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Kinematics of the Chimpanzee Foot During Terrestrial and Arboreal Locomotion

A Dissertation Presented

by

Nicholas Baird Holowka

to

The Graduate School

in Partial Fulfillment of the

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for the Degree of

Doctor of Philosophy

in

Anthropology

(Concentration – Physical Anthropology)

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Nicholas Baird Holowka

We, the dissertation committee for the above candidate for the
Doctor of Philosophy degree, hereby recommend
acceptance of this dissertation.

**Brigitte Demes – Dissertation Advisor
Professor, Department of Anatomical Science**

**William Jungers - Chairperson of Defense
Distinguished Teaching Professor, Department of Anatomical Sciences**

**Susan G. Larson
Professor, Department of Anatomical Sciences**

**Matthew C. O’Neill
Assistant Professor, Department of Basic Medical Sciences
University of Arizona College of Medicine – Phoenix**

**Caley M. Orr
Assistant Professor, Department of Cell and Developmental Biology
University of Colorado School of Medicine**

This dissertation is accepted by the Graduate School

Charles Taber
Dean of the Graduate School
Abstract of the Dissertation

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The adoption of obligate terrestrial bipedality is believed to be the key transition that set early hominins on the path towards the development of advanced social systems and material culture. Critical to this transition was the evolution of a foot that is dramatically different from that of any other living primate. Numerous studies over the past century have investigated the feet of our closest living relatives, the non-human apes, as a means of understanding the evolutionary processes resulting in the modern human foot. None of these studies, however, has been able to quantify foot motion in a non-human ape in a controlled setting to achieve a detailed understanding of the foot function of these animals *in vivo*.

To address this gap, I used a high-speed motion capture system to measure 3-D foot kinematics in two chimpanzees during locomotion on terrestrial and arboreal substrates. I also measured foot kinematics in both humans and chimpanzees during bipedal locomotion while simultaneously collecting pedobarographic data using a pressure-sensing platform. I used these data to address three objectives: 1) Determine the extent to which the chimpanzee foot is adapted for terrestrial *versus* arboreal locomotion, 2) assess interspecies differences in human and chimpanzee foot function, and 3) evaluate the relationship between foot kinematics and plantar pressure distributions in both species.

My results indicate that the chimpanzee foot is a versatile structure, well-suited to both arboreal support grasping *and* proficient terrestrial locomotion *via* general stiffening of the midfoot joints, but with increased mobility of the ankle joint complex. Additionally, I found that the chimpanzee midfoot is less mobile overall during bipedal walking than that of humans, due to the absence of the dramatic joint rotations related to the function of the human longitudinal arch. These findings suggest that chimpanzee foot function makes a good model for that of the earliest hominins, who would have been adept at travel on the ground and in the trees. Later modifications to foot structure enhanced propulsive force production during bipedal locomotion, but at the expense of overall prehensility.

Dedication Page

I dedicate this dissertation to my parents, Barbara and David, who supported and inspired me every step of the way.

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When I began to develop this dissertation project, I heard from multiple sources that one has to be lucky to be successful in non-human primate locomotion research. That is, one must hope that the animals under investigation are compliant research subjects, and will do whatever goofy things the investigator needs for his/her research objective. With my little experience I would say that this is partly true, but it is also contingent on working with a gifted animal trainer, and in Kristin Lasek I got that. Not only did Kristin determine the success of my project through her remarkable bond with Herc and Leo, but she became a good friend who deflated the tension on experimental days and helped to show me the joy of working with nonhuman primates.

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Chapter 1

Background

1.1 Introduction

Fully orthograde bipedalism is one of the defining traits of *Homo sapiens*, and is believed to have been the key characteristic that distinguished the earliest hominins from their ape contemporaries. The adoption of bipedal locomotion is thought to have set hominins on the path towards powerful cognitive capabilities by freeing the forelimbs for use in manipulative activities. This would have paved the way for the development of advanced material culture and eventually, complex social behavior. The evolution of fully-modern human bipedality required a number of dramatic changes to the lower limb, including segment elongation, reorganization of the pelvis and hip joint, and a major architectural overhaul of the foot. Relative to that of all other extant primates, the human foot is a true oddity. Virtually all other primates possess feet specially evolved for powerful pedal grasping. The earliest primates evolved opposable halluces for specialized locomotion on arboreal substrates (Szalay and Dagosto, 1988; Sargis et al., 2007), and later primates retained this feature, as well as other adaptations of the ankle and midfoot joints (Lewis, 1980a; b; Boyer and Seiffert, 2013; Boyer et al., 2015) to maintain proficiency in arboreal locomotion. Even the African apes¹, the closest living relatives of humans, possess powerful grasping halluces, among numerous other pedal features that are believed to represent adaptations to life in the trees. Humans, on the other hand, have completely lost hallucal opposability, and their feet possess a hallmark longitudinal arch that is thought to stiffen the midfoot region to enhance the foot's effectiveness as a lever during push-off in bipedal locomotion.

