040$, $r = 0.832$, $n = 6$) was the only audiometric variable to be significantly correlated with stapedial mass. Excluding *C. jacchus*, notable correlations were also found with high-frequency cutoff ($p = 0.074$, $r = -0.926$, $n = 4$) and **high audible area** ($p = 0.018$, $r = -0.982$, $n = 4$). Using the full speaker dataset, only high audible area ($p = 0.089$, $r = -0.744$, $n = 6$) showed a weak correlation with stapes mass. (The loss of significance for frequency of the second peak is likely related to the inclusion of *Ateles* which had the heaviest stapes in this analysis but a moderately low frequency of the second peak [8 kHz]). **High audible area** ($p = 0.037$, $r = -0.900$, $n = 5$) became highly correlated with stapedial mass, as did high-frequency cutoff ($p = 0.074$, $r = -0.926$, $n = 4$) once *C. jacchus* was excluded. Examination of Figure 7.25 shows that *Ateles* is also influencing the high audible area comparisons. Considering the low sample sizes, these results are

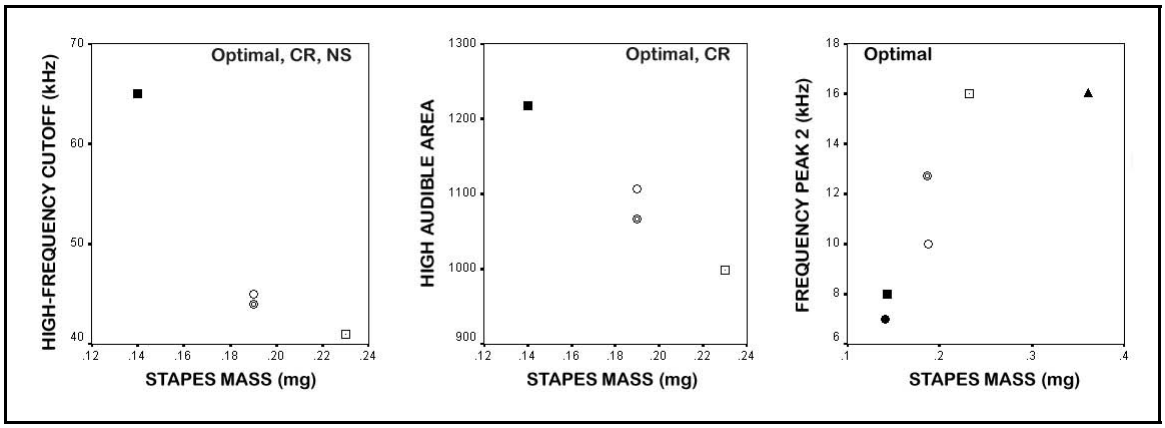

Figure 7.25 - Notable correlations with stapes mass.

suggestive of decreasing high-frequency sensitivity (and possibly frequency of the second peak) with increasing stapes mass.

When the relative mass of the stapes was considered, **total audible area** ($p = 0.024$, $r = -926$, $n = 5$), **range in octaves** ($p = 0.027$, $r = -0.919$, $n = 5$), and **SPL of the second peak** ($p = 0.024$, $r = 0.871$, $n = 6$) were significant using the optimal dataset. Using the full dataset, only **SPL of the second peak** ($p = 0.036$, $r = 0.786$, $n = 7$) was significant although high audible area ($p = 0.097$, $r = -0.734$, $n = 6$) also showed a mentionable correlation which became highly correlated ($p = 0.010$, $r = -0.960$, $n = 5$) after excluding *C. jacchus*. These variables are displayed in Figure 7.26. As with the absolute values, *Ateles* seems to be an outlier in the most of the scatterplots. Regardless, these results suggest that an increase in the relative mass of the stapes is related to an increase in the threshold of the second peak and possibly a decrease in high-frequency sensitivity.

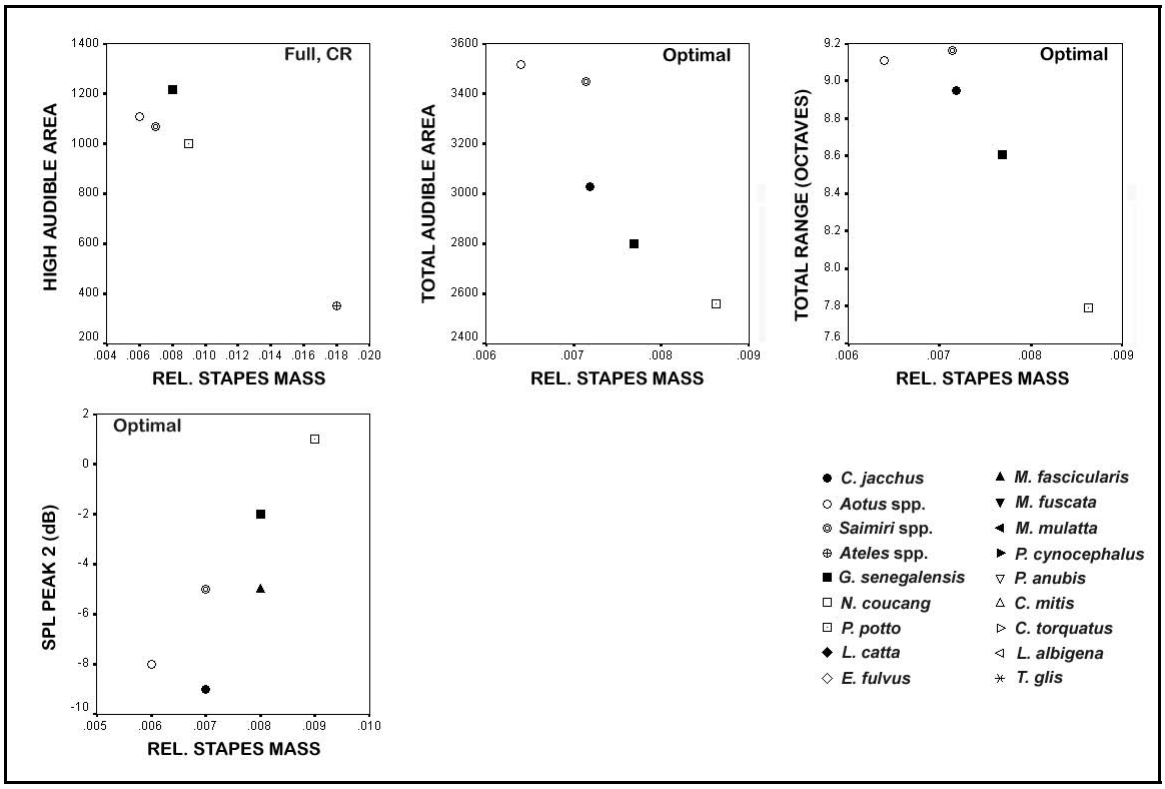

Figure 7.26 - Notable correlations with relative stapes mass.

Ossicular Chain Mass

When the combined mass of all three auditory ossicles was evaluated, no audiometric variables were significant using the optimal dataset whether examining the absolute or relative values. Similarly, using the full speaker dataset, no variables achieved significance using either absolute or relative values. **High audible area** did become significant using both absolute ossicular mass ($p = 0.042$, $r = -0.977$, $n = 5$) and relative ossicular mass ($p = 0.026$, $r = -0.922$, $n = 5$) when *C. jacchus* was excluded (Figure 7.27). These results suggest that increasing ossicular mass is associated with increased high-frequency sensitivity, but the absence of other significant correlations is undoubtedly due in part to the small sample sizes for all comparisons. The lack of congruence between the

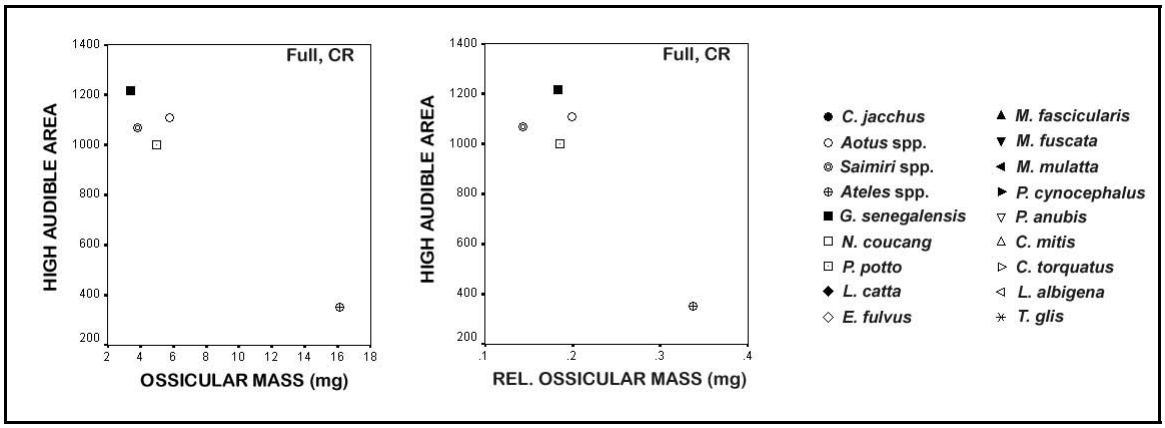

Figure 7.27 - Notable correlations with the combined mass of all three auditory ossicles.

results from the malleus-incus and malleus-incus-stapes mass comparisons (despite the trivial increase in overall mass) is likely explained by the fact that the maximum number of taxa used in any comparison for the full ossicular chain was only seven.

Total Middle Ear Volume

Middle ear cavity volume was the final middle ear structure examined. Total cavity volume will be discussed first before moving on to the influence of the individual cavities. Using the optimal speaker dataset, **low audible area** ($p = 0.026$, $r = 0.727$, $n = 9$) and **SPL @ 250 Hz** ($p = 0.036$, $r = -0.701$, $n = 9$) showed significant correlations with total middle ear volume. High audible area ($p = 0.085$, $r = -0.692$, $n = 7$) was nearing significance excluding *C. jacchus*. Once the full dataset was employed, **low audible area** ($p = 0.018$, $r = 0.724$, $n = 10$), **SPL @ 250 Hz** ($p = 0.023$, $r = -0.705$, $n = 10$), and SPL of the mid-range dip ($p = 0.064$, $r = -0.678$, $n = 8$) showed notable correlations with middle ear volume. These relationships are illustrated in Figure 7.28 and suggest that increased middle ear volume is related most clearly to an increase in low-frequency sensitivity.

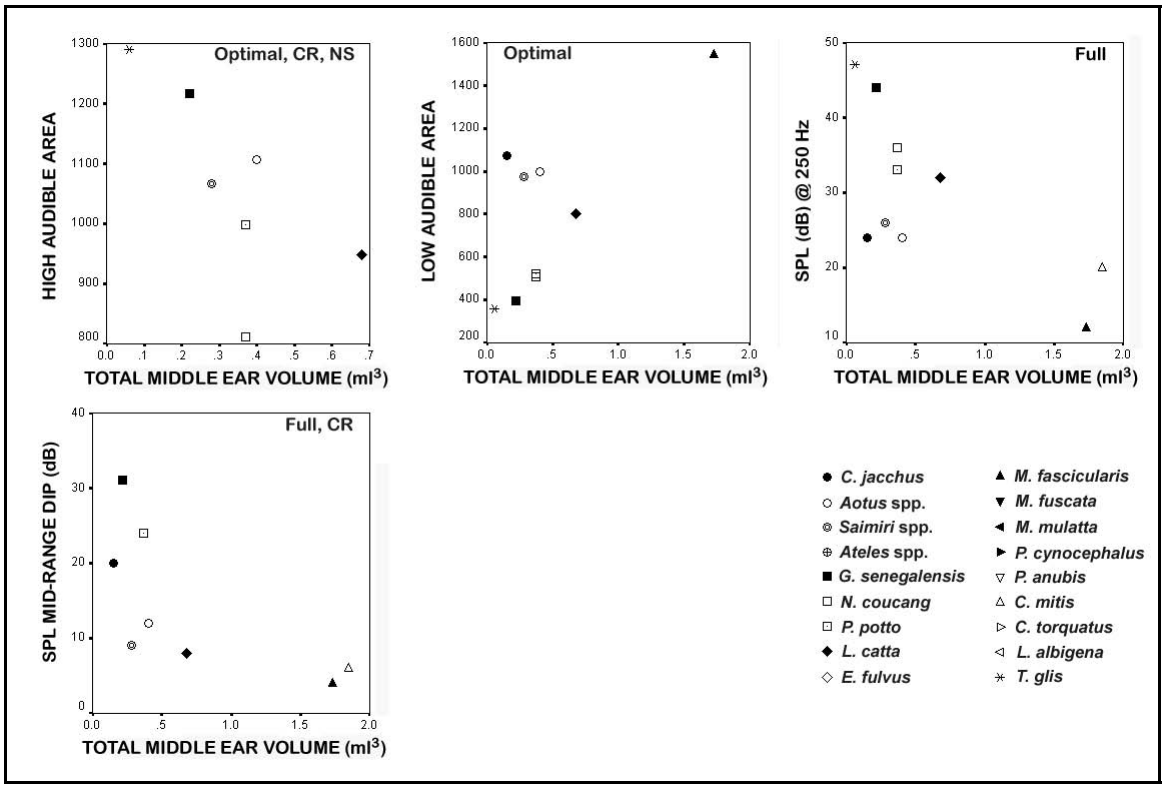

Figure 7.28 - Notable correlations with total middle-ear volume.

Nearly identical results were found when examining the relative total volume of the middle ear cavities. Using the optimal dataset, **low audible area** ($p = 0.040$, $r = 0.690$, $n = 9$) and **SPL @ 250 Hz** ($p = 0.040$, $r = -0.688$, $n = 9$) reached significance while high audible area ($p = 0.083$, $r = -0.694$, $n = 7$) was close excluding *C. jacchus*. The full speaker results included **low audible area** ($p = 0.026$, $r = 0.694$, $n = 10$), **SPL @ 250 Hz** ($p = 0.027$, $r = -0.692$, $n = 10$), and SPL of the mid-range dip ($p = 0.077$, $r = -0.656$, $n = 8$). These variables are shown in Figure 7.29. Obviously, the remarkable similarity dictates that these results can be interpreted in the same way as the absolute values.

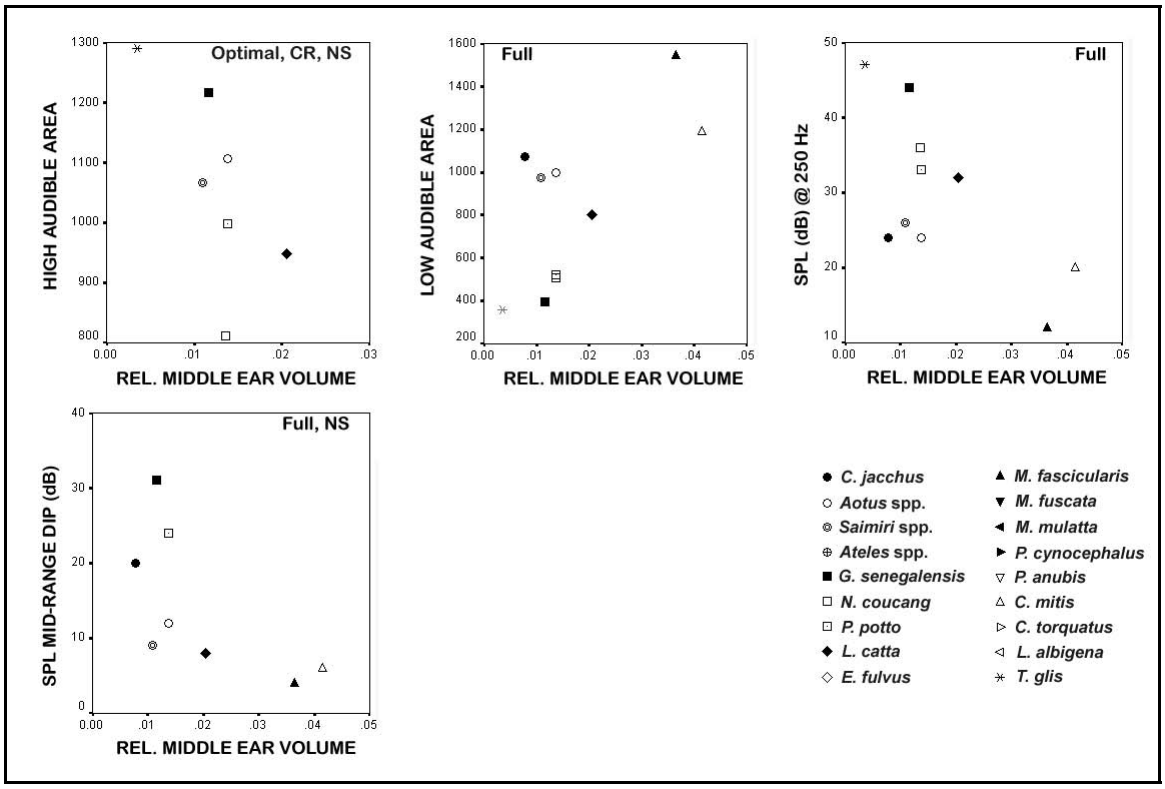

Figure 7.29 - Notable correlations with relative middle-ear volume.

Tympanic Cavity Volume[44]

Examining the volume of the tympanic cavity proper, only frequency of the mid-range dip ($p = 0.099$, $r = -0.731$, $n = 6$) produced a p-value below 0.100 using the optimal speaker dataset. This variable is shown in Figure 7.30. Using the full speaker dataset, no audiometric variables showed a significant relationship with tympanic cavity volume. *C. jacchus* had no significant impact on the high-frequency comparisons. Therefore, tympanic cavity volume appears to be poorly correlated with hearing sensitivity when considering absolute values.

[44] Note that *E. fulvus*, *L. catta*, and *T. glis* were excluded from these analyses since they have a single cavity configuration and comparing this volume to the tympanic cavity volume of other species (with multiple cavity configurations) proved them to be extreme outliers.

Figure 7.30 - Only notable correlation with tympanic cavity volume.

However, when the tympanic cavity was scaled for skull size, several correlations emerged. Using the optimal speaker dataset, high-frequency cutoff ($p = 0.095$, $r = 0.736$, $n = 6$), SPL of the first peak ($p = 0.059$, $r = 0.794$, $n = 6$), **frequency of the first peak** ($p = 0.045$, $r = -0.822$, $n = 6$), and frequency of the mid-range dip ($p = 0.082$, $r = -0.756$, $n = 6$) all showed noteworthy correlations with relative tympanic cavity volume. **High-frequency cutoff** ($p = 0.028$, $r = 0.917$, $n = 5$) became highly correlated after excluding *C. jacchus*. Using the full speaker dataset produced very similar results: high-frequency cutoff ($p = 0.069$, $r = 0.718$, $n = 7$), **frequency of the first peak** ($p = 0.017$, $r = -0.844$, $n = 7$), and **frequency of the mid-range dip** ($p = 0.035$, $r = -0.788$, $n = 7$). Again, removing *C. jacchus* improved the relationship between **high-frequency cutoff** ($p = 0.034$, $r = 0.846$, $n = 6$) and relative tympanic cavity volume. These patterns are displayed in Figure 7.31 and suggest that increases in relative tympanic cavity volume are related to decreases in frequency of the first peak and mid-range dip but increases in the high-frequency limit.

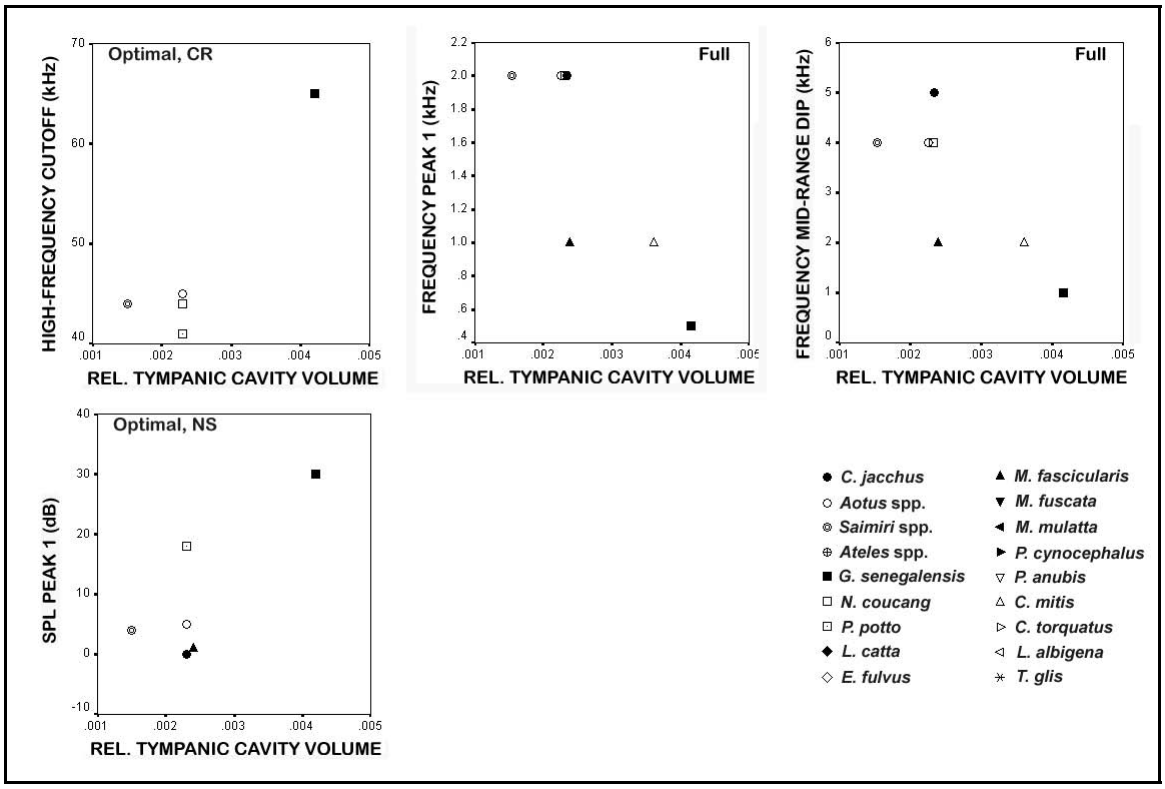

Figure 7.31 - Notable correlations with relative tympanic cavity volume.

Epitympanic Sinus Volume

Moving next to the total volume of the sinuses diverting from the epitympanic recess (collectively termed epitympanic sinuses), weak correlations were found with total audible area ($p = 0.098$, $r = -0.733$, $n = 6$) and range in octaves ($p = 0.066$, $r = -0.782$, $n = 6$) using the optimal dataset. High audible area ($p = 0.070$, $r = -0.847$, $n = 5$) was also nearing traditional significance levels after omitting *C. jacchus*. However, a different pattern appeared when the full dataset was utilized: low audible area ($p = 0.069$, $r = 0.671$, $n = 8$), SPL @ 250 Hz ($p = 0.072$, $r = -0.665$, $n = 8$), and SPL of the mid-range dip ($p = 0.099$, $r = -0.671$, $n = 7$). *C. jacchus* had no influence on the full speaker, high-

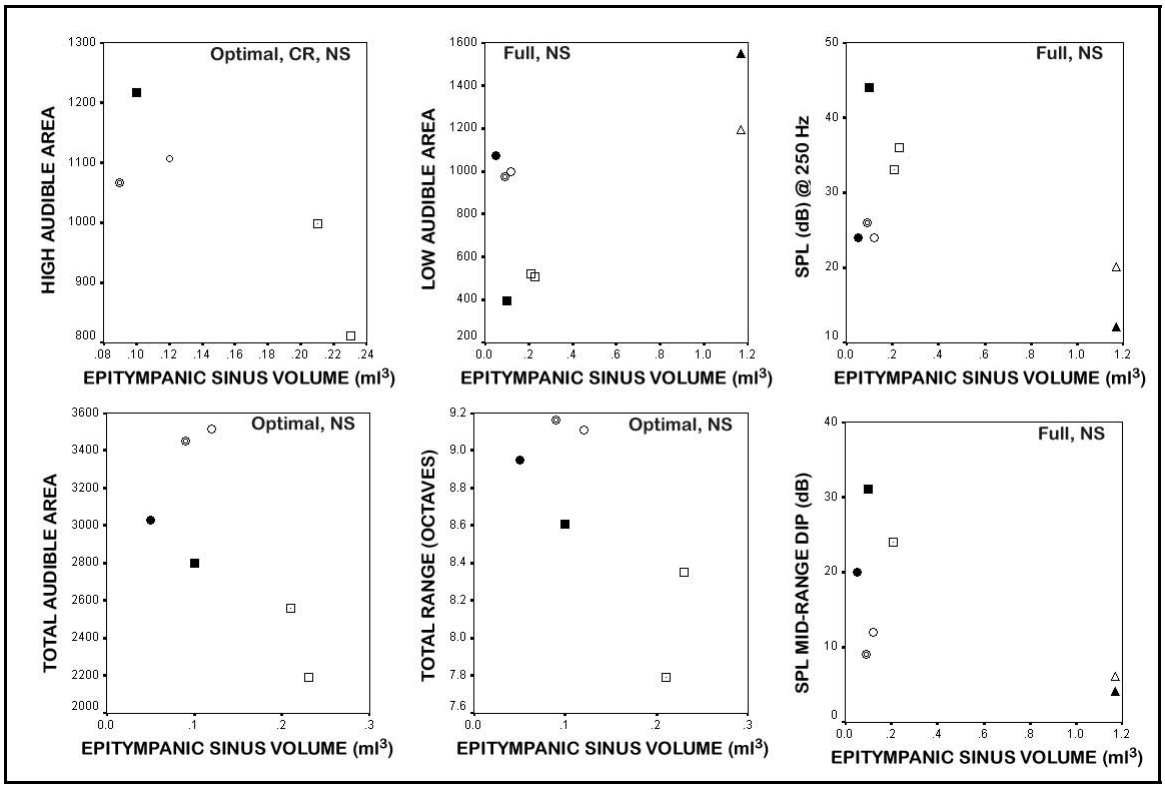

Figure 7.32 - Notable correlations with epitympanic sinus volume.

frequency results. These patterns are shown in Figure 7.32. Meaningful interpretations of these results are problematic due to the non-overlapping relatively low correlations.

Using the optimal speaker dataset to evaluate the relative volume of the epitympanic sinuses, **total audible area** ($p = 0.025$, $r = -0.864$, $n = 6$) and **range in octaves** ($p = 0.025$, $r = -0.867$, $n = 6$) were again found to be significant (although this time they met traditional significance standards). In contrast, no audiometric variables reached significance using the full speaker dataset. *C. jacchus* had no bearing on the high-frequency results for either dataset. The significant variables are shown in Figure 7.33.

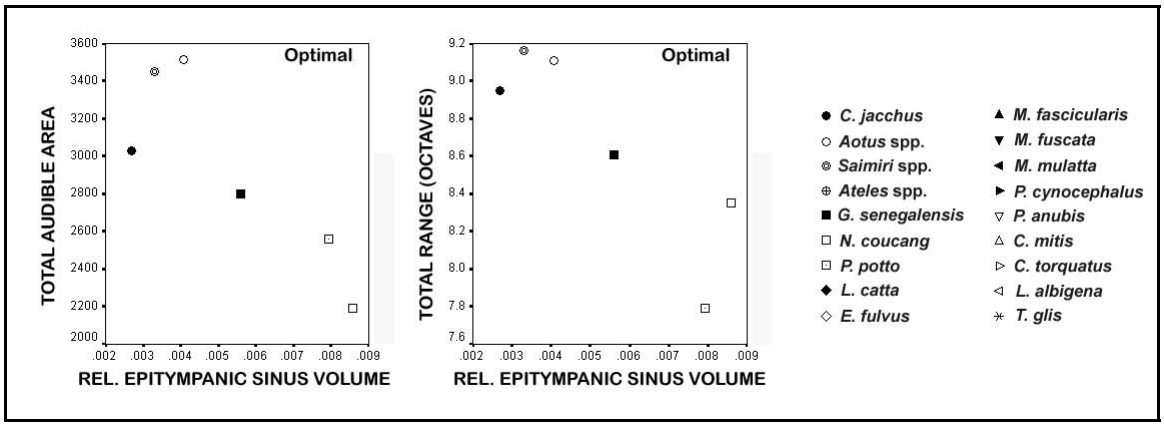

Figure 7.33 - Notable correlations with relative epitympanic sinus volume.

Accessory Cavity Volume

The final cavity volumes to be examined are the accessory cavities located anteromedial to the tympanic cavity itself (termed anterior accessory cavity in anthropoids and medial accessory cavity in lorisoids). Utilizing the optimal speaker dataset, three variables showed a significant relationship with accessory cavity volume: **low audible area** ($p = 0.020$, $r = 0.832$, $n = 7$), **SPL @ 250 Hz** ($p = 0.019$, $r = -0.835$, $n = 7$), and **SPL of the mid-range dip** ($p = 0.032$, $r = -0.850$, $n = 6$). These same variables

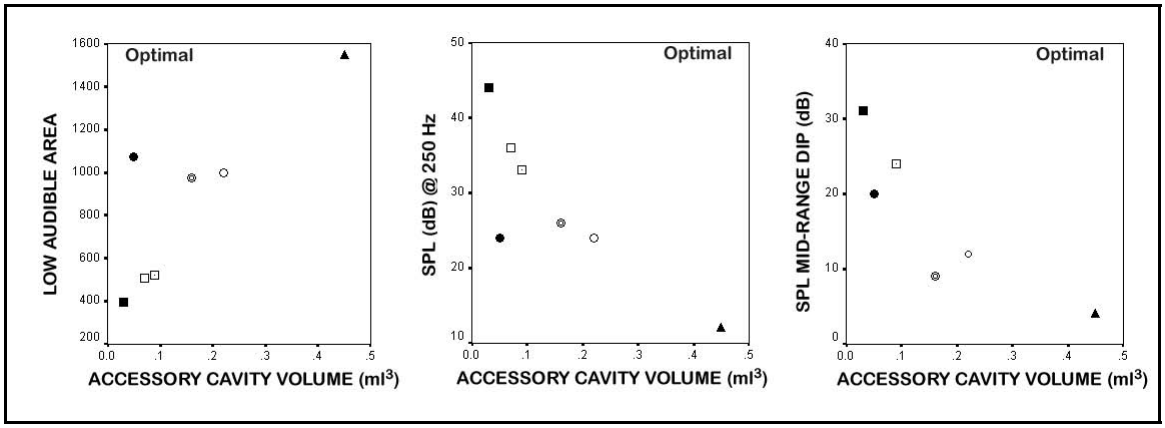

Figure 7.34 - Notable correlations with accessory cavity volume

were also significant using the full speaker data: **low audible area** (p = 0.023, r = 0.779, n = 8), **SPL @ 250 Hz** (p = 0.022, r = -0.782, n = 8), and **SPL of the mid-range dip** (p = 0.017, r = -0.842, n = 7). These relationships are depicted in Figure 7.34. These results suggest that as the volume of the accessory cavity increases, there is a concomitant increase in low-frequency sensitivity and a decrease in the threshold of the mid-range dip.

Looking at the relative volume of the accessory cavities, very similar patterns were found. The optimal speaker results included **low audible area** (p = 0.023, r = 0.824, n = 7), **SPL @ 250 Hz** (p = 0.014, r = -0.856, n = 7), middle audible area (p = 0.092, r = 0.681, n = 7), total audible area (p = 0.092, r = 0.741, n = 6), and **SPL of the mid-range dip** (p = 0.006, r = -0.934, n = 6). Again, the full speaker results perfectly mirrored the optimal speaker results: **low audible area** (p = 0.031, r = 0.753, n = 8), **SPL @ 250 Hz**

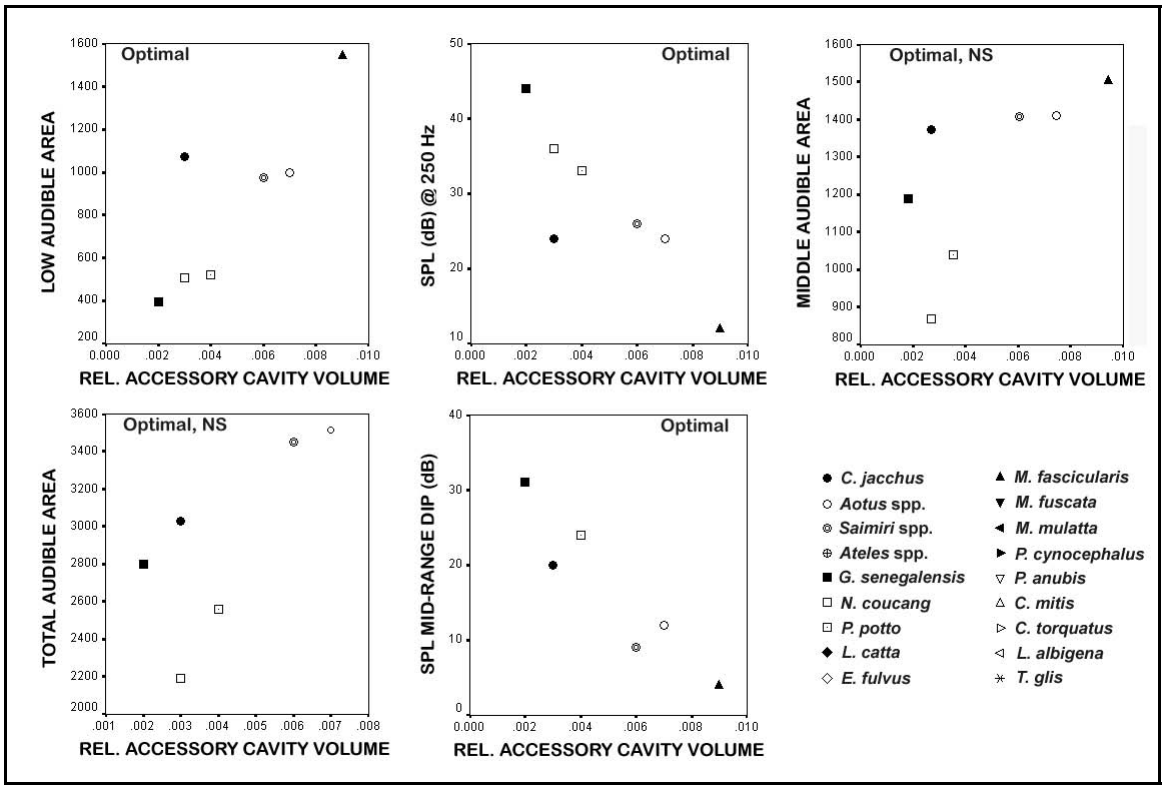

Figure 7.35 - Notable correlations with relative accessory cavity volume.

($p = 0.024$, $r = -0.776$, $n = 8$), middle audible area ($p = 0.096$, $r = 0.627$, $n = 8$), total audible area ($p = 0.074$, $r = 0.710$, $n = 7$), and **SPL of the mid-range dip** ($p = 0.010$, $r = -0.877$, $n = 7$). These findings (Figure 7.35) strengthen the interpretation above for the absolute volume of the accessory cavities and suggest further that the accessory cavities appear to have to largest impact of any cavity on hearing sensitivity.

INNER EAR

Cochlear Length

The final morphometric variable that was analyzed using TIPS data was the length of the cochlea. Using the optimal speaker dataset, there were significant correlations between cochlear length and a familiar host of audiometric variables including **low audible area** ($p = 0.002$, $r = 0.880$, $n = 9$), **SPL @ 250 HZ** ($p < 0.001$, $r = -0.912$, $n = 9$), middle audible area ($p = 0.060$, $r = 0.647$, $n = 9$), range in octaves ($p = 0.091$, $r = 0.634$, $n = 8$) and **SPL of the mid-range dip** ($p = 0.026$, $r = -0.814$, $n = 7$). Six audiometric variables were significant using the full speaker dataset: **low audible area** ($p = 0.002$, $r = 0.853$, $n = 10$), **SPL @ 250 HZ** ($p < 0.001$, $r = -0.876$, $n = 10$), **middle audible are**a ($p = 0.048$, $r = 0.637$, $n = 10$), **total audible area** ($p = 0.044$, $r = 0.679$, $n = 9$), **range in octaves** ($p = 0.030$, $r = 0.716$, $n = 9$), and **SPL of the mid-range dip** ($p = 0.016$, $r = -0.803$, $n = 8$). *C. jacchus* had no effect on the high-frequency comparisons for either dataset. The full speaker dataset correlations are given in Figure 7.36. These results suggest that longer cochlear lengths are associated with increased low- and middle-frequency sensitivity (and therefore total audible area), increased overall range, and decreased threshold of the mid-range dip.

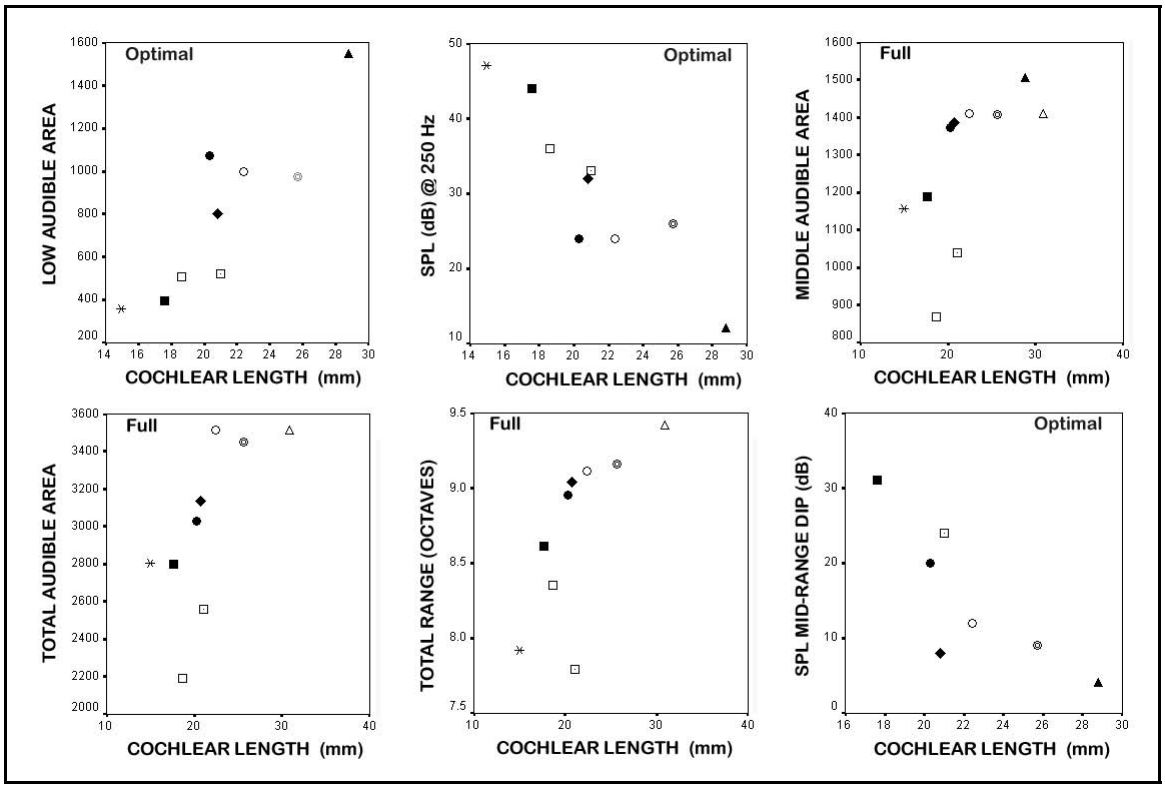

Figure 7.36 - Notable correlations with cochlear length.

In contrast, when relative cochlear length was examined, no variables had a p-value below 0.100 using either the optimal or full speaker datasets. High audible area ($p = 0.059$, $r = 0.688$, $n = 8$) did approach significance (full speaker data) when *C. jacchus* was excluded. This correlation is shown in Figure 7.37.

SUBGROUP COMPARISONS

This section presents the results from comparisons made between subgroups of taxa and between individual species. These analyses were aimed at eliminating some of the confounding factors that can potentially influence the results such as differences in size and measurement error. The first two analyses examined higher taxonomic level

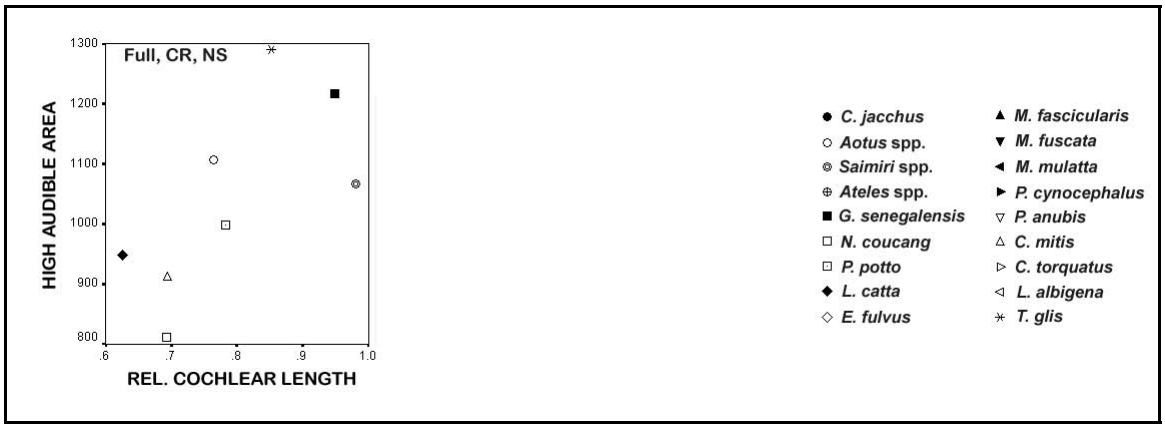

Figure 7.37 - Notable correlations with relative cochlear length.

comparisons between lorisoids and platyrrhines and between platyrrhines and Old World monkeys. In the first analysis, audiometric and morphometric data for the three species of lorisoids (*G. senegalensis*, *N. coucang* and *P. potto*) were compared with three platyrrhines (*C. jacchus*, *Aotus* spp., *Saimiri* spp.). The analysis was designed to test the idea that anthropoids (represented by platyrrhines) have increased low-frequency sensitivity compared with prosimians (represented by lorisoids). Using this particular subgroup of species is advantageous since it helps control for the effects of body size by using species that are of approximately the same size (g-mean of skull size: Mann-Whitney U-test - $p = 0.513$, $Z = -0.655$, $n = 6$).

The second higher-level analysis compared differences in morphometric data between two select platyrrhines and various Old World monkeys. Although Old World monkeys are generally larger in size than New World monkeys, these two comparisons examined relatively large platyrrhines (*Cebus* and *Ateles*) that showed skull sizes in the range of the Old World monkeys tested (see below). Therefore, these analyses can be thought of as "narrow allometric comparisons". The final three contrasts were between

species that were tested in the same laboratories in an attempt to hold measurement error constant. The five comparisons were between species (2 or 3) within the major superfamilies of primates (lemuroids, lorisoids, and ceboids).

Lorisoids vs. Platyrrhines

The first step in this analysis was to compare hearing sensitivity (audiometrics) between lorisoids and platyrrhines. Figure 7.38 shows the audiograms for these six species and it can be seen that one of the most obvious features distinguishing the groups is low-frequency sensitivity. When the audiometric variables were compared (using a non-parametric Mann-Whitney U-test because of small sample size (n = 6)), significant differences were found between lorisoids and platyrrhines in **SPL @ 250 Hz** ($p = 0.046$), **low audible area** ($p = 0.050$), **total audible area** ($p = 0.050$), **middle audible area** ($p = 0.050$), and **range in octaves** ($p = 0.050$). In addition, SPL of the first peak ($p = 0.083$) and SPL of the mid-range dip ($p = 0.083$) were nearing traditional significance levels. Removing *C. jacchus* had no noticeable affect on the high-frequency results. All five significant variables ($p \leq 0.050$) are likely driven by the same general factor - increases in low (and middle) range sensitivity, supporting the observation mentioned above evident in the audiograms.

The next step was to compare mean morphometric values between each group (Table 7.4). Significant differences were detected when comparing **pinna shape ratio** ($p = 0.050$), **ossicular lever arm ratio** ($p = 0.050$), **PTR** ($p = 0.050$), and **ITR** ($p = 0.050$). Unlike the audiometric variables, where only species mean values are available, the morphometric variables can also be compared by considering the individual specimen

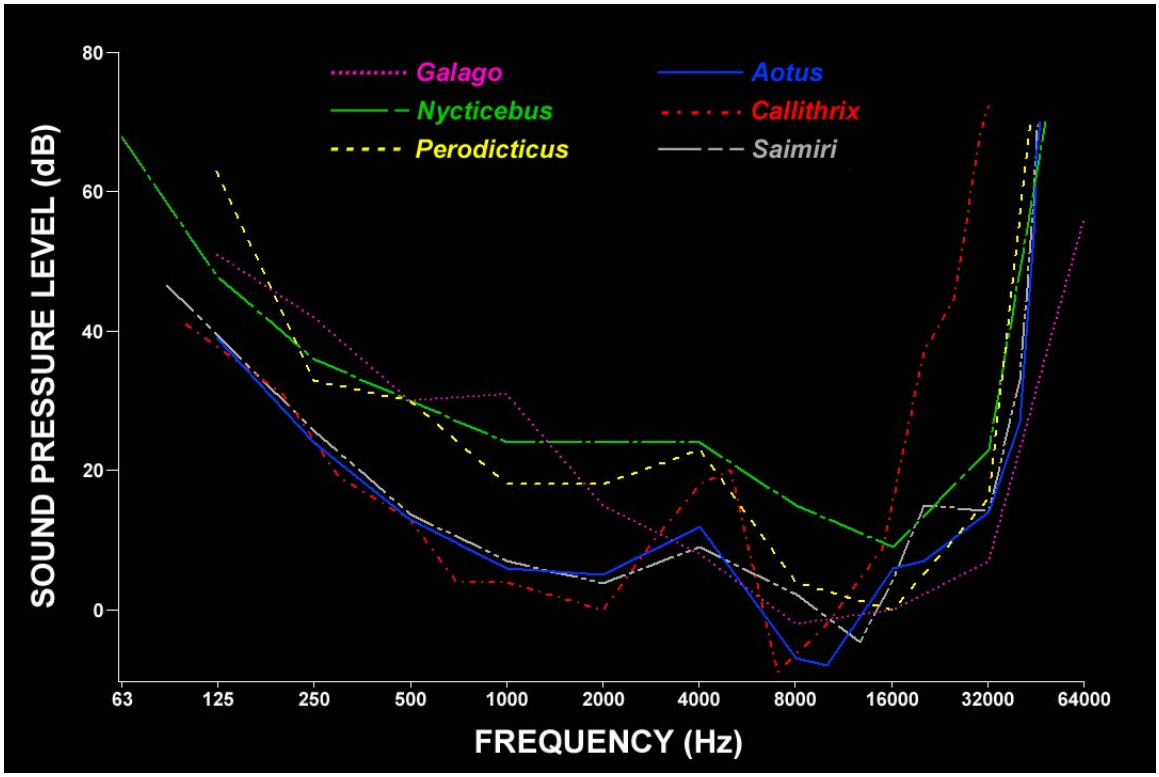

Figure 7.38 - Audiograms of taxa examined in lorisoid versus platyrrhine comparison.

values[45]. This greatly inflates the sample size and statistical power for most comparisons.

Rerunning the analysis using the individual specimen values (a Mann-Whitney U-test was still used to keep the procedure consistent with the previous analyses), several more variables became significant: **pinna shape ratio** ($p < 0.001$, $n = 40$), **interaural distance** ($p < 0.001$, $n = 313$), **malleus lever arm length** ($p = 0.042$, $n = 142$), **incus lever arm length** ($p < 0.001$, $n = 142$), **ossicular lever arm ratio** ($p < 0.001$, $n = 142$), **PTR** ($p = 0.001$, $n = 18$), **ITR** ($p < 0.001$, $n = 18$), **combined malleus-incus mass** ($p = 0.034$, $n = 133$), **tympanic cavity volume** ($p = 0.019$, $n = 18$), **epitympanic sinus volume** ($p = 0.005$, $n = 18$), **accessory cavity volume** ($p = 0.042$, $n = 18$), and **cochlear**

[45] Only adult specimens were used for ossicular mass variables, cavity volume variables, pinna variables, interaural distance, and skull size as was done when calculating the mean values for each taxa. In addition, *S. boliviensis* females were excluded from the *Saimiri* data (see Chapter 6 for explanations).

GROUP		SS	IA	S_p	A_p	A_{tm}	A_{sf}	ACR	LA_m	LA_i	LAR	PTR_{fa}
Ceboids	Mean	**25.0**	**25.2**	**1.23**	**393**	**22.9**	**0.65**	**35.4**	**2.54**	**1.47**	**1.74**	**61.5**
	N	3	3	3	3	3	3	3	3	3	3	3
	SD	5.0	4.5	0.13	64	3.9	0.10	2.2	0.27	0.17	0.07	6.1
Lorisoids	Mean	**23.7**	**23.3**	**1.61**	**427**	**23.1**	**0.61**	**38.9**	**2.80**	**1.29**	**2.17**	**84.6**
	N	3	3	3	3	3	3	3	3	3	3	3
	SD	4.4	4.0	0.08	310	1.5	0.12	5.7	0.11	0.10	0.08	14.1
GROUP		ITR_{fa}	M_m	M_i	M_{mi}	M_s	M_{mis}	V_{me}	V_{tc}	V_{es}	V_{ac}	L_c
Ceboids	Mean	**0.0095**	**1.77**	**2.24**	**4.03**	**0.17**	**4.2**	**0.28**	**0.05**	**0.09**	**0.14**	**22.8**
	N	3	3	3	3	3	3	3	3	3	3	3
	SD	0.0013	0.52	0.96	1.50	0.03	1.5	0.13	0.02	0.04	0.09	2.7
Lorisoids	Mean	**0.0056**	**2.01**	**2.31**	**4.33**	**0.19**	**4.2**	**0.32**	**0.07**	**0.18**	**0.06**	**19.1**
	N	3	3	3	3	2	2	3	3	3	3	3
	SD	0.0011	0.52	0.44	0.91	0.06	1.1	0.09	0.01	0.07	0.03	1.7

Table 7.4 - Mean morphometric variables for platyrrhines (ceboids) and lorisoids. The measurements units are the same as in Table 7.1.

length ($p = 0.005$, $n = 18$). It should also be pointed out that **skull size** also showed a significant difference between lorisoids and platyrrhines ($p = < 0.001$, $n = 297$). The results were nearly identical if parametric statistics (ANOVA) were used instead of non-parametrics.

Many of these results reflect patterns similar to those seen in the TIPS correlational analyses. Increased low-frequency sensitivity is associated with lower values for pinna shape ratio, lever arm ratio, and PTR and higher values for interaural distance, ITR, malleus-incus mass, and cochlear length (the middle-ear cavity volume results will be discussed separately). As before, the trends between low-frequency sensitivity and certain morphometric variables are in the expected direction (from acoustic theory) with the exception of those variables that posit increased mechanical advantage (lever arm ratio, ITR, PTR).

The patterns related to cavity volume were rather interesting and deserve special consideration. Although the total volume of air in the middle-ear cavities did not differ statistically, differences were found when examining the individual cavities. Lorisoids showed slightly (albeit significant) larger tympanic cavities than platyrhhines and

substantially larger volumes for the epitympanic sinus. The larger volume of the epitympanic sinuses in lorisoids may be partly explained by the fact that their cavities are relatively non-trabeculated when compared with platyrrhines (and anthropoids in general). Regardless, the larger volumes found in lorisoids are *not* associated with increased low-frequency sensitivity as might be predicted. In contrast, platyrrhines do show considerably larger accessory cavity volumes than lorisoids. These results could be taken to conclude that accessory cavity volume has a sizeable influence over middle-ear cavity stiffness, and hence low-frequency sensitivity, while the functional role of the other cavities remains elusive.

New World vs. Old World Monkeys

The next two comparisons sought to investigate morphological differences between New and Old World monkeys based on the findings from three audiogram studies that suggested Old World monkeys are generally more sensitive than platyrrhines, especially at lower frequencies (Wendt 1934; Fujita and Elliot 1965; Dalton 1968). The first comparison was between *Cebus* and *Macaca* based on the study by Dalton (1968) that suggested *C. capucinus* was less sensitive than *M. mulatta* at all frequencies tested[46]. In order to maximize sample sizes and number of variables that can be compared, genus means were used for all comparisons and are given in Table 7.5.

One of first observations to take from this comparison is that although macaques have significantly larger skulls than cebus monkeys ($p < 0.001$), they actually have a slightly smaller **interaural distance** ($p < 0.001$) and **tympanic membrane** ($p = 0.006$).

[46] The frequencies tested were from 500 Hz to 8 kHz using the GSR method. See Chapter 3 for more details.

GENUS		SS	IA	S_p	A_p	A_{tm}	A_{sf}	ACR	LA_m	LA_i
Ateles	Mean	**47.9**	**49.8**	**1.38**	**622**	**58.3**	**1.60**	**35.1**	**3.39**	**2.07**
	N	18	25	10	10	27	14	13	6	6
	SD	2.3	2.6	0.13	101	7.0	0.24	6.5	0.19	0.21
Cebus	Mean	**41.1**	**41.9**	**1.37**	**722**	**39.0**	**1.06**	**36.9**	**3.05**	**1.90**
	N	85	94	20	20	76	29	29	37	37
	SD	2.1	2.5	0.07	65	3.9	0.14	5.7	0.19	0.13
Macaca	Mean	**48.7**	**39.8**	**1.27**	**932**	**35.0**	**1.11**	**30.9**	**3.57**	**2.13**
	N	36	36	14	14	8	8	5	10	10
	SD	4.5	3.7	0.09	238	2.9	0.12	3.8	0.39	0.17

GENUS		LAR	PTR_{fa}	ITR_{fa}	M_m	M_i	M_{mi}	M_s	M_{mis}	
Ateles	Mean	**1.65**	**54.6**	**0.0128**	**5.92**	**9.38**	**15.8**	**0.85**	**17.0**	
	N	6	4	4	6	8	8	5	3	
	SD	0.19	15.6	0.0052	1.25	2.61	2.4	0.12	3.4	
Cebus	Mean	**1.61**	**60.1**	**0.0104**	**4.31**	**5.46**	**9.9**	**0.40**	**10.0**	
	N	37	14	14	32	40	35	11	7	
	SD	0.11	8.1	0.0014	0.52	0.76	1.2	0.08	1.0	
Macaca	Mean	**1.67**	**45.5**	**0.0141**	**5.54**	**4.42**	**9.9**	**0.36**	**10.3***	
	N	10	2	2	10	14	4	2		
	SD	0.10	1.5	0.0011	0.67	0.61	1.6	0.05		

Table 7.5 - Genus mean values for morphometric variables comparing *Ateles*, *Cebus* and *Macaca*. Note that the value for *Macaca* M_{mis} (*) was calculated by adding M_m, M_i, and M_s. All other derivative variables based on individual specimens with all individual variables present.