To understand the peculiarities of the human foot and the evolutionary processes that have converted it from a structure designed for grasping into its current form, researchers have frequently taken a comparative approach by investigating the form and function of African ape feet (e.g., Morton, 1922, 1924; Weidenreich, 1923; Tuttle, 1970). Despite their close relationships to humans, African apes possess feet closer to those of most other primates in terms of overall architecture, digit proportions, and of course, hallux opposability. Therefore, researchers have traditionally placed African ape feet in a natural dichotomy with those of humans: feet adapted for arboreal locomotion in the former group versus feet adapted for terrestrial bipedalism in the latter. This dichotomy has formed the basis for numerous hypotheses concerning different aspects of pedal morphology and their relationships to function during locomotion. That is, traditionally, more African ape-like morphology is considered to represent an arboreal adaptation, whereas more human-like morphology is believed to represent an

¹ Throughout this dissertation, I will use the term 'African ape' to refer to extant members of the clade homininae excluding *Homo sapiens*. That is to say, to represent a paraphyletic grade of species including gorillas, bonobos, and chimpanzees.

adaptation for terrestrial bipedalism. These morphologies are then interpreted in the context of how they improve overall foot mechanics during these behaviors.

There is, however, a major logical inconsistency in studies of human and African ape foot morphology that are based upon this dichotomy; that is, all extant African ape species spend considerable amounts of time traveling on the ground (Hunt, 1992; Doran, 1993, 1997; Doran and Hunt, 1994; Sarringhaus et al., 2014), so we should expect their feet to be adapted for terrestrial *as well as* arboreal locomotion. Extant African apes include gorillas, represented by mountain and lowland species, and two species belonging to the genus *Pan*: chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*). Members of these species split their time between life on the ground and in the trees; typically, they use the ground for longer distance travel, but enter the trees to forage and access safe sleep sites (Tuttle, 1986; Doran and Hunt, 1994; Doran, 1997). When on the ground, African apes employ a unique form of quadrupedalism called ‘knuckle-walking’, in which they bear weight on the intermediate phalanges of their forelimbs. In the trees, they use a combination of positional behaviors, including some involving overhead forelimb suspension. Some African apes, such as male chimpanzees and mountain gorillas, spend more time on terrestrial substrates than others (Doran, 1997). However, they all spend more time travelling on the ground than Asian apes (orangutans, gibbons, and siamangs) and most monkeys (Fleagle, 1999).

Nevertheless, due to their close phylogenetic affinity with humans, African apes are often used to represent the arboreal condition in comparative studies of limb morphology, including those focused on the foot. From these studies, researchers have constructed arguments about hominoid pedal adaptations to different locomotor behaviors. Some of these arguments have been tested in experimental studies of African ape locomotion *in vivo*; such studies have also been used to generate new hypotheses about the relationship between human and African ape pedal form and function. These investigations have yielded important insights that have improved our understanding of human foot mechanics and the etiology of foot pathologies (Elftman and Manter, 1935a; Bojsen-Møller, 1979). Additionally, they have dramatically influenced gait reconstructions of fossil hominins, and thereby improved our understanding of the evolution of human bipedalism. However, much is still unknown about African ape foot mechanics. No study has quantified three-dimensional (3-D) motion of the intrinsic foot joints in these species during locomotion. Furthermore, no study has quantified the motion of these joints during travel on arboreal substrates, despite the multitude of functional arguments that assume adaptation to arboreality in the African ape foot. Therefore, in this dissertation I provide 3-D kinematic data for the ankle and intrinsic foot joints in an African ape (the chimpanzee) during locomotion on both arboreal and terrestrial substrates. These data are used to address hypotheses that bear on extant hominoid foot adaptation, as well as human foot evolution. Before describing the more specific objectives of this dissertation, I will provide brief overviews of the comparative anatomy of African ape feet, previous experimental investigations of foot mechanics, and functional interpretations of fossil hominin pedal remains that are based on these studies.

1.2 Comparative Anatomy

Because this dissertation is an investigation of chimpanzee foot kinematics, I will devote this section primarily to the discussion of chimpanzee foot anatomy in comparison to that of humans. In most cases, it can be assumed that the pedal anatomy of the other African apes is similar to that described for chimpanzees, at least relative to the human condition.