The larger tympanic membrane size is also likely driving the significantly larger values for **areal convergence ratio** ($p = 0.032$) and **PTR**[47] ($p = 0.027$) for *Cebus*. Macaques did show significantly longer **lever arms** ($p < 0.001$ for both malleus and incus), although their lever ratio was non-significantly higher. The ossicular mass results are interesting in that macaques have heavier **mallei** ($p < 0.001$), while capuchin monkeys have more massive **incudes** ($p < 0.001$), resulting in their combined mass being nearly equal (and non-significantly different). Potentially, the only variable that would suggest an acoustic advantage for macaques is **pinna area** ($p = 0.001$), which was about one-third larger than that of capuchins. Macaques also had a significantly smaller **pinna shape ratio** ($p = 0.001$).

[47] In addition to the lower value for ITR ($p = 0.003$).

The next analysis looked at *Ateles* compared with Old World monkeys based on the finding by Wendt (1934) that spider monkeys were less sensitive than the three species of cercopithecines (*Cercocebus torquatus*, *Macaca mulatta*, and *Papio anubis*) in his study. Because of the ambiguity relating to the exact species of *Ateles* used by Wendt, and the fact that all three Old World monkeys produced similar audiograms[48], comparisons were made between *Ateles* and macaques using genus mean values. The values for *Ateles* are also given in Table 7.5.

In contrast to the *Cebus* versus *Macaca* comparison, no differences were found in skull size between the genera. However, similar to the previous comparison, New World monkeys (*Ateles*) had a larger **interaural distance** ($p < 0.001$), **tympanic membrane** ($p < 0.001$), **incus mass** ($p = 0.001$), and **pinna ratio** ($p = 0.026$) and a smaller **pinna area** ($p = 0.001$). **Stapedial footplate area** ($p < 0.001$) and **malleus-incus mass** ($p = 0.011$) were also greater in *Ateles*. It is noteworthy to point out that malleus mass did not differ between the genera but incus mass was over twice as small in macaques, resulting in their combined mass being significantly different. Also remarkable is the finding that *Ateles* has a tympanic membrane that is about two thirds larger than that of macaques. As before, the only structures that would appear to provide increased sensitivity for macaques are related to the outer ear while most other variables suggested *Ateles* might be more sensitive, particularly at the lower frequencies.

[48] Stebbins (1973) also found several species of Old World monkeys to have very similar audiograms.

Lemur vs. Eulemur

This comparison looked at differences in morphometric variables between *L. catta* and *E. fulvus*[49]. Two different sources have suggested that differences in high-frequency sensitivity exist between the two species (Mitchell *et al*. 1970; Heffner 2004), with *L. catta* having better high-frequency hearing. In addition, the data presented in Table 3.6 implies that *E. fulvus* is less sensitive at lower frequencies as well. Since the sample sizes for some of the morphometrics were small, non-parametrics (Mann-Whitney U-test) were used to test for differences.

Many of the variables show very similar values between species and few significant differences were found. In particular, the values for interaural distance, tympanic membrane size, cochlear length, pinna area, and combined ossicular mass were nearly identical. Significant differences were detected for **malleus lever arm length** ($p = 0.005$, $n = 21$), **lever arm ratio** ($p < 0.001$, $n = 21$), and **skull size** ($p = 0.001$, $n = 66$). In addition, middle-ear volume ($p = 0.064$, $n = 6$) and incus mass ($p = 0.086$, $n = 34$) were nearing significance levels. Although *E. fulvus* has a slightly larger skull than *L. catta* (**≈** 4%), the only variable that supports the idea that *L. catta* has better high-frequency hearing was pinna ratio (although the difference was non-significant ($p = 0.143$), possibly related to only having a single specimen for *L. catta*). The largest absolute difference between species was in middle-ear volume. Although not quite significant, *L. catta* shows a middle-ear that is over 70% larger than *E. fulvus* so the non-significant finding is almost certainly due to low sample size. The increased bullar volume for *L. catta* could be taken

[49] The species mean values are given in Table 7.1, although the subgroup comparisons calculated the derivative variables slightly differently than for the full group comparisons (the derivatives were based only on specimens that had all individual variables, where as the derivative values in Table 7.1 are based on means for each individual variable).

as support the notion that this species has increased low-frequency sensitivity when compared with *E. fulvus*.

Galago, Nycticebus, and Perodicticus

One of the most striking differences among the lorisoids that have had their hearing tested is that *G. senegalensis* shows a high-frequency cutoff that is over 20 kHz higher than that of the other two species yet has similar low-frequency sensitivity. The data from Heffner and Masterson (1970) also imply that *N. coucang* may have inferior hearing sensitivity at the mid-range frequencies compared with the other two species. The morphometric data for these three species are given in Table 7.1, (although take notice of the footnote above for the *L. catta* and *E. fulvus* comparison) and it can be seen that *G. senegalensis* generally has smaller auditory structures reflecting its overall smaller size. In fact, significant differences were found in **skull size** ($p < 0.001$, $n = 95$) and **interaural distance** ($p < 0.001$, $n = 97$) using a non-parametric Kruskal-Wallis test. Although this test does not allow for post-hoc comparisons, it is evident that it is the smaller values for *G. senegalensis* producing the difference as *N. coucang* and *P. potto* are quite similar.

Numerous morphometric variables also showed significant differences including the six variables involved in calculating transformer ratios: **tympanic membrane area** ($p < 0.001$, $n = 76$), **stapedial footplate area** ($p < 0.001$, $n = 24$), **areal convergence ratio** ($p = 0.014$, $n = 22$), **malleus lever arm length** ($p = 0.002$, $n = 42$), **incus lever arm length** ($p < 0.001$, $n = 42$), and **lever arm ratio** ($p < 0.001$, 42). An interesting feature of these results is that *G. senegalensis* has a smaller tympanic membrane and lever arm lengths but a higher lever arm ratio while *P. potto* had a larger stapedial footplate and

lower PTR[50] than the other species. The relatively small stapedial footplate (and hence high areal convergence ratio) is likely responsible for *N. coucang* having the highest value for PTR.

When examining ossicular mass, all five variables showed significant differences with *G. senegalensis* always having the lightest structures: **malleus mass** ($p < 0.001$, $n = 42$), **incus mass** ($p < 0.001$, $n = 50$), **malleus-incus mass** ($p < 0.001$, $n = 41$), **stapes mass** ($p = 0.040$, $n = 13$), and **malleus-incus-stapes mass** ($p = 0.009$, $n = 10$). No cavity volume measures reached traditional significance levels although total middle-ear volume ($p = 0.066$, $n = 9$), epitympanic sinus volume ($p = 0.061$, $n = 9$), and accessory cavity volume ($p = 0.061$, $n = 9$) were getting close. Tympanic cavity volume was very similar among the three species but interestingly *G. senegalensis* actually had the largest value (although not significantly different). The values for cochlear length are arranged in the expected sequence based on skull size but were found to be only nearing significance ($p = 0.061$, $n = 9$). The most dramatic difference in auditory structures for lorisoids was in **pinna area** ($p = 0.022$, $n = 11$) with *G. senegalensis* having outers ears that were over three times larger than those of either *N. coucang* or *P. potto*. Still, their pinna ratios were similar and not significantly different. Taken as a whole, several auditory structures (e.g., ossicular mass, tympanic membrane area) appear to be related to the increased high-frequency sensitivity in *G. senegalensis*, but the apparent lack of mid-range sensitivity for *N. coucang* is not reflected in the structures measured here.

[50] Statistics were not computed for PTR and ITR because the values for *N. coucang* were calculated from the means of individual structures because no single specimen had all structures present.

Aotus vs. Saimiri

Morphometric variables were compared (using a Mann-Whitney U-test) between *Aotus* and *Saimiri* based on the proposal that *Aotus* is slightly more sensitive than *Saimiri*, particularly on the low-frequency side and around the second peak in sensitivity (see Figure 3.29). Most of the variables showed significant differences between the two genera. *Aotus* is significantly larger than *Saimiri* in **skull size** ($p < 0.001$, $n = 152$), **interaural distance** ($p < 0.001$, $n = 162$), **pinna shape ratio** ($p < 0.001$, $n = 20$), **pinna area** ($p < 0.001$, $n = 20$), **tympanic membrane area** ($p < 0.001$, $n = 172$), s**tapedial footplate area** ($p < 0.001$, $n = 49$), **areal convergence ratio** ($p = 0.005$, $n = 35$), **malleus lever arm length** ($p < 0.001$, $n = 69$), **incus lever arm length** ($p < 0.001$, $n = 69$), **malleus mass** ($p < 0.001$, $n = 66$), **incus mass** ($p < 0.001$, $n = 68$), **malleus + incus mass** ($p < 0.001$, $n = 69$), **all ossicles mass** ($p = 0.003$, $n = 17$), **tympanic cavity volume** ($p = 0.050$, $n = 6$), and **cochlear length** ($p = 0.050$, $n = 6$). The lack of significance for most of the data derived from CT scans (cavity volumes) is almost certainly due to small sample size ($n = 6$) since there is clear separation in their means (Table 7.1). Using parametirc methods (ANOVA) produced qualitatively similar results with the only major exception being that cochlear length became just non-significant ($p = 0.064$).

Most of these results support the idea that *Aotus* shows morphological adaptations (*e.g.*, bigger areas, heavier ossicles, etc.) that should lead to increased sensitivity, particularly at lower frequencies. It is also worth pointing out that *Aotus* had a significantly higher areal convergence ratio, which agrees which theoretical predictions, but is in the opposite direction of that found in the preceding TIPS analysis using the full and optimal speaker datasets. What's more, two morphological variables (pinna shape

ratio and cochlear length) showed patterns that do not support the trend towards more low-frequency tuning for *Aotus*. The first of these is pinna shape, which is taller and narrower in *Aotus*, and should have the influence of lessening low-frequency reception while boosting high-frequency reception (*Aotus* shows only the slightest trend towards increased high-frequency sensitivity - see Table 3.6). The other bizarre finding from this analysis was that *Saimiri* actually has a longer cochlea than *Aotus*. Although this result could obviously be the related to small sample size, it is likely a valid difference since there is absolutely no overlap in the values between the two groups. This finding deserves further investigation.

MORPHOMETRIC – AUDIOMETRIC COMPARISONS USING PICS

In the last few decades, comparative biologists have become concerned that data points from closely related taxa may not be statistically independent - a primary assumption of both parametric and nonparametric techniques. Early attempts to correct for phylogenetic non-independence of data simply avoided comparing individual species and focused the analyses at the generic level (Clutton-Brock and Harvey 1977). However, in addition to addressing non-independence problems, incorporation of phylogenetic information may also be useful for investigating certain adaptive processes such as rates of evolution (Garland *et al*., 1993).

One of the first rigorous attempts to address the phylogenetic non-indepence of most comparative datasets was Felsenstein's independent contrasts (1985), now commonly referred to as PICS (phylogenetic independent contrasts). PICS are calculated by determining the difference in the values for a trait between each sister-taxon pair at the

tips of a phylogenetic tree as well as for internal nodes. These differences are divided by the square root of the sum of their branch lengths to produce the contrast values; the actual data points used for statistical analyses. Another approach that has received considerable attention is the phylogenetic generalized least-squares (PGLS) method. However, recent studies have found that the two approaches are "functionally identical" (Garland and Ives 2000), and in fact that the PICS method is a special case of the PGLS method (Rohlf 2001).

In order to investigate the potential effects of phylogenetic non-independence of the data used in this dissertation, the PICS method was used to reanalyze the previous comparisons using TIPS data (except those comparisons between only two taxa). One of the biggest challenges in using phylogenetic comparative methods, is that the phylogeny (topology and branch lengths) for the comparative dataset must be known. Although it has been shown that type I errors are reduced even if the exact phylogeny is unknown, polytomies area unresolved and/or branch lengths are approximate (Rohlf 2006), the ideal situation is one in which the group under investigation has a relatively well resolved phylogenetic tree. Fortunately, primates have received a considerable amount of attention in this arena of research, and it is possible to generate a phylogeny with reasonable estimates of branching patterns and times since divergence.

The phylogenetic tree representing the taxa in this study is presented in Figure 7.39. The data used to construct this phylogeny were taken from numerous studies (mostly genetic) that focused on specific clades. In many cases, rates of evolution (divergence times) were calibrated using fossils of known age and phylogenetic relatedness. The initial divergence time (in millions of years) between primates and tree

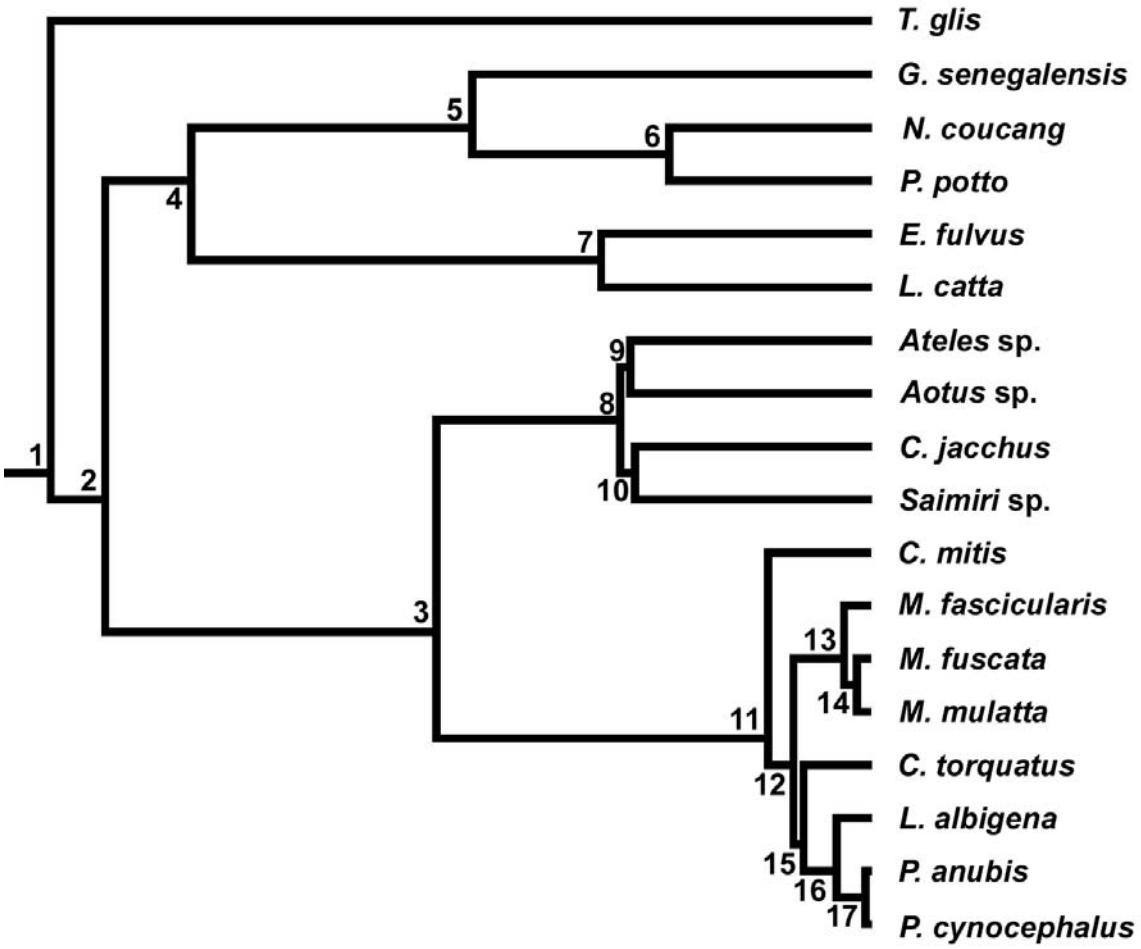

Figure 7.39 - Phylogenetic tree for taxa used in the PICS analysis. Divergence dates for individual nodes (numbers in figure) taken from the literature and described fully in text.

shrews (node 1) was established as 82.8 Mya, that between strepsirrhines and anthropoids (node 2) as 77.2 Mya, and between platyrrhines and catarrhines (node 3) as 43.6 Mya, based on Eizirik *et al*. (2003). The diversification of lemuroids from lorisoids (node 4) was set at 68.5 Mya and of galagids from lorisids (node 5) at 40 Mya, based on Yoder and Yang (2004). The split within lorisids (node 6) was set at 20 Mya and the split within lemurids (node 7) was set at 27 Mya, based on arguments in Ross *et al*. (2004). The initial radiation of extant platyrrhines (node 8) was set at 25 Mya from Porter *et al*. (1997). The split between *Ateles* and *Aotus* (node 9) was set at 24 Mya and between

Saimiri and *Callithrix* (node 10) at 23.5 Mya, again based on Ross *et al.* (2004). The divergence date for *Cercopithecus* from all other cercopithecines (node 11) was set at 10 Mya, also from Ross *et al*. (2004). The split between macaques and other cercopithecines (node 12) was set at 7.5 Mya and between *M. fascicularis* and other macaques at 2.4 Mya (node 13), both based on Tosi *et al*. (2003). The node separating *M. fuscata* from *M. mulatta* (14) was set at 1.15 Mya from Hayasaka *et al*. (1996). The date for the spit between *C. torquatus* and the other papionins (node 15) was set at 6.5 Mya and between *L. albigena* and *Papio* (node 16) at 3.2 Mya, based on *Tosi et al.* (2003). The divergence between *P. cynocephalus* and *P. anubis* (node 17) was set at 0.16 Mya from Newman *et al*. (2004).

To perform the PICS analyses, all morphometric, audiometric, and phylogenetic data were imported into Mesquite 1.12 (Maddison and Maddison 2006). The actual statistics were computed using the PDAP diagnostic chart module (Midford *et al*. 2003). The phylogenetic tree was pruned for individual analyses which used subsets of the full dataset (*e.g*., optimal).

EXTRA-EAR

Skull Size

Similar to the results from the TIPS comparisons, numerous morphometric variables were significantly correlated with skull size using the PICS data. However, seven variables did not show significant relationships with skull size: pinna ratio, pinna area, areal convergence ratio, ossicular lever arm ratio, PTR_{fa}, PTR_{ea}, and tympanic cavity volume. Two of these variables (pinna ratio and areal convergence ratio) were also

non-significant using the TIPS data, but the other four were previously found to be significantly correlated with skull size.

Comparing skull size to the audiometric variables, no significant correlations were found using the optimal speaker dataset. Using the full speaker data, only low audible area ($p = 0.073$, $r = 0.476$, $n = 14$) showed signs of significance. These results are in stark contrasts to the TIPS results where about half of the audiometric variables showed significant correlations with skull size.

Interaural Distance

No significant correlations were found between interaural distance (absolute values) and any audiometric variables using either dataset (optimal or full). In contrast, the TIPS analysis suggested significant associations between interaural distance and a suite of audiometric variables including measures of low, middle and high-range sensitivity. Relative interaural distance (PICS) did show significant correlations with **low audible area** ($p = 0.010$, $r = -0.711$, $n = 11$), SPL of the first peak ($p = 0.099$, $r = 0.550$, $n = 9$), and **SPL of the mid-range dip** ($p = 0.040$, $r = 0.656$, $n = 9$) using the optimal speaker dataset. These results are similar to the TIPS results, except SPL of peak 1 was not significant while SPL @ 250 Hz was significant in the previous analysis. Using the full speaker data, seven variables showed significance levels below 0.100: low-frequency cutoff ($p = 0.078$, $r = 0.655$, $n = 7$); **SPL @ 250 Hz** ($p = 0.008$, $r = 0.620$, $n = 16$), **low audible area** ($p = 0.003$, $r = -0.703$, $n = 14$); **SPL of peak 1** ($p = 0.004$, $r = 0.690$, $n = 140$); **frequency of peak 1** ($p = 0.009$, $r = -.0746$, $n = 14$); **frequency of the mid-range dip** ($p = 0.036$, $r = -0.544$, $n = 14$); and **SPL of peak 2** ($p = 0.003$, $r = -0.683$, $n = 16$).

The three low-frequency variables and SPL of peak 1 are shared with the TIPS results, but the other significant variables from each comparison are completely non-overlapping.

OUTER EAR

Pinna Shape Ratio

Pinna shape ratio was found to be negatively correlated with total audible area ($p = 0.067$, $r = -.0674$, $n = 7$) using the optimal speaker dataset. The same result was found using the full speaker data, although the correlation was a little stronger (**total audible area** - $p = 0.034$, $r = -0.705$, $n = 8$). The pattern of decreasing audible area with increasing pinna shape ratio was also found using the TIPS data, although several other variables were also found to be significant (middle audible area, SPL peak 1, SPL peak 2, SPL of the dip).

Pinna Area

Using the optimal speaker data, the PICS comparison revealed absolute pinna area to be approaching traditional significance with SPL of the first peak ($p = 0.088$, $r = 0.640$, $n = 7$) and SPL of the second peak ($p = 0.057$, $r = 0.618$, $n = 9$), as well as high-frequency cutoff ($p = 0.069$, 0.718, $n = 6$) once *C. jacchus* was eliminated. Very similar results were found using the full speaker data, although high-frequency cutoff was omitted (SPL of the first peak - $p = 0.082$, $r = 0.575$, $n = 9$; **SPL of the second peak** - $p = 0.031$, $r = 0.623$, $n = 11$). These results share no common correlations with the TIPS results which showed correlations with low and mid-frequency sensitivity but not the intensity levels of the peaks in sensitivity.

Relative pinna area (optimal dataset) showed significant correlations with **SPL of the first peak** ($p = 0.029$, $r = 0.759$, $n = 7$) and **frequency of the first peak** ($p = 0.041$, $r = -.0728$, $n = 7$) while frequency of the dip was getting close ($p = 0.100$, $r = -0.621$, $n = 7$). **High-frequency cutoff** ($p = 0.032$, $r = 0.796$, $n = 6$) was also significant excluding *C. jacchus*. The results from the TIPS comparisons were very similar except high-frequency cutoff was non-significant (even without *C. jacchus*). Using the full speaker data, **SPL of the first peak** ($p = 0.015$, $r = 0.735$, $n = 9$) was again significant and frequency of the dip ($p = 0.064$, -0.605, $n = 9$) also showed low p-values. Similar to before, high-frequency cutoff ($p = 0.061$, $r = 0.686$, $n = 7$) suggested a positive correlation with relative pinna area after removing *C. jacchus*. These PICS results share three variables with the full speaker results from the TIPS comparison (SPL of the first peak, frequency of the dip, and high-frequency cutoff) although frequency of the first peak was also previously found to be significant.

MIDDLE EAR

Tympanic Membrane Area

Tympanic membrane area was significantly correlated with **SPL @ 250 Hz** ($p = 0.012$, $r = -0.784$, $n = 8$) and **low audible area** ($p = 0.025$, $r = 0.733$, $n = 8$) using the optimal speaker dataset. These results are the same as those from the optimal speaker TIPS comparisons. Using the full speaker dataset, **SPL of the second peak** ($p = 0.002$, $r = 0.804$, $n = 11$) was found to be significant and high audible area ($p = 0.052$, $r = -0.628$, $n = 9$), frequency of the first peak ($p = 0.060$, $r = -0.612$, $n = 9$), and frequency of the second peak ($p = 0.061$, $r = -0.533$, $n = 12$) all showed p-values below 0.100. **High**

audible area became highly significant ($p = 0.002$, $r = -0.875$, $n = 8$) when *C. jacchus* was excluded from the analysis. The high audible area and frequency of the first peak results reflect those from the TIPS comparison but none of the other significant variables from either analysis were the same.

Examining the relative size of the tympanic membrane, **SPL of the dip** ($p = 0.005$, $r = 0.905$, $n = 6$) and **frequency of the second peak** ($p = 0.007$, $r = -0.822$, $n = 8$) were significant using the optimal speaker dataset. Essentially the same pattern was found using the TIPS data (same variables). **Frequency of the second peak** ($p < 0.001$, $r = -0.843$, $n = 12$) was also significant using the full speaker dataset as was **SPL of the second peak** ($p = 0.023$, $r = 0.648$, $n = 11$). In addition, high audible area ($p = 0.057$, $r = -0.617$, $n = 9$) and frequency of the first peak ($p = 0.096$, $r = -0.554$, $n = 9$) had relatively low p-values using the full speaker dataset. Removing *C. jacchus* only marginally affected the results for high audible area ($p = 0.083$, $r = -0.607$, $n = 8$). These results also resembled those from the TIPS analyses but further suggested one addition correlation that was not previously recognized (SPL of the second peak).

Stapedial Footplate Area

Stapedial footplate area was significantly correlated with **SPL @ 250 Hz** ($p = 0.016$, $r = -0.732$, $n = 9$) using the optimal speaker dataset. The TIPS results also showed this association in additional to significant correlations with three other audiometric variables (low audible area, middle audible area and SPL of the dip). Using the full speaker dataset, **frequency of the first peak** ($p = 0.041$, $r = -0.622$, $n = 10$) and **SPL of the second peak** ($p = 0.049$, $r = 0.556$, $n = 12$) were significant with high audible area (p

= 0.075, r = -0.586, n = 9) also showing low p-values. **High audible area** became highly significant (p = 0.005, r = -0.840, n = 8) after removing *C. jacchus*. The only correlation shared between this analysis and the TIPS analysis is high audible area. The TIPS comparisons also suggested a strong relationship between stapedial footplate area and low-frequency sensitivity similar to the findings using the optimal speaker dataset.

Using the optimal speaker dataset, relative stapedial footplate area showed significant correlations with **SPL of the dip** (p < 0.001, r = 0.945, n = 7) and a weaker relationship with frequency of the second peak (p = 0.078, r = -0.581, n = 9). The full speaker results showed similar patterns with **frequency of the second peak** (p = 0.021, r = -0.601, n = 13) being significant and SPL of the dip (p = 0.092, r = 0.560, n = 9) and frequency of the first peak (p = 0.064, r = -0.576, n = 10) producing p-values below 0.100. With the exception of the frequency of the first peak correlation just mentioned, the TIPS and PICS comparisons produced very similar results involving the same audiometric variables.

Areal Convergence Ratio

Areal convergence ratio (optimal speaker dataset) showed a significant correlation with **middle audible area** (p = 0.045, r = -0.678, n = 8) and weaker relationships with total audible area (p = 0.096, r = -0.627, n = 7) and SPL of the dip (p = 0.067, r = 0.722, n = 6). The PICS comparison using the full speaker dataset produced a different mix of variables: **low audible area** (p = 0.035, r = -0.610, n = 11), **SPL of the second peak** (p = 0.009, r = 0.716, n = 11), **frequency of the second peak** (p = 0.041, r = -0.572, n = 12), SPL @ 250 Hz (p = 0.084, r = 0.519, n = 11), and middle audible area (p = 0.079, r = -

0.525, n = 11). Middle audible area and total audible area were common to the optimal speaker comparisons from both the TIPS and PICS comparison although the TIPS comparison also found correlations with measures of low-frequency sensitivity (SPL @ 250 Hz and low audible area). The full speaker analyses shared only middle audible area between the two comparisons

Malleus Lever Arm Length

The results from the malleus lever arm comparisons (optimal speaker dataset) were similar to those of areal convergence ratio with **SPL @ 250 Hz** ($p = 0.047$, $r = -0.638$, $n = 9$), **low audible area** ($p = 0.007$, $r = 0.783$, $n = 9$), and SPL of the dip ($p = 0.097$, $r = -0.625$, $n = 7$) all producing relatively low significance values. However, using the full speaker dataset, these correlations disappeared and only **frequency of the second peak** ($p = 0.017$, $r = -0.605$, $n = 14$) showed significance with high audible area ($p = 0.097$, $r = -0.587$, $n = 8$) getting close after purging *C. jacchus*. In general, there was little in common between the PICS and TIPS results except SPL @ 250 Hz was found to be significant in both optimal speaker analyses.

The relative malleus lever arm results were similar to the absolute value results in that some of the correlated variables were different between the optimal and full speaker datasets. Using the optimal speaker data, **frequency of the second peak** ($p = 0.045$, $r = -0.643$, $n = 9$) was significant and SPL of the second peak ($p = 0.093$, $r = -0.559$, $n = 9$) also showed signs of being correlated with relative malleus lever arm length. Removing *C. jacchus* also resulted in **high-frequency cutoff** ($p = 0.018$, $r = 0.838$, $n = 6$) and high audible area ($p = 0.071$, $r = 0.714$, $n = 6$) achieving noteworthy correlations. The full

speaker results showed only **SPL @ 250 Hz** ($p = 0.034$, $r = 0.568$, $n = 13$) to be significant, although both **high-frequency cutoff** ($p = 0.004$, $r = 0.849$, $n = 8$) and **high audible area** ($p = 0.013$, $r = 0.779$, $n = 9$) were again significant after expulsing *C. jacchus*. The high-frequency results (high-frequency cutoff and high audible area) were quite similar between the TIPS and PICS comparisons but the only other variable in common was SPL @ 250 Hz (full speaker dataset).

Incus Lever Arm Length

The PICS results from the optimal speaker incus lever arm comparisons resembled those of the malleus in that **SPL @ 250 Hz** ($p = 0.007$, $r = -0.784$, $n = 9$), **low audible area** ($p = 0.002$, $r = 0.852$, $n = 9$), and **SPL of the dip** ($p = 0.028$, $r = -0.721$, $n = 7$) were found to be significant. In addition, middle audible area ($p = 0.073$, $r = 0.589$, $n = 9$) showed relatively low p-values. Also similar to the malleus lever arm results, using the full speaker dataset, only frequency of the second peak ($p = 0.069$, $r = -0.482$, $n = 14$) showed signs of being correlated with incus lever arm length as did high audible area ($p = 0.063$, $r = -0.640$, $n = 8$) after removing *C. jacchus*. The correspondence between the TIPS and PICS results for optimal speaker data was rather good with all the same audiometric variables being significant. However, the full speaker results were mostly non-overlapping with high audible area being the only variable shared by both TIPS and PICS comparisons.

The relative incus lever arm length results (PICS) also reflected those of the relative malleus lever arm. In this case, it was **SPL of the second peak** ($p = 0.033$, -0.672, $n = 9$) that was significant with frequency of the second peak ($p = 0.073$, $r =$ -

0.589, n = 9) getting close. Eliminating *C. jacchus*, **high audible area** (0.007, r = 0.895, n = 6) became significant and high-frequency cutoff (p = 0.094, r = 0.679, n = 6) showed p-values below 0.100, the same as with relative malleus lever arm length results. The similarities continue, with only **SPL @ 250 Hz** (p = 0.021, r = 0.608, n = 13) showing significance using the full speaker data and high-frequency cutoff (p = 0.067, 0.633, n = 8) and **high audible area** (p = 0.002, r = 0.877, n = 8) also achieving low p-values after purging *C. jacchus*. Despite the similitude between the relative malleus and incus lever arm PICS results, the incus TIPS and PICS data matched much better than those of the malleus. The optimal speaker comparisons shared SPL of the second peak and high audible area while the full speaker comparisons shared SPL @ 250 Hz, high audible area, and high-frequency cutoff.

Ossicular Lever Arm Ratio

No variables were found to be significantly correlated with ossicular lever arm ratio using the optimal speaker dataset. Essentially the same pattern was produced using the full speaker dataset (no significant variables), although high-frequency cutoff (p = 0.054, r = 0.659, n = 8) showed relatively low p-values after eliminating *C. jacchus*. These findings contrast strongly with the TIPS results which found six audiometric variables correlated with ossicular lever arm length (using either dataset).

Pressure Transformer Ratio

The PICS results using the optimal speaker dataset showed **middle audible area** (p = 0.036, r = -0.699, n = 8), **total audible area** (p = 0.048, r = -0.711, n = 7), and **SPL**

of the dip (p = 0.035, r = 0.790, n = 6) to have significant relationships with the PTR. These three variables were also found to be significant in the TIPS analysis, although four other significant variables were also detected (SPL @ 250 HZ, low audible area, SPL of the first peak, and SPL of the second peak). Using the full speaker dataset, five audiometric variables produced p-values below 0.100: **SPL @ 250 Hz** (p = 0.028, r = 0.631, n = 11), **low audible area** (p = 0.046, r = -0.584, n = 11), middle audible area (p = 0.074, r = -0.534, n = 11), SPL of the dip (p = 0.059, r = 0.648, n = 8), and SPL of the second peak (p = 0.099, r = 0.498, n = 11). These results also overlapped considerably with the TIPS results with SPL @ 250 Hz, low audible area, middle audible area, and SPL of the dip found in both comparisons. Absent from the PICS results were total audible area and SPL of the first peak.

Impedance Transformer Ratio

Using the optimal speaker data, two variables were significantly correlated with ITR and three had p-values less than 0.100. These include SPL @ 250 Hz (p = 0.060, r = -0.646, n = 8), low audible area (p = 0.082, r = 0.609, n = 8), middle audible area (p = 0.070, r = 0.628, n = 8), **total audible area** (p = 0.037, r = 0.736, n = 7), and **SPL of the dip** (p = 0.037 r = -0.783, n = 6). These five variables were also found to be significant using TIPS data (the TIPS analysis also found SPL of the first and second peaks to have low p-values). The full speaker PICS analysis identified **SPL @ 250 Hz** (p = 0.018, r = -0.665, n = 11), **low audible area** (p = 0.042, r = 0.592, n = 11), SPL of the dip (p = 0.079, r = -0.613, n = 8), and frequency of the second dip (p = 0.057, r = 0.541, n = 12) as showing significant correlations with ITR. Three of these variables (SPL @ 250 Hz, low

audible area, and SPL of the dip) were also represented in the TIPS results, although three additional variables were significant using TIPS data (middle audible area, total audible area, and SPL of the first peak).

Malleus Mass

Malleus mass (optimal data) was significantly correlated with **SPL @ 250 Hz** ($p = 0.013$, $r = -0.781$, $n = 8$) and **low audible area** ($p = 0.013$, $r = 0.783$, $n = 8$) with SPL of the dip ($p = 0.076$, $r = -0.706$, $n = 6$) also having a relatively high correlation coefficient. These results match those found using TIPS data almost exactly. The PICS results using the full dataset showed malleus mass to be highly correlated with **SPL @ 250 Hz** ($p = 0.001$, $r = -0.818$, $n = 11$). High audible area ($p = 0.067$, $r = -0.599$, $n = 9$), SPL at the dip ($p = 0.051$, $r = -0.705$, $n = 7$), and middle audible area ($p = 0.082$, $r = -0.521$, $n = 11$) also showed relatively strong relationships with malleus mass. **High audible area** ($p = 0.002$, $r = -0.883$, $n = 8$) became highly significant after excluding *C. jacchus*. The results also show close agreement with the TIPS results, except the TIPS results also showed a significant correlation with low audible area but did not find a correlation with middle audible area.

Relative malleus mass showed significant correlations exclusively with measures of low-frequency sensitivity using the optimal speaker data: **SPL @ 250 Hz** ($p = 0.024$, $r = -0.735$, $n = 8$) and **low audible area** ($p = 0.037$, $r = 0.698$, $n = 8$). The TIPS comparisons did not detect any significant correlations using the optimal speaker data, although the two aforementioned variables had p-values between 0.100 and 0.200. The full speaker dataset results (PICS) also showed a relationship with low-frequency

sensitivity (**SPL @ 250** - p = -.041, r = -0.596, n = 11), but further suggested that high-frequency hearing (high audible area - p = 0.061, r = -0.609, n = 9) is correlated with relative malleus mass. In fact, **high audible area** (p = 0.006, r = -0.829, n = 8) becomes the audiometric variable with the highest correlation in both the relative and absolute malleus mass comparisons after removing *C. jacchus*. The full speaker TIPS results were very similar to the PICS results with the exception that low audible area also showed a significant correlation with relative malleus mass.

Incus Mass

The only audiometric variable (optimal speaker data) correlated with incus mass was **frequency of the second peak** (p = 0.025, r = -0.699, n = 9). Using the full speaker dataset, no significant variables were found although after removing *C. jacchus* from the high-frequency analyses, **high audible area** (p = 0.029, r = -0.687, n = 9) became significant. The TIPS analysis also found high audible area to be significantly correlated with incus mass (both datasets) but additionally found measures of low-frequency sensitivity (SPL @ 250 HZ and low audible area) and a few other variables significant as well (although not frequency of the second peak as in the PICS analysis).

The PICS analysis for relative incus mass (optimal speaker data) found **frequency of the second peak** (p = 0.015, r = -0.738, n = 9) to be significant and low-frequency cutoff (p = 0.054, r = -0.946, n = 3) to be very close (caution, note the low number of contrasts). The optimal speaker TIPS results also found low-frequency cutoff to have a p-value below 0.100, but found no other variables to be significant. The full speaker PICS comparisons found a significant correlation with **SPL of the second peak** (p = 0.016, r =

0.649, n = 12) and weaker correlations with middle audible area (p = 0.062, -0.531, n = 12), high audible area (p = 0.052, r = -0.598, n = 10), frequency of the first peak (p = 0.064, r = -0.575, n = 10), and frequency of the second peak (p = 0.073, r = -0.493, n = 13). **High audible area** (p = 0.001, r = -0.862, n = 9) became highly significant after *C. jacchus* was removed. The TIPS results illustrated the same pattern as the PICS results regarding high audible area and also showed frequency and SPL of the second peak to be close to traditional significance levels but did not find the other variables listed above to have a correlation with relative incus mass.

Combined Malleus-Incus Mass

When the PICS analysis was applied to the combined mass of the malleus and incus (optimal speaker data), **SPL @ 250 Hz** (p = 0.028, r = -0.723, n = 8) and **low audible area** (p = 0.033, r = 0.709, n = 8) were significant with SPL of the dip (p = 0.065, r = -0.725, n = 6) approaching p = 0.050. The optimal speaker TIPS results were akin, except low audible area had not quite reached traditional significance (still < 0.100). In contrast, the full speaker PICS analysis found a significant correlation with **SPL of the second peak** (p = 0.046, r = 0.610, n = 10) and mentionable correlations with high audible area (p = 0.053, r = -0.626, n = 9), frequency of the first peak (p = 0.093, r = -0.593, n = 8), and SPL of the dip (p = 0.069, r = -0.670, n = 7). As with the PICS analyses of the individual ossicles, **high audible area** (p < 0.001, r = -0.921, n = 8) became highly significant after *C. jacchus* was excluded. The full speaker TIPS results included high audible area and SPL of the dip (as well as SPL @ 250 HZ and low audible

area) but did not find significant associations with the other variables found using PICS (frequency of the first peak and SPL of the second peak).

No significant correlations were found between the relative combined malleus-incus mass and any audiometric variables using the optimal speaker dataset. The same results were produced using the TIPS data. The full speaker PICS results resembled those using absolute values with **SPL of the second peak** ($p = 0.030$, $r = 0.650$, $n = 10$) being significant and high audible area ($p = 0.051$, $r = -0.630$, $n = 9$) and frequency of the first peak ($p = 0.091$, $r = -0.595$, $n = 8$) showing relatively low p-values. Not surprisingly, **high audible area** ($p = 0.001$, $r = -0.890$, $n = 8$) showed a strong relationship with relative malleus-incus mass once *C. jacchus* was ignored. The full speaker TIPS results also found high audible area to be significant but none of the other variables.

Stapes Mass

Stapes mass showed notable correlations with SPL @ 250 Hz ($p = 0.069$ $r = -0.776$, $n = 5$), SPL of the dip ($p = 0.067$, $r = -0.779$, $n = 5$), and **frequency of the second peak** ($p = 0.038$, $r = 0.837$, $n = 5$) using the optimal speaker data. Although based on a low number of contrasts, significant correlations were also detected with **high-frequency cutoff** ($p = 0.029$, $r = -0.971$, $n = 3$) and **high audible area** ($p = 0.027$, $r = -0.973$, $n = 3$) after removing *C. jacchus*. High audible area, high frequency cutoff, and frequency of the second peak were also found to be significant using TIPS data. The PICS results using the full speaker data included total audible area ($p = 0.076$, $r = -0.765$, $n = 5$), middle audible area ($p = 0.075$, $r = -0.708$, $n = 6$), SPL of the dip ($p = 0.067$, $r = -0.780$, $n = 5$), and **SPL of the second peak** ($p = 0.006$, $r = 0.899$, $n = 6$). **High-frequency cutoff**

(same analysis as the optimal speaker dataset) and **high audible area** ($p < 0.001$, $r = -0.993$, $n = 4$) became significant without *C. jacchus* in the analysis. The only variable found to be significant from the full speaker TIPS analysis was high audible area.

Using PICS, no variables were found to be significantly correlated with relative stapes mass using the optimal speaker data. This contrasts with the results using TIPS data (optimal): relative stapes mass is correlated with total audible area, middle audible area, range in octaves, and SPL of the second peak. The full speaker PICS results on the other hand did show significant correlations with **total audible area** ($p = 0.036$, $r = -0.841$, $n = 5$), **middle audible area** ($p = 0.030$, $r = -0.803$, $n = 6$), and **SPL of the second peak** ($p = 0.004$, $r = 0.917$, $n = n = 6$), with high audible area ($p = 0.067$, $r = -0.780$, $n = 5$) getting close. Predictably, omitting *C. jacchus* resulted in **high audible area** ($p = 0.002$, $r = -0.984$, $n = 4$) becoming highly significant. SPL of the second peak and high audible area were also found to be significantly correlated with relative stapes mass using TIPS data.

Ossicular Chain Mass

When PICS were used to analyze the mass of the entire ossicular chain, very few correlations were identified. Using the optimal speaker data, a weak correlation with SPL @ 250 Hz ($p = 0.098$, $r = -0.733$, $n = 5$) was detected. No significant variables were found using optimal speaker TIPS data (although SPL @ 250 Hz did show a p-value of 0.120.) Utilizing the full speaker dataset, a significant relationship was found with **SPL of the second peak** ($p = 0.017$, $r = 0.842$, $n = 6$). **High audible are**a ($p = 0.004$, $r= -0.976$, $n = 4$) also achieved significance after removing *C. jacchus*. The TIPS data

revealed almost exactly the same relationship between high audible area and ossicular chain mass (excluding *C. jacchus*), but no other correlations were found.

Relative ossicular chain mass showed no significant correlations with audiometrics using the optimal speaker data. The TIPS results were the same. However, the full speaker PICS results did show **SPL of the second peak** ($p = 0.022$, $r = 0.827$, $n = 6$) to be correlated and middle audible area ($p = 0.087$, $r = -0.688$, $n = 6$) also showing relatively low p-values. **High audible area** ($p = 0.022$, $r = -0.929$, $n = 4$) became significant after *C. jacchus* was removed. The only significant variable from the full speaker TIPS results was high audible area.

Total Middle Ear Volume

Two significant correlations were found with total middle ear volume using the optimal speaker dataset: **SPL @ 250 Hz** ($p = 0.019$, $r = -0.753$, $n = 8$) and **low audible area** ($p = 0.009$, $r = 0.807$, $n = 8$). The results parallel those of the TIPS analysis except that a weak correlation was also detected with high audible area (minus *C. jacchus*). No significant correlations were found using the full speaker PICS data. The full speaker TIPS data however showed correlations with the common triad, SPL @ 250 Hz, low audible area, and SPL of the dip.

The relative total middle ear volume results using PICS were the same as the absolute values: **SPL @ 250 Hz** ($p = 0.020$, $r = -0.751$, $n = 8$) and **low audible area** ($p = 0.012$, $r = 0.787$, $n = 8$) using the optimal speaker data and no significant variables using the full speaker data. The comparison with the TIPS data was also similar to the absolute

value comparisons: the optimal speaker results were very similar but the TIPS full speaker results found correlations that were absent from the PICS results.

Tympanic Cavity Volume

No significant variables were correlated with tympanic cavity volume using the optimal speaker PICS data. The optimal speaker TIPS significant results were nearly as sparse. The full speaker PICS results showed a significant correlation with only one variable: **frequency of the second peak** ($p = 0.047$, $r = -0.712$, $n = 7$). The full speaker TIPS analysis found no significant variables.

Evaluating the relative volume of the tympanic cavity using PICS (optimal speaker data), two variables showed relatively low p-values: frequency of the first peak ($p = 0.070$, $r = -0.775$, $n = 5$) and frequency of the second peak ($p = 0.095$, $r = -0.676$, $n = 6$). **High-frequency cutoff** ($p = 0.037$, $r = 0.901$, $n = 4$) was also significant after *C. jacchus* was excluded. Frequency of the first peak and high-frequency cutoff (*C. jacchus* removed) were found to be significant using TIPS data, although the TIPS analysis also found correlations with frequency of the dip and SPL of the first peak. The PICS analysis using the full speaker data, also found **frequency of the second peak** ($p = 0.007$, $r = -0.852$, $n = 7$) and **high-frequency cutoff** (minus *C. jacchus* - $p = 0.045$, $r = 0.821$, $n = 5$) to be significant. In this case, only high-frequency cutoff was found to overlap with the TIPS results (which also found frequency of the dip and frequency of the first peak significant).

Epitympanic Sinus Volume

The PICS results for epitympanic sinus volume (optimal speaker data) included SPL @ 250 Hz ($p = 0.056$, $r = -0.743$, $n = 6$) and **low audible area** ($p = 0.032$, $r = 0.797$, $n = 6$). No significant variables were found using the full speaker dataset. The full speaker TIPS results did show SPL @ 250 Hz and low audible area to be approaching significance ($p < 0.100$), but using the optimal speaker TIPS data, the p-values for these variables inched just above the relaxed significance criterion (still less than 0.120).

The PICS results for the relative volume of the epitympanic sinuses were nearly identical to the results for absolute volume. Using the optimal speaker data, SPL @ 250 Hz ($p = 0.078$, $r = -0.702$, $n = 6$) and low audible area ($p = 0.051$, $r = 0.751$, $n = 6$) displayed notable correlations with epitympanic sinus volume and as before, no significant variables were found using the full speaker data. The TIPS results for relative epitympanic sinus volume shared only the finding that no significant variables were detected using the full speaker dataset (the optimal speaker results found total audible area and range in octaves to be significant).

Accessory Cavity Volume

The optimal speaker PICS results for accessory cavity volume included SPL @ 250 Hz ($p = 0.054$, $r = -0.746$, $n = 6$), low audible area ($p = 0.060$, $r = 0.734$, $n = 6$), and **SPL of the dip** ($p = 0.032$, $r = -0.851$, $n = 5$). The only correlation of note using the full speaker data was SPL of the dip ($p = 0.059$, $r = -0.736$, $n = 6$). The TIPS results also found SPL @ 250 Hz, low audible area, and SPL of the dip to be significant (both

datasets) which agrees perfectly with the optimal speaker PICS results but only marginally with the full speaker PICS results.

The relative volume of the accessory cavities showed correlations (optimal speaker data) with SPL @ 250 Hz ($p = 0.097$, $r = -0.674$, $n = 6$), **SPL of the dip** ($p = 0.009$, $r = -0.921$, $n = 5$) and frequency of the second peak ($p = 0.099$, $r = 0.671$, $n = 6$). No significant correlations were found using the full speaker dataset. The TIPS results included SPL @ 250 Hz and SPL of the dip, in addition to low audible area, middle audible area, and total audible area (both datasets). Similar to the absolute accessory cavity comparisons, there was reasonably good agreement between the optimal speaker TIPS and PICS results, but not between the full speaker TIPS and PICS results.

INNER EAR

Cochlear Length

The final PICS comparisons found significant relationships between cochlear length (optimal speaker dataset) and **SPL @ 250 Hz** ($p = 0.018$, $r = -0.777$, $n = 8$), **low audible area** ($p = 0.032$, $r = 0.711$, $n = 8$), and **SPL of the dip** ($p = 0.021$, $r = -0.831$, $n = 6$). **SPL of the dip** ($p = 0.049$, $r = -0.709$, $n = 7$) was also significant using the full speaker dataset but the only other variable even approaching significance was total audible area ($p = 0.081$, $r = 0.610$, $n = 8$). The optimal speaker TIPS results included the three significant variables found using PICS data but also found weaker correlations with middle audible area and range in octaves. Likewise, the full speaker TIPS results also included the two variables listed above but found several other significant correlations as well (SPL @ 250 Hz, low audible area, middle audible area, and range in octaves).

No significant correlations were found between relative cochlear length and any audiometric variable using the optimal speaker data. Weak correlations were detected using the full speaker data with SPL of the dip ($p = 0.083$, $r = 0.646$, $n = 7$) and with high audible area ($p = 0.082$, $r = 0.649$, $n = 7$) once *C. jacchus* was omitted. The TIPS data produced very similar patterns: no significant correlations using the optimal speaker dataset and weak correlations with high audible area and SPL of the dip using the full speaker dataset (although the p-value for SPL of the dip was actually 0.112- just above the significance criterion used here). Next, all of the preceding results (PICS and TIPS) will be summarized and evaluated.

DISCUSSION

Regardless of the statistical method employed (traditional or phylogenetic), the most salient conclusion drawn from the previous analyses is that various aspects of hearing sensitivity are significantly correlated with particular auditory structures from the entire ear (outer, middle and inner). Table 7.6 presents a summary of the significant correlations that were mutual to both the TIPS and PICS comparisons. In just over half of these results (57%), the correlation coefficients (for individual variables) generated using TIPS data were higher than those from PICS data. However, the opposite was true in 58 out of 132 cases (43%), where using phylogenetic statistical procedures actually improved the correlation compared with traditional approaches. Another observation that can be gleaned from Table 7.6 relates to differences between the results produced using either optimal or full-speaker datasets. Using TIPS data, the correlations were higher using the full-speaker dataset in 51% of the cases. In other words, in roughly half

SPL 250	**M_m** (-0.818, -0.832), **A_{tm}** (-0.784, -0.766), **LA_i** (-0.784, -0.871), **L_c** (-0.777, -0.912), **V_{me}** (-0.753, -0.701), **V_{ac}** (-0.746, -0.835), **A_{sf}** (-0.732, -0.864), **M_{mi}** (-0.723, -0.673), **ITR** (-0.665, -0.852), **LA_m** (-0.638, -0.564), **PTR** (0.631, 0.806)
(relative)	**Rel V_{me}** (-0.751, -0.688), **Rel V_{ac}** (-0.674, -0.856), **Rel IA** (0.620, 0.657), **Rel LA_i** (0.608, 0.616), **Rel M_m** (-0.596, -0.717), **Rel LA_m** (0.568, 0.858)
LOW AREA	**LA_i** (0.852, 0.879), **V_{me}** (0.807, 0.727), **M_m** (0.783, 0.681), **ACR** (0.734, 0.832), **A_{tm}** (0.733, 0.696), **L_c** (0.711, 0.880), **M_{mi}** (0.709, 0.650), **ITR** (0.609, 0.859), **PTR** (-0.584, -0.816)
(relative)	**Rel V_{me}** (0.787, 0.690), **Rel IA** (-0.711, -0.691)
LOW CUTOFF	**Rel M_i** (-0.946, -0.924), **Rel IA** (0.655, 0.744)
HIGH AREA	**M_s** (-0.993, -0.982), **M_{mis}** (-0.976, -0.977), **M_{mi}** (-0.921, -0.894), **M_m** (-0.883, -0.853), **A_{tm}** (-0.875, -0.844), **A_{sf}** (-0.840, -0.831), **M_i** (-0.687, -0.733), **LA_i** (-0.640, -0.609)
(relative)	**Rel M_s** (-0.984, -0.960), **Rel LA_i** (-0.895, -0.938), **Rel M_{mi}** (-0.890, -0.894), **Rel M_i** (-0.862, -0.861), **Rel M_m** (-0.829, -0.810), **Rel LA_m** (0.779, 0.769), **Rel L_c** (0.649, 0.688), **Rel A_{tm}** (-0.617, -0.576)
HIGH CUTOFF	**M_s** (-0.971, -0.926), **Rel LA_m** (0.849, 0.791), **Rel A_p** (0.686, 0.621), **Rel LA_i** (0.633, 0.668)
FREQ. PEAK 1	**Rel V_{tc}** (-0.775, -0.822), **Rel A_p** (-0.728, -0.835), **A_{tm}** (-0.612, -0.577), **Rel A_{tm}** (-0.554, -0.553)
SPL PEAK 1	**Rel A_p** (0.759, 0.624), **Rel IA** (0.690, 0.526)
FREQ. PEAK 2	**Rel A_{tm}** (-0.843, -0.660), **M_s** (0.837, 0.832), **Rel A_{sf}** (-0.601, -0.551)
SPL PEAK 2	**Rel M_s** (0.917, 0.786), **REL LA_i** (-0.672, -0.553), **Rel M_i** (0.649, 0.487)
FREQ. DIP	**Rel A_p** (-0.621, -0.781)
SPL DIP	**V_{ac}** (-0.851, -0.850), **L_c** (-0.831, -0.814), **PTR** (0.790, 0.785), **ITR** (-0.785, -0.757), **M_{mi}** (-0.725, -0.736), **LA_i** (-0.721, -0.815), **M_m** (-0.706, -0.721)
(relative)	**Rel V_{ac}** (-0.921, -0.934), **Rel A_{tm}** (0.905, 0.898), **Rel A_{sf}** (0.945, 0.964), **Rel IA** (0.656, 0.614)
TOTAL AREA	**ITR** (0.736, 0.826), **PTR** (-0.711, -0.826), **S_p** (-0.705, -0.798), **ACR** (-0.627, -0.624), **L_c** (0.610, 0.679)
MIDDLE AREA	**PTR** (-0.699, -0.820), **ACR** (-0.678, -0.699), **ITR** (0.628, 0.786), **LA_i** (0.589, 0.659)

Table 7.6 - Audiometric-morphometric correlations that were significant in both the TIPS and PICS comparisons. The numbers in parentheses are the Pearson's correlations coefficients - the first number is from the PICS analysis and the second number is from the TIPS analysis. The morphometric variables are listed from highest to lowest correlation coefficients based on the PICS values. Note that for SPL @ 250 Hz, low audible area, high audible area, and SPL of the mid-range dip, the correlations based on absolute and relative values have been separated for ease of interpretation.

the cases the correlations were improved by adding more taxa (full-speaker), but the other half of the time the coefficients became lower. In contrast, when PICS data were used, the correlations were higher using the optimal dataset in 71% of the cases.