1.2.1 Bony Anatomy

Compared to those of humans, chimpanzees possess relatively elongate pedal phalanges, particularly in the lateral digits (2-5) (Midlo, 1934; Schultz, 1963). In addition to their great length, the proximal and intermediate phalanges of chimpanzees and other great apes are markedly curved, which is an adaptation to adjust to the high strains incurred by the bending moments produced by digital flexor muscles during arboreal substrate grasping (Preuschoft, 1970). In contrast to their relative digit length, chimpanzees possess relatively shorter midfoot regions than humans (Schultz, 1963; Lovejoy et al., 2009). This means that the anteroposterior length of the region including the cuboid, navicular, and cuneiform bones is relatively short, which Lovejoy et al. (2009) argue reduces the overall mechanical efficiency of the foot when acting as a lever during push-off. Chimpanzees also possess relatively shorter calcaneal tubers than humans, meaning that their triceps surae muscles have lower relative mechanical advantage (Schultz, 1963; Holowka and O'Neill, 2013). Their tubers are significantly more slender than those of humans as well, which has been argued to limit their ability to resist strains during touchdown of terrestrial locomotion (Latimer and Lovejoy, 1989). The degree of torsion of the metatarsal bases relative to their heads indicates the presence of a low transverse arch in the feet of chimpanzees (Morton, 1924; Elftman and Manter, 1935a), but does not indicate longitudinal arching, as in humans (Pontzer et al., 2010; Ward et al., 2011; Drapeau and Harmon, 2014). Chimpanzees also possess a relatively shorter first metatarsal than humans, likely reflecting the role of hallux in pedal grasping, and its relative contribution to push-off during terrestrial locomotion (Wunderlich, 1999; Jungers et al., 2009).

Additional bony features can be used to distinguish the foot bones of humans and chimpanzees. Chimpanzees lack a lateral plantar process of the calcaneus, which may reduce their ability to resist the strains incurred at touchdown during bipedal locomotion (Zipfel et al., 2011; O'Neill et al., 2015). They do, however, possess a prominent peroneal trochlea, which is greatly reduced in humans (Stern and Susman, 1983). The peroneal trochlea is the anchorage point for the peroneal retinaculum, which serves as a pulley for the peroneus longus and peroneus brevis muscles. It therefore has been argued to reflect the relative size of these muscles compared to those in humans, as well as their activity during arboreal locomotion (Stern and Susman, 1983). However, it has also been suggested to serve as an additional weight-bearing feature of the chimpanzee calcaneus, performing a similar function to the human lateral plantar process, and requiring chimpanzees to bear weight on the lateral sides of their feet (Lewis, 1983; Latimer and Lovejoy, 1989). Another feature argued to bear weight in chimpanzees is the navicular tuberosity, which is greatly expanded relative to the human condition, according to 3-D geometric morphometric analyses (Harcourt-Smith, 2002; Jungers et al., 2009). Harcourt-Smith and Aiello (2004) have suggested that this feature indicates substantial medial midfoot weight support in chimpanzees, although Lovejoy et al. (2009) argue that the tuberosity is only large relative to the rest of the bone, which is anteroposteriorly short compared to that in humans.

Numerous aspects of pedal joint articular surface morphology have been argued to be indicative of differences in joint orientation and overall mobility in humans and chimpanzees. These include features of the talocrural and subtalar joints, which have been described as comprising the 'upper' and 'lower' ankle joints, respectively (Elftman and Manter, 1935a). Chimpanzees possess a talar trochlea characterized by a lateral margin that is taller than the medial margin, indicating a more inverted neutral position of the chimpanzee foot relative to the leg than that in humans (Latimer et al., 1987). The anterior and posterior margins of the talar

trochlea also describe a wider conical angle than those in humans, resulting in greater foot inversion and external rotation at higher dorsiflexion angles, which is thought to optimally position the foot during arboreal support grasping (Lewis, 1980a; Latimer et al., 1987). The chimpanzee subtalar joint axis of rotation is believed to be more medially oriented but less dorsally inclined than that in humans, resulting in a more favorable disposition for placing the foot against arboreal substrates (Elftman and Manter, 1935a; Lewis, 1980b). Additionally, the posterior articular facet of the chimpanzee subtalar joint possesses a greater relative degree of curvature than that in humans (Latimer and Lovejoy, 1989; Prang, 2016), and the chimpanzee talar and calcaneal articular surfaces remain congruent over a broader range of motion at this facet (Rose, 1986). These features are thought to enable chimpanzees to load their subtalar joints in a greater range of inversion and eversion postures than humans, and potentially provide a greater range of joint motion overall.