The most frequent correlations were between a variety of morphometric variables and measures of low frequency sensitivity. However, high-frequency sensitivity, peaks in

sensitivity and overall sensitivity also proved to be associated with various parts of the auditory system. One of the most surprising variables not among the significant morphometric variables common to both TIPS and PICS analyses was interaural distance[51]. This finding suggests that once phylogeny is taken into account, interaural distance has little influence on hearing sensitivity (contra Masterson *et al*. 1969; Heffner 2004). The other morphometric variables (absolute values) that are completely absent from Table 7.6 include pinna area, lever ratio, tympanic cavity volume and epitympanic sinus volume. The following section will address the influence of morphometric variables (only the ones common to both TIPS and PICS comparisons) on each region of the audiogram with comments on how these findings relate to theoretical predictions and previous studies.

Low-Frequency Sensitivity

Among the three measures of low-frequency sensitivity used here, SPL @ 250 Hz showed the highest number of significant correlations with morphometric variables. A total of 10 variables (absolute values) were negatively correlated with SPL @ 250 Hz, and an additional variable (PTR) showed a positive relationship[52]. The ordering of the variables (from highest to lowest correlation coefficients) using PICS data was as follows: malleus mass, tympanic membrane area, incus lever arm length, cochlear length,

[51] However, keep in mind that numerous morphometric variables were correlated with interaural distance using TIPS data.

[52] By definition (Chapter 2), PTR and ITR are inversely correlated and that simple pressure gain models suggest PTR is proportional to auditory sensitivity (inversely proportional to auditory thresholds), while the same models predict an inverse relationship between ITR and auditory sensitivity.

total middle-ear volume, accessory cavity volume, stapedial footplate area, combined malleus-incus mass, ITR, malleus lever arm length, and PTR. Using TIPS data, the order was rearranged in the following sequence: cochlear length, incus lever arm length, stapedial footplate area, ITR, accessory cavity volume, malleus mass, PTR, tympanic membrane area, total middle ear volume, combined malleus-incus mass, and malleus lever arm length. A few structures such as cochlear length, incus lever arm length, malleus mass, and accessory cavity volume were found on the top half of the list regardless of the statistical method, while the other variables jumped around considerably in the overall ordering. The negative correlation between most of these variables and SPL @ 250 Hz suggests that as structures get larger, low frequency sensitivity is increased (a lower threshold at 250 Hz). However, the correlations with PTR and ITR both imply that an increase in the overall transformer ratio is associated with a *decrease* in low-frequency sensitivity.

A similar list of morphometric variables was found to be correlated with low audible area. In this case, eight variables were positively correlated while a ninth showed a negative correlation (again PTR). The order of correlation coefficients derived using PICS for these variables was: incus lever arm length, total middle-ear volume, malleus mass, accessory cavity volume, tympanic membrane area, cochlear length, combined malleus-incus mass, ITR and PTR. Using TIPS data the list was rearranged in the following order: cochlear length, incus lever arm length, ITR, accessory cavity volume, PTR, total middle-ear volume, tympanic membrane area, malleus mass, and combined malleus-incus mass. In this analysis, only incus lever arm length and accessory cavity volume were found at the top of both lists. As with SPL @ 250 Hz, increases in the

values for most variables are related to increases in low-frequency sensitivity with the exceptions of PTR and ITR. No morphometric variables (absolute values) common to both analyses were found to be correlated with low-frequency cutoff. Undoubtedly, the limited number of taxa for which this audiometric variable is available severely constrains its utility.

These results support the basic concept that increases in middle-ear structure size (ossicular mass, cavity volumes, tympanic membrane and stapedial footplate areas) result in heightened low-frequency sensitivity (Howell 1932; Legouix and Wisner 1955; Mundie 1963, Lay 1972; Webster and Webster 1972, 1977; Henson 1974; Møller 1974; Fleischer 1978; Rosowski and Graybeal 1991; Rosowski 1992). Furthermore, they agree with ideas proposing that decreased cochlear length (and presumably basilar membrane length) also results in decreased low-frequency sensitivity (West 1985; Rosowski and Graybeal 1991; Echteler *et al*. 1994). These general conclusions are strengthened by the subgroup comparisons between lorisoids and platyrrhines and between *Aotus* and *Saimiri*. In contrast, increases in overall transformer ratios (PTR and ITR) are not associated with increased low-frequency sensitivity and in fact show the opposite relationship.

High-Frequency Sensitivity

The second highest number of correlations was found with measures of high-frequency sensitivity. High audible area showed negative correlations with stapes mass, malleus-incus-stapes mass, malleus-incus mass, malleus mass, tympanic membrane area, stapedial footplate area, incus mass, and incus lever arm length (in order from highest to lowest significant correlations). The ordering was exactly the same whether considering

the PICS or TIPS results. Clearly, this list is dominated by morphometric variables that are related to the mass of the ossicles although the inclusion of tympanic membrane and stapedial footplate areas is also intriguing. These findings show that as ossicular mass decreases and tympanic membrane and stapedial footplate areas get smaller there is increased sensitivity to high-frequency sounds.

The relative values for most of these variables (and a few additional ones) were also correlated with high audible area. Negative correlations were found with relative stapes mass, relative malleus-incus mass, relative incus mass, relative malleus mass, and relative tympanic membrane area while positive correlations were found with relative incus lever arm length, relative malleus lever arm length, and relative cochlear length. The order of highest to lowest correlation coefficients (Table 7.6) was very similar whether using PICS or TIPS data. A handful of morphometric variables also illustrate significant correlations with high-frequency cutoff. Topping the list is stapes mass which shows a negative correlation with high-frequency cutoff, followed by positive correlations with relative malleus lever arm length, relative pinna area, and relative incus lever arm length.

These results concur with the findings from previous researchers that ossicular mass and middle-ear areas (tympanic membrane and stapedial footplate) are inversely related to high-frequency hearing (Rosowski and Graybeal 1991, Rosowski 1992, Hemilä *et al*. 1995). These findings are further supported by the lorisoid comparison presented above which found *G. senegalensis* to have increased high-frequency sensitivity associated with reduced middle-ear structures. A notable pattern evident in the high-frequency correlations is that relative ossicular mass still shows the expected relationship

with high-frequency hearing (more mass, less sensitivity) even after factoring in skull size.

These findings also suggest that there might be tradeoffs between high- and low-frequency sensitivity, since measures of ossicular mass showed negative correlations with high audible area but positive correlations with low audible area and SPL @ 250 Hz. To examine this possibility further, the covariation between audiometric variables was examined and the significant results are presented in Table 7.7. One of the first observations to take from these results is that measures of low-frequency sensitivity are correlated with numerous other audiometric variables. For example, as low audible area increases, range in octaves, total audible area, and middle audible area all increase and there is a reduction in SPL of the mid-range dip and SPL of the first peak (the exact same variables were covarying with SPL @ 250 Hz). More interestingly, as low-frequency sensitivity increases, high-frequency cutoff decreases supporting the idea that there is some tradeoff between high-and low-frequency hearing. However, the fact that high audible area was the only other audiometric variable that high-frequency cutoff was significantly correlated with also suggests that losses in high frequency sensitivity are not directly proportional to gains in low-frequency sensitivity. In other words, if tradeoffs between losses and gains were essentially equal, one would not expect to see increases in overall sensitivity (range and total audible area) associated with increases in low-frequency sensitivity. Therefore, it appears that some primates have increased their overall sensitivity by increasing their low-frequency sensitivity with only a slight detriment to high-frequency sensitivity.

Audiometric 1	Audiometric 2	r	p	n
Low Audible Area	SPL @ 250 Hz	-0.968	< 0.001	12
	SPL of the Dip	-0.844	0.002	10
	SPL Peak 1	-0.796	0.006	10
	Range in Octaves	0.875	0.001	10
	Total Audible Area	0.862	0.001	10
	Middle Audible Area	0.831	0.001	12
	High-Frequency Cutoff	-0.677	0.032	10
SPL @ 250 Hz	SPL of the Dip	0.83	0.002	10
	SPL Peak 1	0.808	0.005	10
	Range in Octaves	-0.797	0.006	10
	Total Audible Area	-0.758	0.011	10
	Middle Audible Area	-0.739	0.006	12
	High-Frequency Cutoff	0.787	0.007	10
Low-Frequency Cutoff	Range in Octaves	-0.972	0.006	5
High Audible Area	High-Frequency Cutoff	0.814	0.004	10
Range in Octaves	SPL of the Dip	-0.765	0.027	8
	Frequency Peak 2	-0.831	0.003	10
	Total Audible Area	0.844	0.002	10
	Middle Audible Area	0.839	0.002	10
Total Audible Area	SPL of the Dip	-0.856	0.007	8
	Frequency Peak 2	-0.697	0.025	10
	Middle Audible Area	0.948	< 0.001	10
Middle Audible Area	SPL of the Dip	-0.857	0.002	10
	SPL Peak 1	-0.797	0.006	10
SPL Peak 1	SPL of the Dip	0.808	0.005	10
Frequency Peak 1	Frequency of the Dip	0.974	<0.001	10

Table 7.7 – Covariation between audiometric variables. Correlations between variables (optimal speaker-derived dataset with *Callithrix jacchus* removed) were tested using Pearson's correlation coefficients. The most notable patterns from these findings are that measures of low-frequency sensitivity are associated with overall sensitivity while measures of high-frequency sensitivity are not. This implies that, although high- and low-frequency sensitivity are negatively correlated, the tradeoffs are not directly proportional.

Peaks in Sensitivity

Although not as common as low and high-frequency correlations, a few morphometric variables showed consistent patterns with various measures of peaks in sensitivity. Frequency of the first peak showed negative correlations with relative tympanic cavity volume, relative pinna area, tympanic membrane area and relative tympanic membrane area (in this order from highest to lowest correlations using PICS data). SPL of the first peak showed positive correlations with only two variables: relative pinna area and relative interaural distance. Curiously, relative pinna area was correlated with both audiometric variables showing that as relative pinna area increases there is an increase in the threshold of the first peak (less sensitive) but a decrease in the frequency.

The finding that tympanic membrane area is negatively correlated with frequency of the first peak is consistent with the findings of Rosowski (1992) who compared these variables in a broad sample of mammals. However, the lack of a correlation between tympanic membrane area and SPL of the first peak does not support suggestions by Khanna and Tonndorf (1978) that these two variables show a negative relationship (*i.e.*, that a larger eardrum collects more acoustic energy resulting in a lower threshold). It should be noted, however, that these researchers were comparing tympanic membrane area with the maximum peak of sensitivity which is not necessarily the same as the metric used here (first peak in sensitivity).

Frequency of the second peak showed a negative correlation with relative tympanic membrane area (as with frequency of the first peak) and relative stapedial footplate area as well as a positive correlation with stapedial mass. While the middle-ear area results generally agree with the notion that larger areas (even relative) are associated

with a decrease in the frequency of best sensitivity (Rosowski 1992), the stapedial mass results are perplexing. These results suggest that the frequency of the second peak actually increases with increasing stapedial mass, counter to ideas put forth by Fleischer (1978) and conventional wisdom.

Three relative variables were correlated with SPL of the second peak. Relative stapedial mass and relative incus mass showed positive relationships while relative incus lever arm length showed a negative relationship. These findings suggest that increases in relative ossicular mass are linked with increasing threshold of the second peak in sensitivity (less sensitivity). On the other hand, increases in the relative length of the incus lever arm are associated with increased sensitivity at the second peak (lower thresholds). As with SPL of the first peak, these findings do not support the notion by Khanna and Tonndorf (1978) that tympanic membrane area is negatively correlated with the threshold (SPL) of the peak in sensitivity. But again, the shortcoming with comparing these results to previous studies is that earlier investigators generally denoted only a single peak in sensitivity which in reality could equate to either the first or second peaks as defined in this dissertation. Perhaps additional, more illuminating light could be shed on the relationships between peaks in sensitivity and morphological variation if a more standardized approach were taken.

Frequency of the mid-range dip showed a significant correlation (positive) with only one morphometric variable: relative pinna area. SPL of the mid-range dip showed a positive correlation with PTR and negative correlations with accessory cavity volume, cochlear length, ITR, malleus-incus mass, incus lever arm length, and malleus mass. The order of these variables from highest to lowest correlations was only slightly altered

when considering the coefficients produced using TIPS (Table 7.6). Most of these findings suggest that as auditory structures get bigger, the mid-range dip gets smaller or at least its threshold gets lower. The exceptions, not surprisingly, are PTR and ITR which show that as PTR gets higher, or ITR gets lower, the threshold of the dip increases. It's worth pointing out that all of these variables were also correlated with measures of low-frequency sensitivity (low area and SPL @ 250 Hz). In fact, SPL of the dip is significantly correlated with both low audible area ($p = 0.002$, $r = -0.844$, $n = 10$) and SPL @ 250 Hz ($p = 0.002$, $r = 0.830$, $n = 10$). A possible interpretation of these findings is that as low-frequency sensitivity increases (presumably due to increasing middle-ear structures and cochlear length) there is a concomitant decrease in the magnitude of the mid-range dip although the functional causes for this association remain obscure.

Overall Sensitivity

Although overall range in octaves did not prove to be significantly correlated with any morphometric variables that were common to both analyses (PICS and TIPS), total audible area and middle audible area did show consistent correlations. Total audible area showed positive correlations with ITR and cochlear length and negative correlations with PTR, pinna ratio and areal convergence ratio. This indicates that a longer cochlea and lower pinna ratio are associated with an increased total audible area. However, increased areal convergence ratio and transfer ratios are correlated with a decrease in total audible area - the complete opposite from theoretical predictions (Weber 1851, Helmholtz 1863, Békésy 1960, Dallos 1973)! Similar trends were revealed in relation to middle audible

area: positive correlations were found with ITR and incus lever arm length and negative correlations were detected with PTR and areal convergence ratio.

Closing Remarks

Although it could be argued that the conclusions reached in this chapter are conservative because they are based only on variables that were significant in both TIPS and PICS analyses, the patterns illustrated by the common variables are robust and basically unaffected by statistical procedures. This adds confidence to the interpretations of the form to function relationships. In any case, most of the results provide added support for many long standing theories and general notions about auditory functional morphology. For example, cochlear length and numerous middle-ear structures (cavity volumes, ossicular mass, tympanic and stapedial areas) appear to exert a considerable influence over low-frequency sensitivity. At the same time, the mass of the ossicular chain also seems to play a key role in determining high-frequency sensitivity. Taken as a whole, these findings also reinforce the idea that all three regions of the auditory system (outer, middle and inner) are important for determining the overall patterns of hearing sensitivity (Manley 1972; Rosowski 1992; Ruggero and Temchin 2002).

In spite of this extensive list of functional associations that agree with expectations, the greatest departures from theoretical predictions come from measures that are hypothesized to increase the sound pressure of incoming waves (areal convergence ratio, lever arm ratio, PTR and ITR). The pattern was repeated several times where a higher transformer ratio value was associated with a decrease in sensitivity. This remains true whether considering low-frequency sensitivity, peaks in sensitivity or

overall sensitivity. These results should cast serious doubt on studies that have used these measures to directly compare hearing performance in various taxa (*e.g*., Wever and Lawrence 1954, Hunt and Korth 1980; Masali *et al*. 1992).

The obvious question raised by this last finding is that if middle ear transformer ratios are not positively associated with absolute hearing thresholds, then what is their functional or adaptive role? For the ossicles at least, it may well be that we are overestimating the true lever arm lengths (Chapter 2), and that little or no mechanical advantage is afforded by the apparent differences between malleus and incus lever arms (Khanna and Tonndorf 1972, 1978; Kelly and Prendergast 2001). Another possibility is that the dimensions and positions of the ossicles are simply a product of the placement of the ectotympanic ring relative to the oval window. In other words, as the eardrum gets repositioned due to changing cranial architecture (or just increases in size), the malleus and incus get dragged along with no acoustic advantage (or disadvantage) as to their respective "lever arm" lengths. Finally, these results could also be taken as support for the idea that the ultimate role of the malleus-incus complex is not for increasing pressure but to protect the inner ear from being overstimulated by excessively loud sounds (Huttenbrink 1996). In the end, we are still in the early stages of understanding ossicular function despite hundreds of years of research. This is ironic considering the fact that the malleus-incus complex is one of the defining traits of mammals.

Regardless, none of this addresses the finding that areal convergence ratio, PTR, and ITR also produced results that run counter to expectations. This finding is even more perplexing than the ossicular results since it is generally well accepted that the reduced surface area of the stapedial footplate, compared with that of the tympanic membrane,

results in a pressure increase[53]. The most likely explanation for these patterns is that other factors are offsetting the mechanical advantage produced by the middle ear transformer mechanism. One possibility is that the species with higher transformer ratios (generally strepsirrhines) also have much higher cochlear impedances. The differences in cochlear length between similarly sized anthropoids and prosimains may be indicative of differences in cochlear architecture that have an influence on cochlear impedance. However, since virtually nothing is known about cochlear impedance in any non-human primate, this possibility will remain speculative until sufficient research is conducted aimed at this problem. Conversely, it is also possible that groups with higher transformer ratios commonly have a lower acoustic input pressure at the tympanic membrane. The finding that pinna shape ratio (although not pinna area) was positively correlated with total audible area could be suggestive of such an influence.

Lastly, a third possibility relates to the degree of fixation of the ossicles. As was discussed in Chapter 2, the torsional stiffness of the malleus-incus complex is largely determined by the degree of rigid attachment to the surrounding bones and this will have an impact on the elastic reactance (stiffness) of the middle ear. A higher stiffness will favor the reception and transmission of higher frequencies but diminish that of lower frequencies Also briefly mentioned in Chapter 2 was that "lower" primates (prosimians) and tree shrews are apparently characterized by having a "transitional" middle ear type, which has an intermediate degree of torsional stiffness, compared with the freely mobile-type (low stiffness) found in "higher" primates (Fleischer 1978). This is suggestive that

[53] This also relates to PTR and ITR since the areal convergence ratio has a disproportionate influence, compared with the ossicular lever arm ratio, on the overall transformer values.

animals with a transitional middle ear type may have higher transformer ratios as an adaptation to help partially overcome the higher torsional stiffness of their middle ears.

Any of these possibilities could partially explain that negative relationship between middle ear transformer ratios and hearing thresholds (particularly at lower and middle frequencies). However, there is clearly much future research to be done on these topics before a better understanding of the role of the middle ear transformer mechanism is completely understood. The next and final chapter will use the functional relationships defined here to investigate the hearing in a few select fossil taxa relevant to primate evolution.

CHAPTER 8

Introduction

The preceding chapter revealed numerous auditory structures that showed tight relationships with hearing sensitivity regardless of the statistical approach employed. The strongest correlations were between low-frequency sensitivity and morphological variables such as cochlear length, tympanic membrane and stapedial footplate area, malleus and incus mass, and middle-ear cavity volume (in particular total middle-ear volume and accessory cavity volume). Since these structures have the potential to be preserved in fossils, it is possible to evaluate certain aspects of hearing sensitivity in extinct taxa and begin to develop a general picture of the evolution of primate audition. This chapter used CT data obtained from fossils to compare auditory morphology and predict certain aspects of hearing sensitivity in three taxonomic groups which represent early members of major evolutionary radiations.

Plesiadapids

The geologically oldest and generally most primitive fossil specimens examined were members of the order †Plesiadapiformes. These extinct primate-like animals were traditionally considered a suborder of Primates but are now generally recognized as their

own order, although they still maintain a sister-group relationship with euprimates[54] (Cartmill 1974; Beard 1990; Fleagle 1999). Thus, they occupy an interesting phylogenetic position intermediate between tree shrews and primates and present the possibility to shed light on aspects of primate origins related to hearing. The first species examined was †*Pronothodectes gaoi*, a relatively small (~400g - Doug Boyer, unpublished data) omnivore that lived during the middle-late Paleocene of North America. CT scans of two petrosals from different specimens were examined (UALVP 43098 and DB 047). The next plesiadapiform species examined was †*Plesiadapis tricuspidens*, a medium-sized (~1300g) herbivore from the late Paleocene-early Eocene of North America and Europe (Fleagle 1999). CT scans of five petrosals representing different individuals uncovered in France were investigated (1371, 17415, 17416, 17417, 17418). These two species are of particular interest because their predicted body mass is within the ranges of the small and medium-sized primates used in the extant comparative sample (Chapter 7). These scans were generously obtained from Douglas Boyer at Stony Brook University.

All of the plesiadapiform specimens were scanned at the Center for Quantitative Imaging, Penn State University using the OMNI-X HD-600 High-resolution CT scanner. The scans for *P. gaoi* had a slice thickness of 49.1 µm with the resulting cubic voxels close to isometric (pixel size was 43.9 µm for UALVP 43098 and 40µm for DB 047). The scans for *P. tricuspidens* had a slice thickness of 0.05811 µm and a pixel size of 50 µm. The final images were 16 bit TIFF files. Auditory measurements were taken on these specimens using the same CT procedures and protocols as defined in Chapter 4. Since

[54] Euprimates are considered "primates of modern aspect" (Rose and Bown 1991) and include all extant primate taxa and fossils that can be attributed to living groups as well as those from the families Omomyidae and Adapidae.

these specimens preserved only the inner ears, measurements were generally limited to cochlear length and occasionally oval window dimensions. However, isolated stapedes (one from each species) were discovered in the vestibule and estimates of the stapedial footplate were also taken. These represent the first known stapedes from these two taxa.

Early Anthropoids

The next fossil species examined was †*Aegyptopithecus zeuxis*, an early anthropoid primate from the early Oligocene of Egypt. This species had an estimated body mass of between 6 and 7 kg, was diurnal, and probably fed largely on fruits (Kay and Simons 1980, Fleagle 1999). Although *A. zeuxis* lacked some of the auditory features found in later catarrhines (see below), it is generally considered a primitive stem catarrhine because of its reduced dental formula (2.1.2.3), bony configuration of its neurocranium (Fleagle and Rosenberger 1983), and astragalar morphology (Seiffert and Simons 2001). However, in many ways its auditory morphology most closely approximates that found in the last common ancestor of New and Old World anthropoids in possessing an anterior accessory cavity, lacking a bony ear tube and stapedial artery, and in having the tympanic ring fused to the lateral surface of the auditory bulla (Simons 1972; Cartmill *et al*. 1981).

A recently discovered cranium (CGM 85785) was the specimen used in this study as a representative of †*A. zeuxis*. This skull was also scanned at the Center for Quantitative Imaging, Penn State University using the OMNI-X HD-600 High-resolution CT scanner. CGM 85785 was scanned with a slice thickness of 63.79 μm and a pixel size of 56 μm, and reconstructed as 16 bit TIFF images. Although this specimen is moderately

well preserved, the only measurement currently able to be taken was cochlear length[55]. These scans were graciously provided by Elwyn Simons and Erik Seiffert from Duke University and Oxford University, respectively.

Early Platyrrhines

The final fossil species investigated was †*Homunculus patagonicus*, an early New World monkey from the early-middle Miocene of Argentina. These were medium sized (2 -3 kg) diurnal monkeys that probably had a mixed folivorous/frugivorous diet (Kay *et al.* 2005). Although †*H. patagonicus* is considered a stem platyrrhine, they still maintained several features of the skull that reflect primitive anthropoid characteristics (*e.g.*, bony configuration around pterion). Still, in most ways they resemble extant platyrrhines and have been linked with modern pitheciines based on facial morphology (Tauber 1991).

A recently discovered skull (skull 1) presented the opportunity to investigate several features of the auditory region. This skull was scanned at the University of Texas High-Resolution X-ray CT Facility with a slice thickness of 48.43 μm and a pixel size of 44.92 μm (reconstructed as 16 bit TIFF images). The excellent state of preservation of this specimen permitted four auditory structures to be measured including the volumes of the middle-ear cavities, the area of the tympanic ring, the area of the oval window, and the length of the cochlea. The scans were kindly made available by Richard F. Kay of Duke University.

[55] The middle-ear was filled with matrix which made precise thresholding difficult for all but the cochlea.

Analysis and Results

Before proceeding to the comparison of the morphology and predicted hearing capabilities in these fossil species, it is first necessary to look at the methods and limitations of the procedures to be used in the analysis. Although it is fairly straightforward to use regression analyses to predict unknown values using traditional data (*i.e*. TIPS), developing predictive statistics for phylogenetic methods is more involved. The major challenge results from the fact that PICS regression analysis forces the intercept through the origin (Felsenstein 1985). The results produced by such an analysis will give a slope value that can be applied to raw data (TIPS), but Mesquite does not provide an estimate of the y-intercept (other than zero which is not useful for predicting raw values). Fortunately, the "problem of the intercept" can be solved rather easily (Rohlf 2001). Garland and Ives (2002) have shown that the y-intercept for a slope based on PICS data can be estimated by forcing the regression line through estimates of the root node values for the x and y variables. This is expressed by the relationship:

(8.1) $$b = y^{RN} - (m * x^{RN})$$

where b is the intercept, y^{RN} is the root node value of the y variable, m is the phylogenetically adjusted slope, and x^{RN} is the root node value of the x variable. Once the intercept is determined, it and the phylogenetically adjusted slope can be used in the standard slope-intercept form for a linear equation ($y = mx + b$). Although Mesquite does not give the y-intercept, it does provide a method for estimating the root node values for x and y by using the "trace characters" function in the tree window option (Maddison and

Maddison 2006). As this method was applied here, the ancestral character states were reconstructed using squared-change parsimony and the slope was based on least squares regression.

One last question to consider is how accurate are the regression equations based on the functional relationships defined here (Chapter 7) for estimating unknown audiometric values? To address this issue, known values were compared with predicted values using a jack-knife procedure. The exact method involved removing a species from the dataset, calculating the slope and intercept, and then comparing predicted value using this slope and intercept with the actual value for the removed species. This procedure was repeated for every taxon in the sample using both PICS and TIPS regression equations. The morphometric variables that were used included tympanic membrane area, stapedial footplate area, middle-ear cavity volume and cochlear length. The audiometric variable that was predicted was SPL @ 250 Hz using the optimal speaker dataset[56].

The mean differences between actual and predicted values for SPL @ 250 Hz are given in Table 8.1. In general, these results suggest that it is possible to predict SPL @

Variable	TIPS	PICS
A_{tm}	6.75	7.375
A_{sf}	4.875	5.625
V_{me}	7.75	8.375
L_c	3.125	6.125
Mean	**5.625**	**6.875**

Table 8.1 - Mean differences between known and predicted values for SPL @ 250 Hz using tympanic membrane area, stapedial footplate area, middle-ear cavity volume, and cochlear length as the predictive variables. Variable abbreviations defined in Chapter 4.

[56] *Callithrix jacchus* was removed from the optimal speaker dataset because the audiogram for this species appears to show some irregular audiometric values (see Chapter 7).

250 Hz with an average range of ± 5.6-6.9 dB. Using TIPS data however, cochlear length showed a mean difference between the expected value and the predicted value of just over ± 3 dB. One reason why the TIPS estimate shows a lower margin of error than the PICS estimate may be related to the fact that the correlation between cochlear length and SPL @ 250 Hz was very high using TIPS (r = -0.922) but only moderately high using PICS (r = -0.767). It is also interesting that all the morphometric variables did slightly better for prediction using the TIPS data compared with using the PICS data. Still, except for the relatively large difference in cochlear length estimates, the difference between statistical approaches for the other variables was less than 1 dB. Figure 8.1 shows the

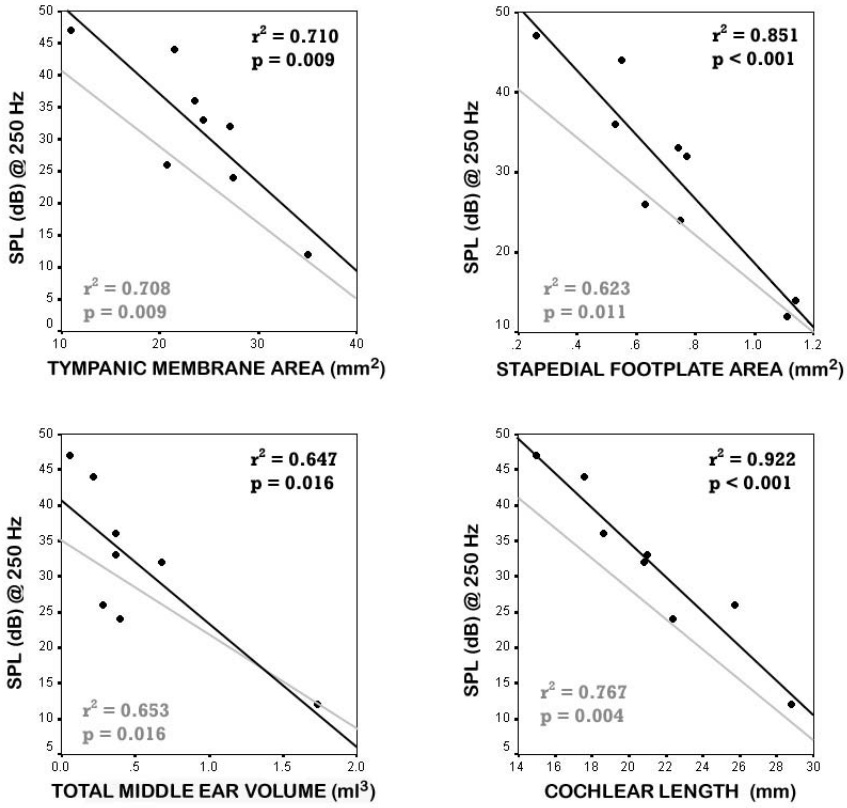

Figure 8.1 - Regression lines for four morphometric variables versus SPL @ 250 Hz computed using both PICS (grey line) and TIPS (black line) data.

regression lines for each variable computed using both TIPS and PICS. As can be seen from this figure, the PICS regression lines have a shallower slope and always have a lower y-intercept. Also noteworthy is the observation that the PICS line for cochlear length falls completely below the raw data values. These results suggest that the method used here to estimate the y-intercepts may be underestimating the true intercept values. Therefore, only TIPS regressions will be used to predict hearing sensitivity in fossils. And at last, onto the results.

Homunculus patagonicus

The first fossil species to be presented is *Homunculus patagonicus*. Not only is this fossil the geologically youngest of the taxa studied here (~17mya), but it is also the

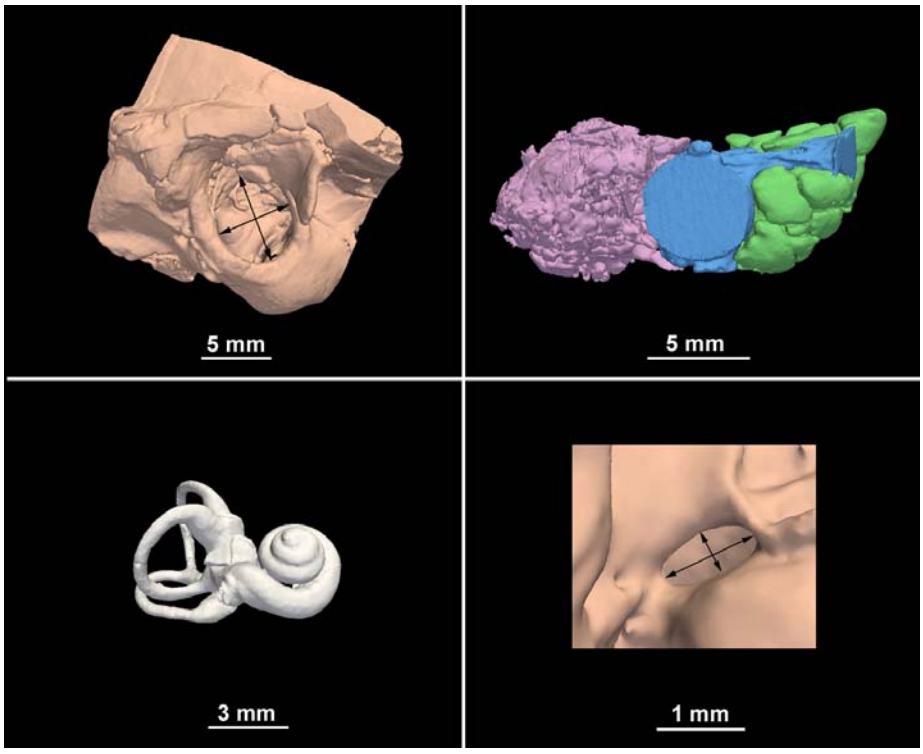

Figure 8.2 - Three-dimensional models used to take auditory measurements in *Homunculus patagonicus*. See Chapter 4 for details about CT measurement methods.

best preserved. Figure 8.2 shows images of the three-dimensional models that were used to take the auditory measurements and illustrates the excellent state of preservation of the middle and inner ears. The only structure that was difficult to measure was the oval window, although estimates of its dimensions were still taken. Table 8.2 presents the measurements obtained for all fossil species as well as mean values for superfamilies of the extant comparative sample.

The auditory structures in *Homunculus* are more similar in size and configuration to other platyrrhines than to the other primate taxa examined. *Homunculus* shows a particular affinity with *Saimiri* and *Aotus* despite its slightly larger overall size. For example, the values for both cochlear length and oval window area were nearly identical to those of *Saimiri*, while the size of the tympanic ring was somewhat intermediate between *Saimiri* and *Aotus* (see Table 7.1 for exact values for *Saimiri* and *Aotus*). The total volume of the middle-ear cavities was moderately larger than the genus means for either *Aotus* or *Saimiri* but still fell within the upper range for *Aotus*. *Homunculus* also displays the typical platyrrhine pattern in having the largest portion of the middle-ear cavity volume contained within the (anterior) accessory cavity.

Taxa	A_{tm}	A_{sf}	V_{me}	V_{tc}	V_{es}	V_{ac}	L_c
H. patagonicus	**23.7**	**0.56***	**0.48**	**0.10**	**0.18**	**0.20**	**24.5**
Platyrrhine Mean	22.9	0.65	0.28	0.05	0.09	0.14	22.8
A. zeuxis							**25.7**
Catarrhine Mean	46.1	1.25	1.79	0.14	1.17	0.49	29.9
Lorisoid Mean	23.1	0.61	0.32	0.07	0.18	0.06	19.1
Lemuroid Mean	27.1	0.72	0.54				21.0
P. tricuspidens		**0.80***					**17.0**
P. gaoi		**0.67***					**15.4**
T. glis	11.0	0.26	0.06				15.0

Table 8.2 - Auditory measurements taken on fossils and group means for extant sample. Asterisks indicate questionable values due to the difficulty in taking the measurement. See Chapter 4 for variable abbreviations.

Using these values, several audiometric variables were predicted for *Homunculus* and are given in Table 8.3. The statistics used to derive these values are given in Appendix 46. The predicted values for SPL @ 250 Hz range from 24-32 dB producing a mean value of 29 dB. The value predicted using cochlea length (24 dB) is very similar to the ancestral state value of 25 dB estimated for the node marking the divergence of extant platyrrhines[57] (node 8 - Figure 7.39) using squared-change parsimony (Midford *et al*. 2003; Madison and Madison 2006). Accessory cavity volume produced a similar prediction for SPL @ 250 Hz (27 dB). Considering the fact that cochlear length and accessory cavity volume showed the highest r^2 values of these variables and the finding that cochlear length showed the best predictive power of any of the variables examined (Table 8.1 and Figure 8.1), the best estimate of SPL @ 250 Hz for *Homunculus* is probably between 24-27 dB (mean = 25.5 dB). The predicted values for high audible area (1051) and SPL of the mid-range dip (14) also agree quite well with the estimated ancestral state values for node 8 (1072 and 10 dB respectively).

	SPL 250	High Area	SPL Dip
A_{tm}	32 ± 17	1051 ± 395	
V_{me}	32 ± 19		
V_{ac}	27 ± 11		16 ± 20
L_c	24 ± 9		12 ± 19
mean	**29**		**14**

Table 8.3 - Estimated audiometric values for *H. patagonicus* using equations derived from TIPS data. Estimates were rounded to the nearest whole number. Stapedial footplate area was not used for audiometric predictions because of the uncertainty in this measurement.

[57] This is not meant to imply that *H. patagonicus* is the common ancestor of extant platyrrhines, but that this nodal value represents an estimate for platyrrhines closest to the geologic time of fossil New World monkeys such as *H. patagonicus*.

Aegyptopithecus zeuxis

The next fossil specimen to be discussed is the ~30 million year old *Aegyptopithecus zeuxis* skull (CGM 85785). The only precise measurement able to be taken was cochlear length. This measurement is also given in Table 8.2 and CT models of the cochlea are presented in Figure 8.3. The cochlear length value for *A. zeuxis* falls at the bottom end of the values for catarrhines but still is longer than any non-catarrhine examined. This relatively smaller length is still surprising since *A. zeuxis* is similar in size to *M. fascicularis* yet has a cochlear length that is about 3 mm shorter. It is worth noting that *A. zeuxis* also had a relatively smaller cranial capacity than extant catarrhines (Simons 1995). The predicted value for SPL @ 250 Hz using this length was 21 ± 9 dB. This value is slightly higher (less sensitive) than the estimated value of 17 dB for the last common ancestor of the catarrhines examined (node 11 - Figure 7.39).

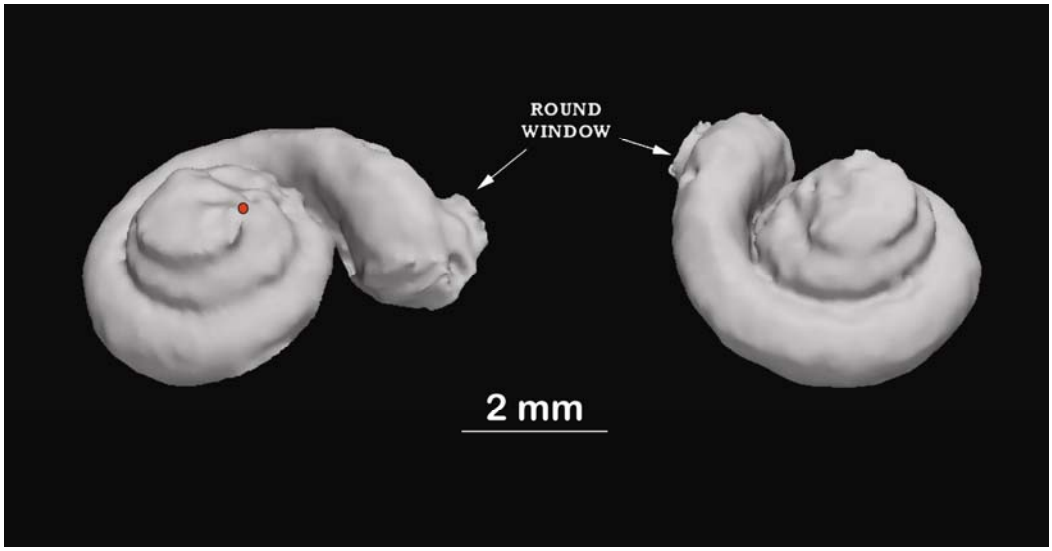

Figure 8.3 - Two views of the three-dimensional CT model used to measure the outer circumference of the cochlea for *Aegyptopithecus zeuxis* (CGM 85785). The measurements start at the cochlear edge of round window and end at the apex of the spiral (red dot).

Plesiadapis tricuspidens

The five, ~55 million year old *Plesiadapis tricuspidens* petrosals (Figure 8.4) presented the opportunity to examine intra-specific variation in auditory morphology. The values for cochlear length and stapedial footplate area are given in Table 8.4. The range for cochlear length in 4 of the 5 specimens is only 0.5 mm but specimen 17415 shows a value that is almost a full millimeter shorter than the next smallest specimen. These measurements produce a mean cochlear length value for *P. tricuspidens* of 17 mm which falls below the mean values for all of the extant taxa examined except tree shrews (Table 8.2). These cochleae appear even more relatively short when one considers that the estimated body mass for *P. tricuspidens* was around 1300g, larger than the average for any of the lorisoid or platyrrhine species with cochlear length measurements.

Using the mean value of 17 mm produces the predicted value for SPL @ 250 Hz of 42 ± 4 dB. Considering the shortest and longest cochleae for these specimens only moderately alters these values: 44 dB and 41 dB, respectively, and are appreciably higher the estimated ancestral state value of 34 dB for the basal node (1) separating tree shrews from primates (Figure 7.39).

Species	Spec. #	L_c	A_{sf}
P. tricuspidens	1371	17.3	0.62*
	17415	16.1	0.63*
	17416	17.2	0.73
	17417	17.5	1.13*
	17418	17.0	0.88*
Mean		**17.0**	**0.80**
P. gaoi	43098	15.6	0.67*
	DB 047	15.3	
Mean		**15.4**	**0.67**

Table 8.4 - Auditory measurements taken on *Plesiadapis tricuspidens* and *Pronothodectes gaoi* specimens. Note that A_{sf} is actually oval window area for all specimens except 17418 and 43098. Asterisks indicate questionable measurements.

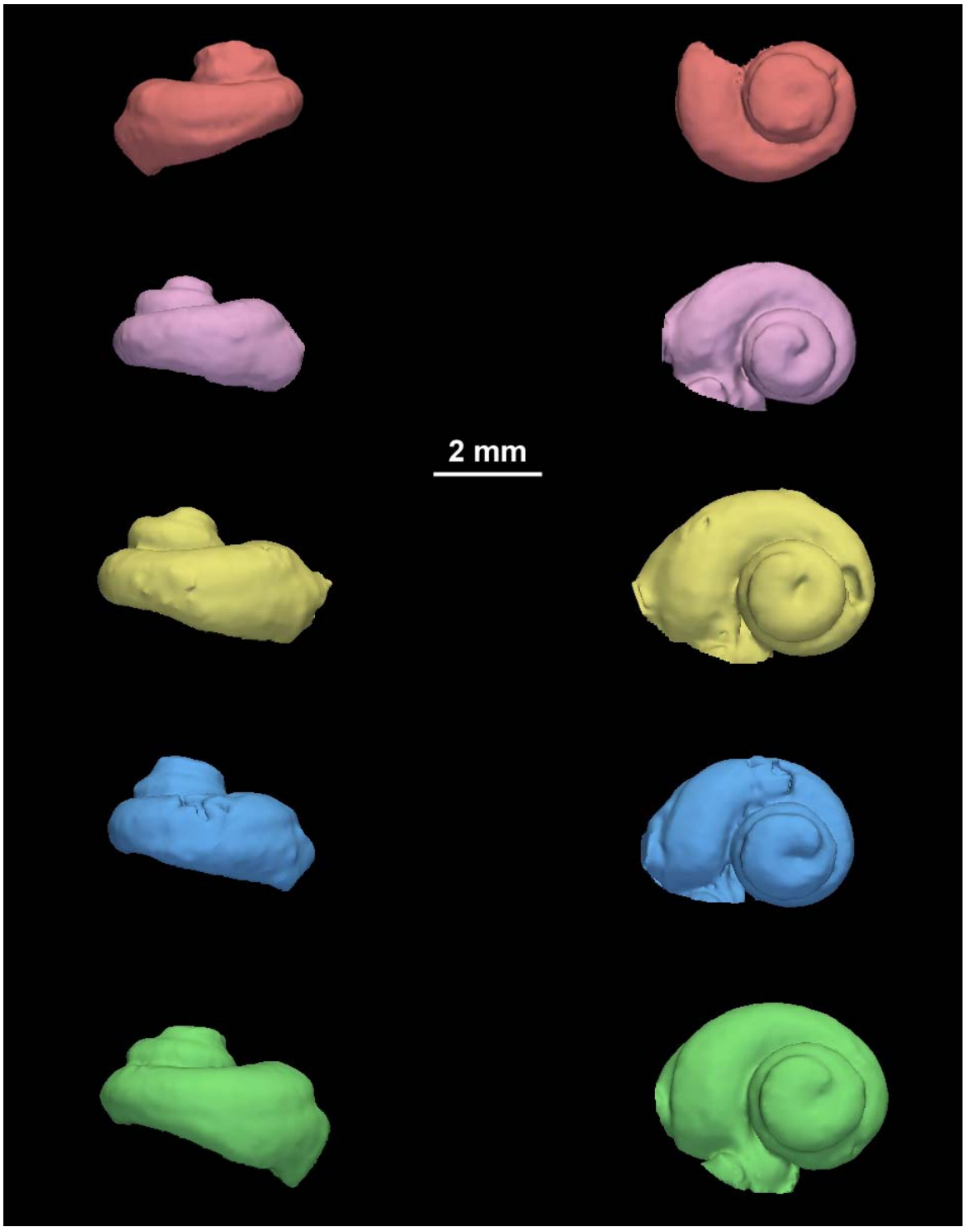

Figure 8.4 - Two different views of CT models of the five *Plesiadapis tricuspidens* cochleae. Red models are from specimen 1371, lavender models are from 17415, yellow models are from 17416, blue models are from 17417, and green models are from 17418.

The estimates for stapedial footplate area are also given in Table 8.4. Most of the measurements were difficult to obtain and 17416 was the only specimen to produce estimates with a reasonable degree of confidence. The stapedial footplate value of 1.13 mm^2 for 17417 is considerably larger than those for all the other specimens which may indicate a significant degree of measurement error. However, this specimen also had the longest cochlea of the group, suggesting that the stapedial footplate estimate is deviating in the proper direction but may be overestimated. It is also interesting that the one actual stapedial footplate that was measured (17418 - Figure 8.5) produced a value that is moderately close to the "solid" estimate from 17416. The values for these specimens (17416 = 0.73 mm^2, 17418 = 0.88 mm^2) straddle the mean for the group, suggesting a species mean value of 0.80 mm^2. In contrast to the cochlear length estimate for *P. tricuspidens*, this value is longer than the mean values for all of the extant groups except catarrhines (Table 8.2). Due to the uncertainty in these estimates, audiometric variables will not be predicted in *P. tricuspidens* using stapedial footplate area.

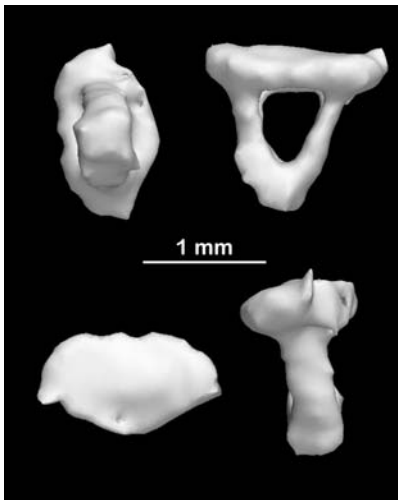

Figure 8.5 - CT models of the stapes discovered within the vestibule of *P. tricuspidens* (17418). The small flanges extending from the footplate are an artifact of the model making process where the stapes had to be segmented from the surrounding structures.

Pronothodectes gaoi

The final, smallest, and oldest (~ 60 mya) fossil species to be discussed is *Pronothodectes gaoi*. The auditory measurements taken on the two specimens of *P. gaoi* are also given in Table 8.4 and Figure 8.6 shows the CT models for both cochleae and the partial stapes that were assayed. The measurements for cochlear length are shorter than any primate examined and are only marginally longer (probably inconsequentially) than the value for tree shrews (Table 8.2). This is intriguing since the estimated body mass for *P. gaoi* is almost three times the size of that for tree shrews. As with *P. tricuspidens*, the estimated area of the stapedial footplate in *P. gaoi* is relatively large compared with the extant primates, although this measurement is also considered only an approximation. Using the mean value of 15.4 mm for cochlear length yielded predicted value for SPL @ 250 Hz of 46 ± 5 dB, considerably higher than the estimated value of 34 dB for node 1.

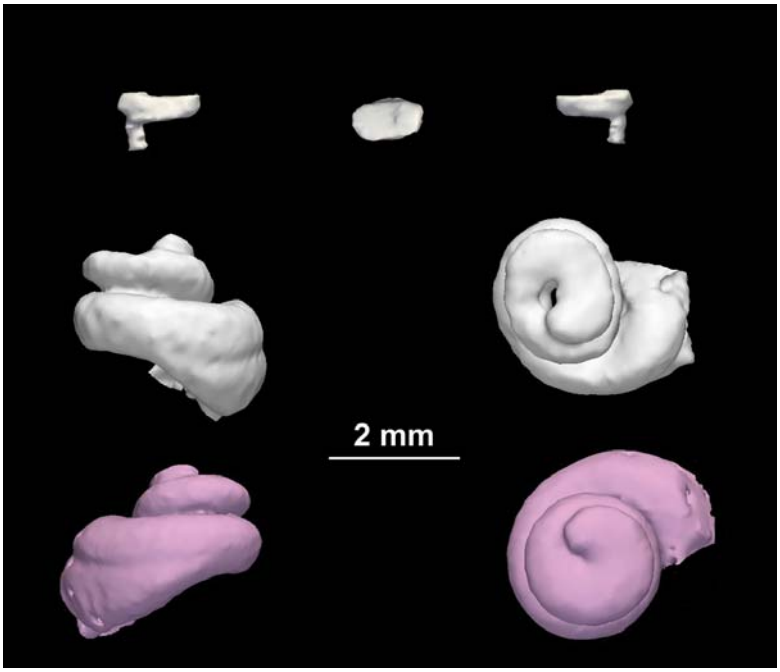

Figure 8.6 - CT models of the partial stapes and cochleae for two specimens of *P. gaoi*. The images in white are from specimen 43098 and those in lavender are from DB 047.

Discussion

Figure 8.7 displays the optimal speaker audiograms along with the predicted values of SPL @ 250 Hz for all fossils. There is fairly distinct separation in the low-frequency sensitivity of the extant groups and *H. patagonicus* and *A. zeuxis* both fall close to their respective group values. Even with the relatively wide confidence intervals, their low-frequency sensitivity appears to be better than that of any of the prosimians examined. *P. tricuspidens* and *P. gaoi*, on the other hand, both illustrate values that place them between lorisoids and tree shrews. This apparent lack of low-frequency sensitivity is interesting, particularly in *P. tricuspidens*, since primates of equal or smaller size show considerably better sensitivity in this range. For example, *P. tricuspidens* has a predicted body mass (1300g) that is slightly larger than the medium-sized platyrrhines and lorisoids examined here, but has a predicted SPL @ 250 Hz that is several decibels above the values for *N. coucang* and *P. potto* (36 and 33) and over a dozen decibels above the

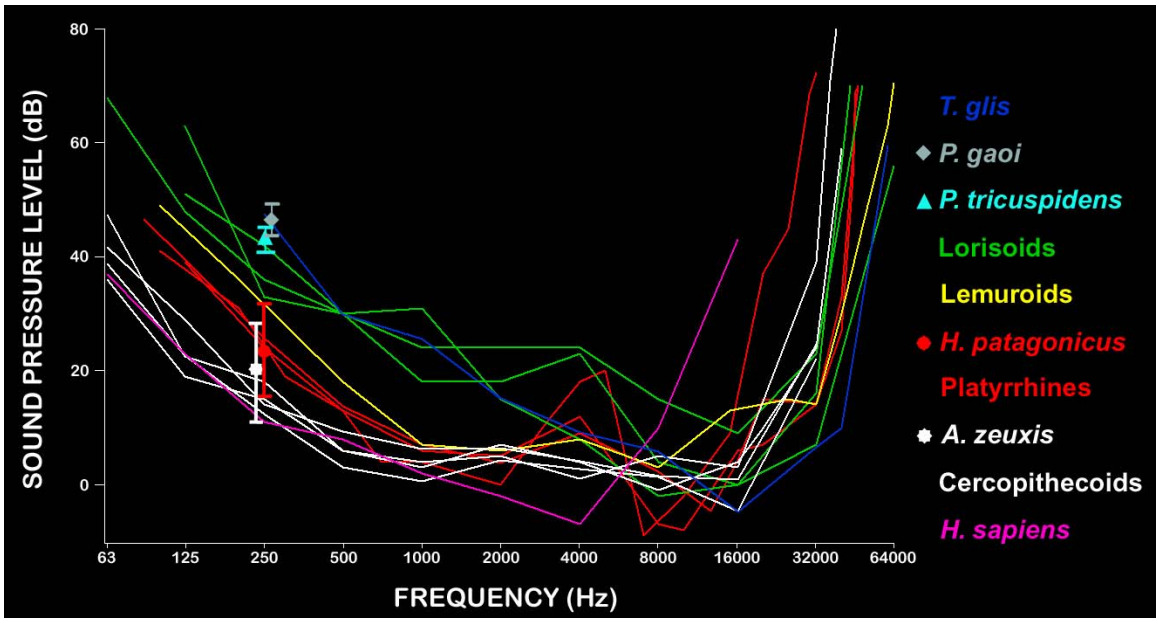

Figure 8.7 - Optimal speaker audiograms and predicted values of SPL @ 250 Hz for the four fossil species.

values for *Aotus* sp. and *Saimiri* sp. (24 and 26). Similarly, *G. senegalensis* shows a value of 44 dB for SPL @ 250 Hz, very similar to the predicted value for *P. gaoi*, yet is approximately half the size (210g and ~400g, respectively).

If these data are put into an evolutionary context (Figure 8.8), it becomes evident that primates have been progressively increasing their low-frequency sensitivity from the purported ancestral mammalian condition (or at least the tree shrew-like condition) which emphasized high-frequency sensitivity (Masterson *et al.* 1969). This progression appears to have occurred in two adaptive shifts. The first shift seems to coincide with the initial radiation of the order (or at least Euprimates) and the second shift apparently happened at the divergence between prosimians and anthropoids. Obviously, one method for increasing low-frequency sensitivity is to increase body size which will generally result in an overall increase in skull size and auditory anatomy. As has been shown here and elsewhere, larger auditory structures (*e.g.*, eardrums, ossicular mass, bullar volume, cochlear length) increase sensitivity to low-frequency sounds. However, the trends evident in Figure 8.8 can not simply be explained as the result of following the basic principle of Cope's law (that animals tend to increase in body size over geological time).

The data presented here suggest that plesiadapiforms (at least the species examined) had not reached the primate-level of low-frequency sensitivity despite being relatively large. There also appears to be a distinct difference in low-frequency sensitivity between anthropoids and prosimians that is not strictly associated with differences in body size. This was best illustrated by the comparison between like-size platyrrhines and lorisoids, where the New World monkeys showed significantly better low-frequency

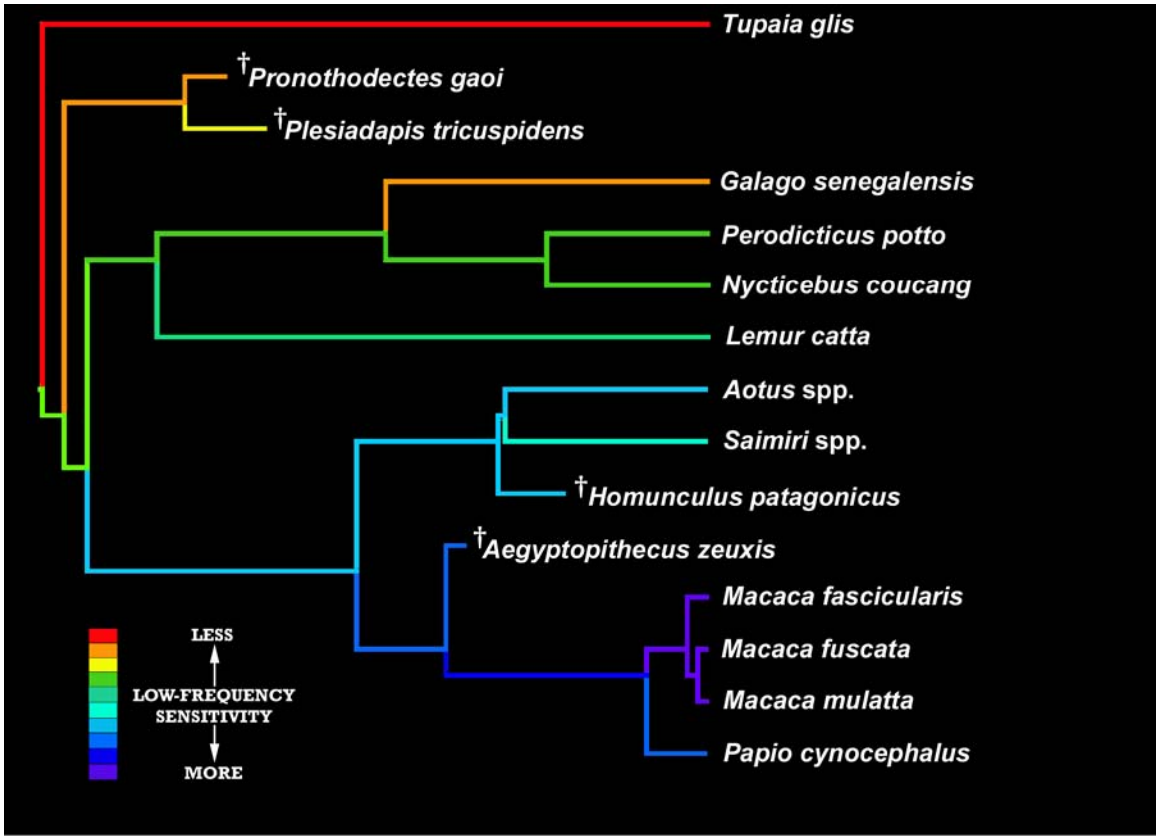

Figure 8.8 - Low-frequency sensitivity based on SPL @ 250 Hz for extant and fossil taxa. Squared-change parsimony (extant data) was used to estimate the nodal values.

sensitivity, yet with only minimal losses in high-frequency sensitivity (Table 3.6 and Figure 7.38). There may still be other adaptive shifts within primate auditory evolution that have not yet been fully realized or validated (*e.g.*, lemuroids versus lorisoids, platyrrhines versus catarrhines).

These findings, plus the results presented in Table 7.7 (covariance of audiometric variables), can be interpreted to support the hypothetical sequence of primate hearing evolution presented in Figure 8.9. This evolutionary sequence proposes that the first shift in primate hearing was achieved by adding a minor second peak on the low-frequency side that led to a marginal increase in low-frequency sensitivity with only slight losses in high-frequency. The second shift was achieved by further expanding the low peak in

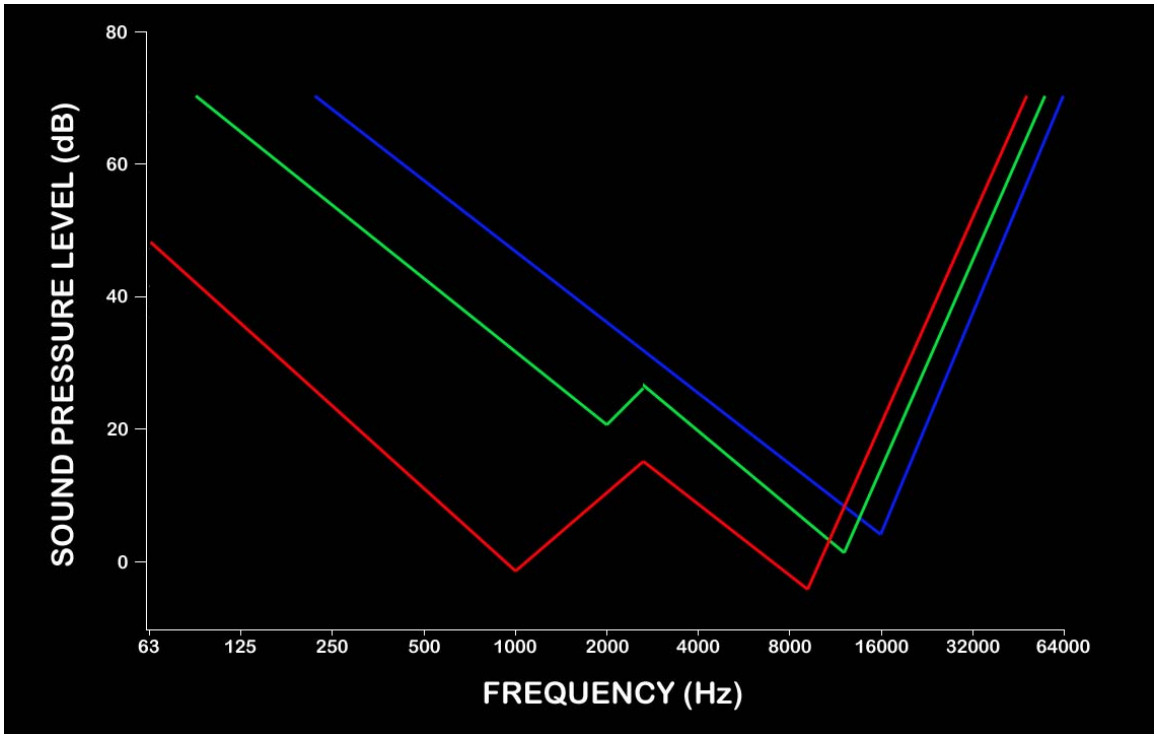

Figure 8.9 – Hypothetical sequence of the evolution of primate hearing. Blue curve represents the primitive (tree shrew-like) condition, green curve represents the first adaptive shift in low-frequency sensitivity, and red curve represents the second adaptive shift in low-frequency sensitivity. Note the relatively large increases in low-frequency sensitivity compared with the relatively small decreases in high-frequency sensitivity.

sensitivity to the point that the animals (anthropoids) were now receptive to a considerably larger portion of the low audible field. As the SPL of the low peak became lower, not only was low-frequency sensitivity increased, but apparently the SPL of the notch between the peaks was also lowered (Table 7.7).

While there is still much to be learned vis-à-vis the proximate mechanisms by which primates (and other mammals) have achieved these adaptive shifts, several notable distinctions in auditory anatomy have been identified. One of the most conspicuous morphological trends has been towards increasing cochlear length (and presumably basilar membrane length) which facilitates an increase in the sensory neuroepithelia (organ of Corti) that transduces mechanical vibrations into neurological impulses. In this

way, a larger range of frequencies[58] can be represented on the basilar membrane without a significant loss at one particular end of the frequency spectrum. This pattern has obvious advantages over simply retuning the basilar membrane by altering the stiffness gradient that determines its receptivity to particular frequencies (see Chapter 2).

However, it may not be so straightforward to simply "roll-out" the basilar membrane to expand hearing sensitivity. For one thing, the cochlea is located in a tightly packed region, and increasing sensitivity to low-frequency sounds by lengthening the basilar membrane would require expanding the apical end of the cochlea. For another thing, an increase in the peripheral sensory neurons necessitates a concomitant increase in neural processing and storage ability. In other words, there seems to be a need to increase relative brain size (at least those areas related to audition) which could be constrained by basic metabolic demands (the expensive-tissue hypothesis - Aiello and Wheeler 1995). Another possibility is that there could be selection against increasing low-frequency sensitivity even at relatively larger body sizes. If a species is ecologically adapted to high-frequency specializations, then increasing the reception of low-frequency sounds could result in partial masking of the biologically more important high-frequency sounds. This might be the case for animals that use high-frequency communication (which is more cryptic and difficult to localize) or for predators that prey on animals that make high-frequency sounds, such as insects.

[58] It is also possible to increase the resolution of a particular frequency range without actually increasing the overall range in frequencies. However, this does not seem to be the case in most primates since the increase in low-frequency sensitivity does not appear to be associated with an equal loss in high-frequency sensitivity. Humans may present an exception to this pattern whereby high-frequency sensitivity was lost in order to increase sensitivity to mid-range frequencies. Although conjectural, this may be related for a need for high-fidelity resolution of the prominent frequencies in human speech.

Either possibility could hypothetically explain the lack of cochlear length expansion (and presumably low-frequency sensitivity) in plesiadapiformes compared with extant and fossil primates. Their dietary reconstructions, however, do not support the ideal that it was strict insectivory (particularly in *P. tricucspidens*) that might have been driving high-frequency selection. These species may simply not have had the neocortical space needed for more sensory input (the same case might be made for visual adaptations). Future studies comparing encephalization quotients to the acuity and perception of different sensory modalities may help identify physiological and adaptive constraints that ultimately place limits on the evolution of various sensory systems, particularly hearing.

The next logical question to ask is: what are the selective pressures that led to the increased low-frequency sensitivity characteristic of euprimates compared with other closely related taxa? One of the long standing ideas in primate evolution is that primates have shifted from a primarily olfaction based foraging strategy to one that relies more heavily on vision (Cartmill 1974, 1992). However, the role of hearing in this context has rarely been discussed although the same basic arguments might also apply. Below I present one *possible* scenario that may explain auditory evolution in primates, particularly the increase in low-frequency sensitivity.

As the earliest primates began to shift towards an emphasis on visual adaptations, their emphasis on olfactory cues for long-range communication diminished. Anyone that has spent time in the jungles knows that vision works well for close range observations, but because of vegetation and topography, its utility is inversely related to distance. However, auditory cues have a much larger active (audible) space (Figure 8.10) and can

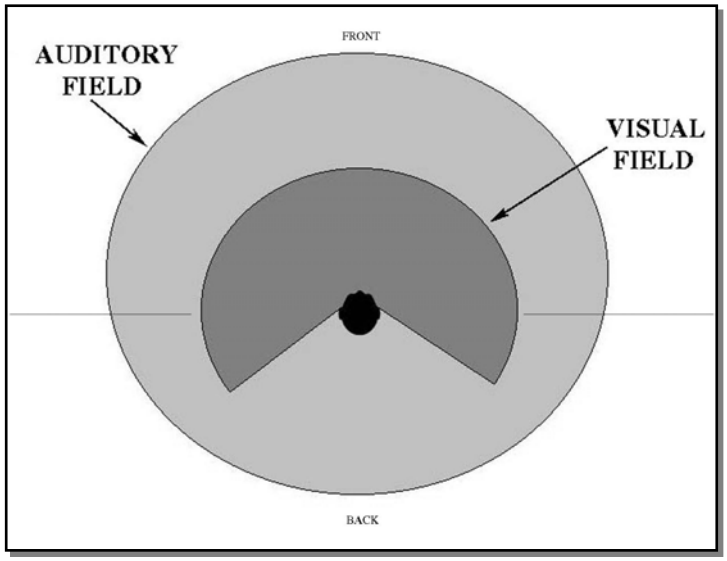

Figure 8.10 - In closed environments such as jungles, hearing can generally detect environmental stimuli at a greater distance and from a wider range of directions compared with vision.

propagate information about the signaler up to several kilometers. Thus, the first stages of primate evolution witnessed not only a modification towards visual reliance but also towards increased auditory sensitivity at low frequency.

One possibility is that the neocortical expansion required for increased visual acuity could have acted as an exaptation for increased auditory sensitivity. The problem with this argument is that it has often been noted that brain size was relatively small in the earliest known fossil primates, including early anthropoids (Simons 1995). It is worth noting however that *A. zeuxis* had a relatively short cochlea and cranial capacity for a catarrhine, yet still produced a predicted value for SPL @ 250 Hz that was at the bottom end of the extant catarrhine range. These findings suggest that it may have been the expansion of the peripheral sensory neurons (*i.e.*, organ of Corti and possible the photoreceptors of the eye) that led to an increase in neocortex size and that a relatively

small brain does not preclude increased sensory perception. This could also be taken to suggest that increased low-frequency sensitivity progressed gradually from the primitive anthropoid condition (platyrrhine-like?) to the extant catarrhine condition (Figure 8.8), and that these gradual increases in low-frequency sensitivity selected for gradual increases in brain size. It will be interesting to try and tease apart this chicken and egg question by comparing the rates of evolution between cochlear size and neocortex size and by attempting to isolate specific regions of the brain expansion (*e.g.*, auditory cortex).

The second stage in primate auditory evolution may have been related to the shift from nocturnality to diurnality. As anthropoid primates moved "into the light" (Ross 2000), several factors could have selected for increased low-frequency sensitivity. For one, diurnal primates (and mammals) generally live in larger groups than nocturnal ones, most likely in response to increased predation pressures (Crook and Gartlan 1966). Larger group size often translates into more group spread and hence the need to communicate over greater distances. Since low-frequency vocalizations travel further with less perturbation from biotic factors, low-frequency communication (hearing and vocalizations) would be advantageous for animals trying to communicate over relatively long distances.

In addition to increasing the potential distance over which vocal communication can be effective, better sensitivity could lead to a larger variety and better perception of complex calls in the vocal repertoire, such as those characterizing many diurnal primates (Petter and Charles-Dominique 1979). Although these adaptations and the benefits conferred by them would have been slight initially, continued selection ultimately

produced the auditory specializations embodied by living and recently extinct primates. Although mostly speculative, this scenario could be tested by evaluating the hearing capabilities in more fossils, gaining a better understanding of the tradeoffs associated with particular sensory specializations, and investigating the ecological pressures that influence hearing and vocal communication.

Regardless of vagaries surrounding the precise selective pressures that have led to differences in primate hearing, we are beginning to understand the morphological adaptations that engender these differences. As has been demonstrated here, one of the primary mechanisms by which primates have increased hearing sensitivity is by increasing the length of the cochlea. It also appears that primates have altered the shape and size of the outer ears and augmented the general size of many middle-ear structures (*e.g*., the connecting passage between the tympanic cavity and additional cavities such as the accessory cavity). However, the functional implications of variation in several auditory structures remain enigmatic. One is the functional significance of differences in ossicular lever arm lengths and areal convergence ratios. Another is the influence on hearing sensitivity of differences in middle-ear cavity configurations. Obviously, there is much research yet to done on primate (and vertebrate) auditory functional morphology.

Concluding Remarks

In the end, this dissertation raised many more questions than it answered. Still, the overarching goal was achieved in that it was demonstrated that differences in primate auditory structure are associated with differences in hearing sensitivity and that these relationships can be used to evaluate hearing in fossils. The application of these

functional relationships (in this dissertation) has only scratched the surface of the possible insights that can be gained from these data. The next step will be to assess more fossils to help strengthen and expand the conclusions reached here and to investigate species representing intermediate stages in primate auditory evolution (*e.g.*, Adapids), as well as unique radiations (*e.g.*, sub-fossil lemurs). As more auditory sensitivity data become available for living primates it will be possible to further test and refine the functional relationships defined here. It will also be interesting to explore the sensitivity and morphology in some of the unstudied extant primate species with apparent auditory specializations (e.g., tarsiers, Aye-Ayes). The final step will be to integrate our understanding of primate auditory functional morphology with the ecology of living species in order to better understand the pressures that helped shape particular hearing patterns. Although this scientific journey has come to an end, the winds of curiosity will continue to propel my exploration towards gaining a better understanding of the evolution and functional morphology of hearing in primates and other animals.

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APPENDICES

APPENDIX 1 – Elder 1934

Freq. (Hz)	*dB SPL	Moos R-L diff (dB)	Bokar R-L diff (dB)	Bimba R-L diff (dB)
128	30.3	3.51	0.06	
256	18	2.98	0.53	
512	10.3	0.89	3.03	3.63
1024	1.8	0.18	11.49	0.12
2048	-2.8	3.21	1.43	8.39
4096	7.3	8.57	4.52	2.98
8192	5	4.94	0.95	5.65
		mean R-L diff	mean R-L diff	mean R-L diff
		3.47	3.15	4.15

*Based on graphs in Green 1971, Stebbins 1971, and Gillette *et al*. 1973

APPENDIX 2 – Wendt 1934

	C. torquatus		*A. paniscus* #3		*A. paniscus* #4	
Freq. (Hz)	*dB SPL	**dB SPL	*dB SPL	**dB SPL	*dB SPL	**dB SPL
64	40	34	54	48	51	45
128	38	29	39	30	45	36
256	14	8	24	18	28	22
512	4	6	20	22	12	14
1024	-8	-4	3	7	0	4
2048	-11	-5	8	14	8	14
4096	3	5	24	26	23	25
8192	-15	-3	-9	3	-10	2
16384	1	25	14	38	17	41

	P. anubis		*M. mulatta*	
Freq. (Hz)	*dB SPL	**dB SPL	*dB SPL	**dB SPL
64	43	37	38	32
128	34	25	28	19
256	10	4	4	-2
512	2	4	1	3
1024	0	4	-3	1
2048	-7	-1	-5	1
4096	27	29	3	5
8192	-22	-10	-22	-10
16384	-5	19	1	25

* Based on Sivian and White (1933) corrective factor
** Based on ISO (1961) corrective factor

APPENDIX 3 – Harris 1943

M. mulatta Freq. (Hz)	Huba dB SPL	Meta dB SPL	Gris dB SPL	Hercules dB SPL	Jercules dB SPL	Mean dB SPL
63			46			46
125	18.8		20.5	16.6	26	20
250		12.5	14.5			14
500	4.2		5.8	7	10.4	7
1000	-1		-6.6	-0.4	0.3	-2
2000	2.6	-3.4	-11.8			-4
4000	2.8		-0.4	-1	6.4	2
8000			-9.5			-10

M. sinica Freq. (Hz)	Mussilini dB SPL	Jun dB SPL	Mean dB SPL	M. sp. dB SPL	Genus mean dB SPL
63	43.9		43.9		
125	18.4	18.6	18.5		
250	12.7	12	12.35		
500	8.9	2.5	5.7		
1000	1.6	-4.1	-1.25		
2000	-0.7	-12	-6.35		
4000	7.8	-2.5	2.65		
8000	-16	-8.4	-12.2		

APPENDIX 4 – Seiden 1957

C. jacchus Freq. (Hz)	#1 dB SPL	#2 dB SPL	#3 dB SPL	#5 dB SPL	#6 dB SPL	Mean dB SPL	Range dB
100	46	50	32	38	40	41	18
200	33	37	29	21	34	31	16
300	20	24	16	16	19	19	8
500	12	13	15	15	10	13	5
700	6	4	1	1	8	4	7
1000	3	5	3	3	9	4	6
2000	-3	1	0	3	1	0	6
3000	0	16	10	16	14	11	16
4000	5	26	15	23	22	18	21
5000	9	19	19	22	31	20	22
7000	-18	-11	-12	-3	-1	-9	17
10000	-9	2	-12	5	6	-2	18
15000	-3	5	-2	27	17	9	30
20000	29	39	45	58	38	42	29
25000	30	43	61	67	68	54	38
30000	60		79	79		73	19
35000	72					72	

APPENDIX 4 continued – Seiden 1957

Adjusted Freq. (Hz)	*Adjusted C. jacchus Mean dB SPL*
100	41
200	31
300	19
500	13
700	4
1000	4
2000	0
3000	11
4000	18
5000	20
7000	-9
10000	-2
15000	9
20000	37
25000	44.9
30000	68.5
32000	72.3

APPENDIX 5 – Clack and Herman 1963

Freq. (Hz)	dB SPL
1000	-4
2000	-8
4000	-2
8000	0
16000	9

APPENDIX 6 – Semenoff and Young 1964

M. nemestrina Freq. (Hz)	H RMS volts	I RMS volts	J RMS volts	Mean RMS volts
130	35.3	30	14.2	27
250	17.1	5.7	3.8	9
500	7.7	-7.4	-4.2	-1
1000	-21.2	-20.6	-24.6	-22
2000	-13.7	-20.1	-17.5	-17
4000	-0.4	3	-5	-1
8000	31.5	27.2	39.5	33

APPENDIX 6 continued – Semenoff and Young 1964

Human Freq. (Hz)	X RMS volts	Y RMS volts	Z RMS volts	Mean RMS volts
130	9.3	2.9	2.1	5
250	-18.3	-17.1	-9.5	-15
500	-27.1	-30.3	-30.3	-29
1000	-33.1	-29.5	-35.1	-33
2000	-27.1	-29.9	-34.7	-31
4000	-15.1	-11.5	-20.3	-16
8000	18.9	15.3	4.9	13

APPENDIX 7 – Fujita and Elliot 1965

S. scuireus Freq. (Hz)	Double-Grill Mean dB SPL	Reward #3 dB SPL	Reward #10 dB SPL	Mean dB SPL	Range dB
63	52	31	46	39	15
125	40	33	20	27	13
250	23	17	17	17	0
500	13	7	-3	2	10
1000	3	-3	*14	-3	17
2000	-5	3	*17	3	14
4000	6	4	-2	1	6
8000	7	5	-4	1	9
16000	-2	-13	-13	-13	0
32000	7	16	15	16	1

S. scuireus Freq. (Hz)	Shock #3 dB SPL	Shock #18 dB SPL	Mean dB SPL	Range dB
63	47	47	47	0
125	29	29	29	0
250	16	16	16	0
500	12	10	11	2
1000	9	3	6	6
2000	4	4	4	0
4000	2	2	2	0
8000	6	0	3	6
16000	1	-3	-1	4

*Excluded from mean

APPENDIX 8 – Fujita and Elliot 1965

M. fascicularis Freq. (Hz)	Reward #1 dB SPL	Reward #2 dB SPL	Mean dB SPL	Range dB
63	32	38	35	6
125	27	17	22	10
250	15	10	13	5
500	8	1	5	7
1000	3	-3	0	6
2000	13	3	8	10
4000	12	5	9	7
8000	-4	6	1	10
16000	-2	-12	-7	10
32000	28	16	22	8

M. fascicularis Freq. (Hz)	Shock #1 dB SPL	Shock #2 dB SPL	Shock #27 dB SPL	Mean dB SPL	Range dB
63	38	43	43	41	5
125	24	24	21	23	3
250	10	12	15	12	6
500	0	0	6	2	6
1000	-1	1	3	1	4
2000	2	2	1	2	1
4000	0	-8	5	-1	13
8000	6	-2	1	2	8
16000	-5	-2	-2	-3	3

APPENDIX 9 – Fujita and Elliot 1965

M. mulatta Freq. (Hz)	Reward #5 dB SPL	Reward #6 dB SPL	Mean dB SPL	Range dB
63	31	31	31	0
125	25	17	21	8
250	18	11	15	7
500	9	4	7	5
1000	5	7	6	2
2000	4	9	7	5
4000	0	4	2	4
8000	-8	-5	-7	3
16000	-15	-12	-14	3
32000	12	18	15	5

M. mulatta Freq. (Hz)	Reward #5 dB SPL	Reward #6 dB SPL	Reward #7 dB SPL	Reward #26 dB SPL	Mean dB SPL	Range dB
63		43	40	37	40	6
125	28	18	28	17	23	11
250	24	6	16	12	15	18
500	9	6	9	0	6	9
1000	9	3	9	-1	5	10
2000	4	4	14	4	7	10
4000	2	-3	5	-9	-1	14
8000	-4	-11	-4	-7	-7	7
16000	-6	-13	-9	-6	-9	7

APPENDIX 10 – Behar *et al*. 1965

M. mulatta Freq. (Hz)	#24 dB SPL	#60 dB SPL	#1114 dB SPL	Thersa dB SPL	Mean dB SPL
50	56.6	52.1	41.4	56.2	52
100	37.5	42.3	29.2	42.4	38
125	30.5	29.8	28.6	36.1	31
250	12.5	14.1	12.4	12.9	13
500	12.6	10.2	3.3	7.8	8
1000	9.9	13.4	1.4	2.7	7
2000	9.2	6.4	-3.4	12	6
4000	18.9	11.8	2.1	13.3	12
6300	12.5	11.2	-0.6	-0.4	6
8000	18.2	14	4.3	3.2	10
10000	14.2	11.6	3.6	1.7	8
12500	8.2	5.6	-2.3	-2.4	2
16000	12.8	10.2	3.6	-2.2	6
20000	14.2	13.2	9.2	6.4	11
25000	29	24.2	13	4.6	18
31500	22.3	28.6	17.7	10.5	20

Human Freq. (Hz)	RW dB SPL	JF dB SPL	ML dB SPL	AI dB SPL	RL dB SPL	JA dB SPL	RA dB SPL	Mean dB SPL
50	40.6	39.1	43.9	43.3	39.3	41.8	45.6	42
100	25	36.5	35.5	25.6	33.6	26.7	32.8	31
125	16.7	28.5	23.9	19.9	20.7	21.7	23.6	22
250	3.8	18.4	6.2	13.4	7.7	6.1	11.4	10
500	6.7	18	8.6	11.3	6.7	3.3	9.4	9
1000	1	6.3	-5.7	5.1	-2.9	-3.1	2.7	0
2000	-1.7	3.1	1.3	8.8	3.5	-2.1	16.3	4
4000	1.3	-3.2	-4.5	-4.2	-9.7	-12.8	-1.3	-5
6300	10	8.4	12.3	-2.9	12.4	5.3	10.2	8
8000	5.5	9.7	15.7	17.5	14	6.5	20.4	13
10000	14.4	6.3	29	18.1	22.5	18.2	27.9	19
12500	23.4	30.9	51.9	20.9	26.6	26.3	41.5	32
16000	38	63.5	54.5	61.8	73.8	34.9	79	58
20000	93.8		82.7	98.4	76	92.5		89

APPENDIX 11 – Farrer and Prim 1965

Pan Age	High Limit (Hz)	Range (Hz)	Human Age	High Limit (Hz)	Range (Hz)
4	26543		5-9	20676	
5	25865		10-14	20059	
6	24067		15-19	18441	
			20-24	18441	
			25-29	17176	
			30-34	16794	

APPENDIX 12 – Stebbins *et al*. 1966

M. fascicularis Freq. (Hz)	M-2 dB SPL	M-3 dB SPL	M-6 dB SPL	Mean dB SPL	Range dB	*M. nemstrina* dB SPL
60	44	41	37	41	7	39
125	26	32	24	27	8	24
250	19	25	24	23	6	22
500	10	17	6	11	11	16
1000	1	2	-1	1	3	4
2000	16	19	6	14	13	8
4000	12	18	24	18	12	15
8000	15	6	0	7	15	4
10000	14	19	8	14	11	18
15000	2	13	13	9	11	10
20000	39	29	14	27	25	20
30000	35	32	32	33	3	40
40000	43	44	46	44	4	80
45000	74	82	92	83	18	

APPENDIX 13 – Clack 1966

M. mulatta Freq. (Hz)	c2 L1 dB SPL	c2 L2 dB SPL	c2 R1 dB SPL	c2 R2 dB SPL	c2 Binaural dB SPL
125	24	32	27	30	
250	14	10	0	11	
500	4	1	4	4	
1000	-4	-1	1	-3	-3
2000	-3	4	1	-10	-6
4000	1	24	6	20	0
8000	8	-5	-11	-9	-12
16000	14	19	-14	-17	-16

M. mulatta Freq. (Hz)	c4 L1 dB SPL	c4 L2 dB SPL	c4 R1 dB SPL	c4 R2 dB SPL	c4 Binaural dB SPL
125	17	21	32	41	
250	2	0	13	18	
500	-13	-14	-1	3	
1000	-15	-11	0	-1	-13
2000	-7	-9	10	17	-8
4000	-1	2	31	35	-6
8000	-9	-7	32	34	-3
16000	-10	-15	24	39	6

M. mulatta Freq. (Hz)	*Mean dB SPL	**Mean dB SPL		Human Freq. (Hz)	Monaural dB SPL
250	9			250	34
500	-3			500	12
1000	-5	-7		1000	3
2000		-7		2000	6
4000		7		4000	3
8000		-9		8000	23

*Based on more sensitive ear
**Based on both ears

APPENDIX 14 – Dalton 1968

C. capucinus Freq. (Hz)	Mean GSR dB SPL	GSR Range dB	ECR 3L4 dB SPL
500	13	15	33
1000	15	12	29
2000	18	4	29
4000	15	7	28
8000	7	14	23

M. mulatta Freq. (Hz)	CS #3014 dB SPL	*CS #518 dB SPL	GSR #3014 dB SPL	*GSR #518 dB SPL
500	-5	12.9	5	20
1000	-2.5	22.9	5	25
2000	9	17.2	10	20
4000	-13.4	-13.1	5	-1
8000	-11.1	-11	0	-5

M. mulatta Freq. (Hz)	ECR #583 dB SPL	ECR #614 dB SPL
500	15	25
1000	10	20
2000	5	20
4000	15	30
8000	5	35

*Subject suffered from otits media

APPENDIX 15 – Dalton *et al*. 1969

M. Mulatta Freq. (Hz)	#508 dB SPL	#557 dB SPL	#566 dB SPL	#608 dB SPL	Mean dB SPL	Range dB
500	10	8	4	0	6	10
1000	8	4	-1	-2	2	10
2000	-3	0	-4	-5	-3	5
4000	-6	-8	-12	-7	-8	6
8000	-4	-9	-13	-4	-8	9

APPENDIX 16 – Heffner *et al*. 1969

G. senegalensis Freq. (Hz)	A dB SPL	B dB SPL	C dB SPL	D dB SPL	Mean dB SPL	Range dB
125				51	51	
250	47	44		40	44	7
500	30	20	39	29	30	19
1000	28	37		29	31	9
2000	19	17	16	10	16	9
4000	7	17	-1	11	9	18
8000	3	5	2	-16	-2	21
16000	6	10	-3	-14	0	24
32000	4	8	19	-3	7	22
64000	57	61			59	4

APPENDIX 17 – Heffner and Masterson 1970

N. coucang Freq. (Hz)	A dB SPL	B dB SPL	Mean dB SPL	Range dB
63	69	66	68	3
125	46	50	48	4
250	34	39	37	5
500	26	33	30	7
1000	26	22	24	4
2000	20	28	24	8
4000	22	26	24	4
8000	24	6	15	18
16000	14	4	10	10
32000	32	16	24	16
48000	69	70	70	1

P. potto Freq. (Hz)	A dB SPL	B dB SPL	Mean dB SPL	Range dB
125	63		63	
250	38	28	33	10
500	44	17	31	27
1000	28	8	18	20
2000	27	6	17	21
4000	33	13	23	20
8000	14	-5	5	19
16000	3	-2	1	5
32000	16	16	16	0
43000	70	70	70	0

APPENDIX 18 – Gourevitch 1970

M. nemestrina Freq. (Hz)	A dB SPL	B dB SPL	Mean dB SPL	Range dB
125	46	44	45	2
250	33	24	28	9
500	19	17	18	2
800	13		13	
1000	14	5	9	9
1500	21	5	13	16
2000	11	0	6	11
3000	4		4	
3500	14		14	
4000	17	14	16	3
5000	17	19	18	2
6000	11		11	
7000	16		16	
8000	11	5	8	6
17000	11	6	8	5

APPENDIX 19 – Mitchell *et al*. 1970

L. catta Freq. (Hz)	#2023 dB SPL	#3183 dB SPL	Mean dB SPL	Range dB
100	51	50	51	1
200	44	48	46	4
500	33	34	34	1
1000	21	15	18	6
2000	22	13	18	9
4000	23	37	30	14
8000	27	26	27	1
15000	64	15	40	49
25000	67	19	43	48
40000		14	14	

E. fulvus Freq. (Hz)	#3442 dB SPL	#3368 dB SPL	Mean dB SPL	Range dB
100	51	47	49	4
200	46	32	39	14
500	37	27	32	10
1000	38	9	24	29
2000	20	16	18	4
4000	41	22	32	19
8000	32	21	27	11
15000	32	29	31	3
25000	37	9	23	28
40000		41	41	

E. macaco Freq. (Hz)	#2548 dB SPL	#2549 dB SPL	Mean dB SPL	Range dB
100	51	51	51	0
200	46	37	42	9
500	23	30	27	7
1000	15	22	19	7
2000	34	18	26	16
4000	39	19	29	20
8000	22	27	25	5
15000	19	18	19	1
25000	18	16	17	2
40000		19	19	

APPENDIX 20 – Mitchell 1970; Mitchell *et al*. 1971

L. catta Freq. (Hz)	#674 dB SPL	#2023 dB SPL	#2034 dB SPL	#4059 dB SPL
100	48	51	52	44
200	29	39	44	35
500	8	30	20	21
1000	0	16	4	8
2000	1	9	2	7
4000	6	14	5	7
8000	-2	4	11	-1
15000	0	16	8	4
25000	3	17	-4	12
32000	7	30	8	5
40000	22	37	22	26

L. catta Freq. (Hz)	#2311 dB SPL	Mean dB SPL	Range dB
100	51	49	8
200	31	36	15
500	17	19	23
1000	8	7	16
2000	9	6	8
4000	9	8	9
8000	5	3	13
15000	6	7	16
25000	19	9	23
32000	8	12	25
40000	34	28	15

APPENDIX 21 – Gillette *et al*. 1973

L. catta Freq. (Hz)	Mean dB SPL
100	49
200	36
500	18
1000	7
2000	6
4000	8
8000	3
15000	13
25000	15
32000	14
40000	30
50000	49
60000	63

70000	86
75000	94

APPENDIX 22 – Green 1970, 1975

S. scuireus Freq. (Hz)	Reward #1 dB SPL	*Reward #2 dB SPL	Reward #4 dB SPL	Reward #5 dB SPL
125	65		55	64
250	43		48	47
500	29	33	32	33
1000	16	26	17	17
2000	18	28	16	16
4000	17		13	17
8000	3	15	10	10
16000	19	22	19	16
32000	28		20	27
40000	79		65	37
46000	82		83	71

S. scuireus Freq. (Hz)	Reward Mean dB SPL	Reward Range dB	Shock #4 dB SPL
125	61	10	66
250	46	5	50
500	31	4	27
1000	17	1	16
2000	17	2	14
4000	16	4	13
8000	8	7	8
16000	18	3	15
32000	25	8	20
40000	60	42	44
46000	78	12	60

*Excluded from mean

APPENDIX 23 – Pugh *et al*. 1970

M. nemstrina Freq. (Hz)	Pre-operative dB SPL	Post-operative dB SPL	Difference dB
63	60	64	4
125	51	57	6
250	45	51	6
500	29	39	10
1000	15	14	
2000	8	6	
4000	17	20	
8000	6	4	
16000	32	33	

APPENDIX 24 – Stebbins 1973

Cercopithecinae Freq. (Hz)	Mean dB SPL
60	47
63	45
125	29
250	17
500	8
1000	0
2000	7
4000	14
8000	0
16000	23
32000	57
45000	80

APPENDIX 25 – Beecher 1974

A. trivergatus Freq. (Hz)	1 dB SPL	2 dB SPL	Mean dB SPL	Range dB	*S. scuireus* Freq. (Hz)	Mean dB SPL
125	38	40	39	2	125	47
250	25	23	24	2	250	33
500	11	15	13	4	500	19
1000	6	6	6	0	1000	9
2000	4	6	5	2	2000	7
4000	12	12	12	0	4000	15
8000	-8	-6	-7	2	8000	1
10000	-7	-9	-8	2	10000	-4
16000	7	4	6	3	16000	14
20000	7	7	7	0	20000	15
32000	16	11	14	5	32000	17
40000	28	26	27	2	40000	33
44000	54	54	54	0	44000	58
45000	67	64	66	3	45000	69

APPENDIX 26 – Pfingst *et al*. 1975

Human (H1) Freq. (Hz)	Reaction Time dB SPL	Clinic dB SPL	Forced Choice dB SPL
125	46		40
250	22	25	18
500	8	11	1
1000	3	9	-2
2000	6	10	-3
4000	11	13	10
8000	18	15	17
16000	38		38
17000	75		71

Human Freq. (Hz)	*Curve A dB SPL	*Curve B dB SPL	*Curve C dB SPL
125	46	34	27
250	22	17	13
500	8	6	4
1000	3	1	-2
2000	6	0	-1
4000	11	0	19
8000	18	14	11
16000	39	29	29
18000	75	72	89

Human Freq. (Hz)	H1 dB SPL	H5 dB SPL	Mean dB SPL	Range dB
125	27	29	28	2
250	13	14	14	1
500	4	14	9	10
1000	-2	0	-1	2
2000	-1	-1	-1	0
4000	19	12	16	7
8000	11	8	10	3
16000	28	62	45	34
18000	89		89	

*See text for calibration procedures used for each curve

APPENDIX 26 continued – Pfingst *et al*. 1975

M. mulatta Freq. (Hz)	M1 dB SPL	M2 dB SPL	Mean dB SPL	Range dB
125	42	35	39	7
250	24	21	23	3
500	16	19	18	3
1000	5	8	7	3
2000	7	10	9	3
4000	12	11	12	1
8000	-2	2	0	4
16000	1	12	7	11
32000	22	28	25	6
45000	84	62	73	22

APPENDIX 27 – Pfingst *et al*. 1978

M. mulatta Freq. (Hz)	Mean dB SPL	Standard Deviation dB
125	39	19.5
250	25	12.5
500	17	8.5
707	14	
1000	9	4.5
1414	6	3
2000	7	3.5
2828	13	6.5
4000	16	8
5656	10	5
8000	6	3
10000	7	
11312	5	2.5
16000	7	3.5
22624	12	6
32000	29	14.5
40000	53	26.5
41000	60	
43000	70	
45300	79	39.5

APPENDIX 28 – Lonsbury-Martin and Martin 1981

M. mulatta Freq. (Hz)	Mean dB SPL	Standrad Deviation dB
354	24	5
500	21	4
704	12	4
1000	11	6
1408	7	5
2000	9	5
2816	16	7
4000	18	4
5632	14	5
8000	5	7
11264	9	4
16000	8	5
22528	5	5
32000	32	8

APPENDIX 29 – Heinz et al. 1982

P. cynocephalus Freq. (Hz)	AL dB SPL	MA dB SPL	LE dB SPL	MO dB SPL	Mean dB SPL	Range dB
62	50	46			48	4
125	23	22			23	1
250	17	19			18	2
500	-3	4	14	7	6	17
1000	-4	7	6	1	3	11
2000	2	7	10	9	7	8
4000	-2	12	6	5	5	14
8000	4	7	-5	-9	-1	16
16000	2	5	-3	7	3	10
20000	11	7			9	4
32000	24	24			24	0
40000	53	63			58	10

APPENDIX 30 – Bennett *et al*. 1983

M. mulatta Freq. (Hz)	Old Group Replication	A1 dB SPL	A2 dB SPL	A3 dB SPL	Mean dB SPL	Range dB
125	1	43.5	49.8	47.7	45.0	3.1
	2	46.8	47.1	47.1		
	3	41.3	44.0	38.3		
500	1	31.4	36.8	30.1	32.0	8.2
	2	27.7	39.6	32.3		
	3	26.4	33.6	26.1		
2000	1	21.5	41.3	34.7	35.0	21.6
	2	22.9	46.5	36.9		
	3	24.1	45.7	38.3		
4000	1	18.7	24.9	13.1	20.0	11.8
	2	11.6	26.3	18.8		
	3	18.2	31.9	16.0		
16000	1	28.1	19.7	6.8	21.0	7.0
	2	24.1	16.3	12.3		
	3	35.5	30.5	17.8		
22627	1	60.5	nr	30.6	49.0	26.1
	2	63.2	nr	28.2		
	3	nr	nr	48.3		
32000	1	nr	nr	nr		
	2	nr	nr	nr		
	3	nr	nr	nr		

M. mulatta Freq. (Hz)	Middle-aged Group Replication	B1 dB SPL	B2 dB SPL	Mean dB SPL	Range dB
125	1	32.7	32.7	31.0	0.8
	2	29.8	29.8		
	3	28.1	30.5		
500	1	17.2	19.3	16.0	3.0
	2	16.3	13.8		
	3	10.5	19.8		
2000	1	19.8	17.5	19.0	0.5
	2	17.7	20.7		
	3	17.9	18.5		
4000	1	4.3	0.7	3.0	3.5
	2	4.2	0.7		
	3	5.5	2.1		
16000	1	18.3	14.1	17.0	1.9
	2	14.8	22.2		
	3	14.7	17.3		
22627	1	23.1	15.6	24.0	4.2
	2	28.1	17.5		
	3	26.9	32.5		
32000	1	46.1	64.7	61.0	16.0

	2	53.6	68.8		
	3	60.4	74.5		

APPENDIX 30 continued – Bennett *et al*. 1983

M. mulatta Freq. (Hz)	Young Group Replication	C1 dB SPL	C2 dB SPL	Mean dB SPL	Range dB
125	1	38.3	29.7	33.0	7.6
	2	39.7	31.8		
	3	32.0	25.7		
500	1	24.8	10.3	13.0	12.2
	2	18.1	3.6		
	3	15.1	7.4		
2000	1	12.3	0.1	6.0	12.8
	2	11.4	-0.5		
	3	12.8	-1.7		
4000	1	3.9	-2.1	0.0	3.3
	2	-2.6	0.1		
	3	4.1	-2.6		
16000	1	7.8	2.6	9.0	5.1
	2	10.3	9.3		
	3	15.6	6.7		
22627	1	15.6	13.3	16.0	4.5
	2	17.5	15.0		
	3	20.7	11.9		
32000	1	40.1	31.0	37.0	11.3
	2	41.2	33.0		
	3	47.3	30.8		

APPENDIX 31 – Brown and Waser 1984

C. mitis Freq. (Hz)	M1 dB SPL	M2 dB SPL	Mean dB SPL	Range dB
63	50	50	50	0
125	30	28	29	2
250	20	20	20	0
500	12	7	10	5
1000	6	4	5	2
2000	5	7	6	2
4000	4	4	4	0
8000	10	8	9	2
16000	5	11	8	6
32000	12	22	17	10
45000	50	50	50	0

Human Freq. (Hz)	LS dB SPL	DG dB SPL	DO dB SPL	CB dB SPL	Mean dB SPL	Range dB
63	60	58	57	56	58	4
125	37	37	37	37	37	0
250	24	25	23	22	24	3
500	8	16	11	11	12	8
1000	9	4	4	2	5	7
2000	9	10	-1	6	6	11
4000	8	0	-7	4	2	15
8000	15	6	15	13	12	9
16000	34	35	23	41	33	18

APPENDIX 32 – Brown 1986

L. albigena Freq. (Hz)	Mean dB SPL
63	54
125	29
250	18
500	13
800	2
2000	6
4000	6
8000	5
16000	11
32000	16

APPENDIX 33 – Smith *et al*. 1987

E. patas	Pre-Treatment			Post-Treatment	
	M-157	M-155		M-157	M-155
Freq. (Hz)	dB SPL	dB SPL	Freq. (Hz)	dB SPL	dB SPL
63	97		63	90	
125	88	73	125	80	94
250	58	67	250	52	57
370	48	49	370	49	50
500	36	43	500	43	35
715	27	30	715	42	35
1000	26	25	1000	53	25
1400	24	22	1400	52	31
2000	24	26	2000	61	21
2850	28	21	2850	70	45
4000	26	18	4000	76	61
5700	28	20	5700	82	72
8000	17	10	8000	66	70
11200	37	0	11200	73	79
23000	48	18	16000	80	90
32000	57	71			
40000	71				

APPENDIX 34 – Owren *et al*. 1988

Freq. (Hz)	Human dB SPL	Range dB	*C. aethiops* dB SPL	Range dB
63	61	10	62	10
88	53	7	54	7
125	42	5	42	1
176	33	16	34	6
250	21	8	26	6
353	11	14	16	5
500	6	6	8	3
707	2	13	3	4
1000	2	3	-2	4
1400	7	7	-4	4
2000	11	11	6	3
2828	13	18	8	6
4000	15	15	3	8
5657	13	18	-2	12
8000	16	16	5	15
11313	38	21	4	0
16000	35	19	12	20
22625	49		16	11
32000			15	17
34895			13	8
38054			16	3
40000			22	17
42000			34	11
43000			38	14
45000			60	11

APPENDIX 34 continued – Owren *et al*. 1988

Freq. (Hz)	*C. neglectus* dB SPL	Range dB	*M. fuscata* dB SPL	Range dB
63	59	10	68	10
88	55	22	58	16
125	43	13	48	18
176	34	14	38	19
250	27	9	32	17
353	16	3	21	12
500	11	5	15	13
707	7	11	9	12
1000	4	4	3	12
1400	3	7	3	14
2000	15	5	11	10
2828	12	5	15	12
4000	9	8	10	9
5657	2	4	2	10
8000	4	8	8	5
11313	7	9	10	7
16000	6	9	9	10
22625	18	12	18	6
32000	22	16	21	13
34895	24	12	23	23
38054	29	22	36	30
40000	47	30	49	26
42000	57	23	63	7
43000	50		63	
45000	>72		>72	

APPENDIX 35 – Kojima 1990

P. troglodytes Freq. (Hz)	Pen dB SPL	Popo dB SPL	Mean dB SPL	Range dB	Human Freq. (Hz)	dB SPL
125	44	54	49	10	125	35
250	25	35	30	10	250	16
500	13	17	15	4	500	3
1000	14	6	10	8	1000	3
2000	23	13	18	10	2000	3
4000	23	23	23	0	4000	3
8000	5	-4	1	9	8000	23
16000	13	15	14	2	16000	73
24000	26	23	25	3		
32000	86	82	*84	4		
32000						

* text gives a value of 90 dB

APPENDIX 36 – Smith and Olszyk 1997

M. fuscata Freq. (Hz)	M03 R dB SPL	M03 L dB SPL	Mean dB SPL	M04 R dB SPL	M04 L dB SPL	Mean dB SPL
73	62	61	62	57	59	58
176	59	52	56	51	45	48
250	55	47	51	42	40	41
500	42	42	42	34	32	33
1000	29	23	26	20	18	19
2000	17	15	16	13	8	11
4000	15	11	13	17	16	17
5657	10	8	9	8	9	9
8000	6	2	4	1	2	2
11313	8	8	8	3	4	4
16000	13	15	14	7	14	11
22625	6	5	6	3	4	4
30500	16	17	17	14	17	16

Freq. (Hz)	M05 R dB SPL	M05 L dB SPL	Mean dB SPL	M06 R dB SPL	M06 L dB SPL	Mean dB SPL	Mean All dB SPL
73	54	62	58				59
176	42	53	48	46	47	47	50
250	39	48	44	42	38	40	44
500	30	42	36	33	33	33	36
1000	17	23	20	19	16	18	21
2000	8	15	12	12	9	11	13
4000	14	11	13	14	14	14	14
5657	11	8	10	5	6	6	9
8000	-2	1	-1	2	-2	0	1
11313	3	7	5	11	5	8	6
16000	15	14	15	15	13	14	14
22625	0	5	3	3	5	4	4
30500	16	16	16	15	22	19	17

APPENDIX 37 – Jackson *et al*. 1999

M. fuscata Freq. (Hz)	#286 dB SPL	#605 dB SPL	#638 dB SPL	Mean dB SPL	Range dB
8			83		
12.5	81	77	76	78	5
16	71	73	72	72	2
25	63	66	60	63	6
32	56	57	57	57	1
63	37	35	37	36	2
125	18	19	19	19	1
250	13	15	17	15	4
500	7	2	10	6	8
1000	4	5	3	4	2
2000	7	0	9	5	9
4000	4	-2	1	1	6
8000	8	0	6	5	8
16000	9	1	0	3	9
32000	41	37	38	39	4
36000	77	64	72	71	13
40000	92	85	89	89	7

Human Freq. (Hz)	CC dB SPL	HH dB SPL	JM dB SPL	LH dB SPL	PH dB SPL
4	101	100	101	101	100
8	95	92	95	95	95
16	88	78	83	87	87
32	63	58	62	65	62
63	38	39	39	34	38
125	20	12	17		21
250	14	13	7		11
500	11	14	8		10
1000	-11	-8	-2		-4
2000	-10	-14	9		-14
4000	-11	-2	-4		-13
8000	14	17	4		2
16000	14	41	28		17
18000	67	81	77		66
20000	91	>91	92		>91
22000	>91	>91	>91		>91

APPENDIX 37 continued – Jackson *et al*. 1999

Human Freq. (Hz)	RH dB SPL	SM dB SPL	Mean dB SPL	Range dB
4	100	101	101	1
8	92	92	94	3
16	86	68	82	20
32	56	42	58	23
63	29	34	36	10
125	12	21	17	9
250	7	8	10	7
500	10	7	10	6
1000	1	2	-4	13
2000	-20	-10	-10	29
4000	-12	-19	-10	17
8000	4	13	9	15
16000	49	4	26	34
18000	85	51	71	34
20000	>91	91		
22000	>91	>91		

APPENDIX 38 – Lasky *et al*. 1999

M. mulatta Freq. (Hz)	Mean dB SPL	Standard Deviation dB
125	43	2
250	33	1.9
500	30	1.4
1000	18	1.9
2000	27	2.7
4000	22	1.8
8000	13	1.5

APPENDIX 39 – Heffner 2004

E. fulvus Freq. (Hz)	Mean dB SPL
72	60
*8000	-1
43000	60

* best frequency

APPENDIX 40 – Mean *M. fascicularis* free-field audiogram

M. fascicularis Freq.(Hz)	*Mean dB SPL
63	38.8
125	22.6
250	12.4
500	3
1000	0.6
2000	4.2
4000	2.8
8000	1.4
16000	-4.6
32000	22

*Based on Fujita and Elliot 1965

APPENDIX 41 – Mean *M. mulatta* closed-field audiogram

M. mulatta Freq. (Hz)	*Mean dB SPL
125	39
250	25
354	22.5
500	19
707	13
1000	10
1414	6.5
2000	8
2828	14.5
4000	17
5656	12
8000	5.5
10000	7
11312	7
16000	7.5
22624	8.5
32000	30.5
40000	53
41000	60
43000	70
45300	79

*Based on Pfingst *et al*. 1978 and Lonsbury-Martin and Martin 1981

APPENDIX 42 – Mean *M. mulatta* free-field audiogram

M. mulatta Freq. (Hz)	*Mean dB SPL
63	41.8
125	29
250	14
500	9.3
1000	6.3
2000	6.6
4000	4.2
8000	1.5
16000	0.8
32000	24.6

*Based on Behar *et al*. 1965,
Fujita and Elliot 1965, and Bennett *et al*. 1983

APPENDIX 43 – Mean *M. nemestrina* closed-field audiogram

M. nemestrina Freq. (Hz)	*Mean dB SPL
87	41.5
125	34.5
250	25
500	17
1000	6.5
2000	7
4000	15.5
8000	6
15000	9
16000	12
20000	20
30000	40
32000	48
40000	80

*Based on Stebbins *et al*. 1966
and Gourevitch 1970

APPENDIX 44 – Mean *P. troglodytes* closed-field audiogram

P. troglodytes Freq. (Hz)	*Mean dB SPL
125	39.5
250	24
500	12.5
1000	6
2000	7.5
4000	15
8000	3
16000	14
24000	25
28800	80

* Based on Elder 1934, 1935,
Farrer and Prim 1965, and Kojima 1990

APPENDIX 45 – Mean *S. scuireus* open-field audiogram

S. scuireus Freq. (Hz)	*Mean dB SPL
87	46.5
125	39.5
250	25.8
500	13.8
1000	7
2000	3.8
4000	9
8000	2.3
12650	-4.6
16000	4.3
20000	15
32000	14.3
40000	33
44000	58
45000	69
46000	70

*Based on Fujita and Elliot 1965
and Beecher 1974

APPENDIX 46 – Regression statistics for fossil hearing predictions

Regression	Slope	Intercept	S.E.
L_c vs. SPL @ 250 Hz	-2.433	83.430	3.404
L_c vs. SPL of the Dip	-1.678	53.509	6.815
A_{tm} vs. SPL @ 250 Hz	-1.383	64.705	6.545
A_{tm} vs. High Audible Area	-15.890	1428	157.46
V_{me} vs. SPL @ 250 Hz	-17.328	40.653	7.218
V_{ac} vs. SPL @ 250 Hz	-69.231	40.936	3.607
V_{ac} vs. SPL of the Dip	-45.875	25.573	6.507