Researchers have also pointed out several major differences between humans and chimpanzees at the joints comprising the transverse tarsal joint complex: the calcaneocuboid joint, and the talonavicular joint. The human calcaneocuboid joint is distinguished from that of chimpanzees, and other African apes, by the presence of a pronounced, inferomedially positioned calcaneal process on the proximal articular surface of the cuboid. This feature is believed to allow close-packing of the calcaneocuboid joint during the midfoot supination² that accompanies push-off in a human step (Bojsen-Møller, 1979). This process is much reduced, and more centrally located in chimpanzees, and is believed to serve as a pivot about which transverse tarsal joint complex inversion and eversion can occur during arboreal locomotion (Lewis, 1980b). The talonavicular joint articular surfaces are larger and more strongly curved in chimpanzees than in humans (Sarmiento and Marcus, 2000; Zipfel et al., 2011), potentially facilitating a greater range of motion in chimpanzees at this joint. Elftman and Manter (1935a) suggested an even more nuanced model of transverse tarsal joint complex function in chimpanzees. They argued that both the talonavicular and calcaneocuboid joints possess two orthogonal axes of rotation, one of which is relatively mediolaterally oriented, and the other of which is more vertically oriented. In humans, the mediolateral axes of both joints are slightly offset, preventing sagittal plane rotation across the transverse tarsal joint complex. In chimpanzees, however these axes are aligned to create a single mediolateral transverse tarsal joint axis of rotation. As a consequence, Elftman and Manter argued, chimpanzees possess greater sagittal plane mobility at this joint complex than humans.

Among the tarsometatarsal joints, chimpanzees and other African apes diverge most obviously and dramatically from humans at the first metatarsal-medial cuneiform joint. African apes possess a highly curved joint surface that, when combined with the strong torsion of the first metatarsal, enables a larger range of motion and opposability of the hallux against the lateral digits. Humans, in contrast, possess a flat, forward facing joint surface that is designed to restrict motion between the hallux and the other digits. On the lateral side of the foot, chimpanzees possess relatively curved articular surfaces at their cuboid-metatarsal joints (DeSilva, 2010; Proctor, 2013), which have been argued to contribute to midfoot sagittal plane mobility. Humans,

² Use of the terms ‘pronation’ and ‘supination’ follows the definitions provided by Root et al. (1977). Pronation is a combination of motion in three planes: eversion (coronal plane), abduction (transverse plane), and dorsiflexion (sagittal plane). Supination is a combination of inversion (coronal plane), adduction (transverse plane), and plantarflexion (sagittal plane).

in contrast, possess relatively flat joint surfaces, which are thought to improve joint stability but limit mobility.

Finally, several aspects of metatarsophalangeal joint morphology have been attributed to functional differences in humans and chimpanzees. Human metatarsal heads are characterized by ‘dorsal doming’, in which the articular surface projects dorsally above the superior surface of the metatarsal head (Latimer and Lovejoy, 1990a). This feature is thought to enable humans to accommodate high metatarsophalangeal joint dorsiflexion angles at push-off during walking. Chimpanzees, on the other hand, possess more plantarly oriented heads, which are thought to provide greater stability during pedal grasping. Additionally, humans possess mediolaterally broad dorsal surfaces of their metatarsal heads, which are thought to result in tightening of collateral ligaments to close-pack these joints at high dorsiflexion angles (Susman et al., 1984). Chimpanzees, however, possess superiorly narrow metatarsal heads, suggesting reduced ability to accommodate high forces during dorsal excursion. Additionally, the articular surfaces of the phalangeal bases in humans present a relatively dorsal ‘cant’, increasing dorsiflexion range of motion at the metatarsophalangeal joints (Stern and Susman, 1983; Latimer and Lovejoy, 1990a). The proximal phalangeal bases are generally less canted in chimpanzees, potentially reflecting less use of these joints in high dorsiflexion angles during locomotion.

1.2.2 Soft Tissue Anatomy

The most obvious, major difference in the soft tissue anatomy of the feet of humans and chimpanzees concerns the plantar aponeurosis. In humans, this structure is a thick, broad ligamentous band that attaches posteriorly to the medial process of the calcaneal tuberosity, and courses anteriorly towards the digits. Along the way it gives off superficial fibers that insert onto the skin of the sole of the foot, and deeper fibers that cross the metatarsophalangeal joints and attach to the plantar surfaces of the proximal phalanges. In humans, this structure functions as a truss, tightening as the digits are dorsiflexed, such as occurs during push-off in a walking step. This tightening of the aponeurosis pulls the metatarsal heads inferiorly and posteriorly relative to the calcaneus, supinating the foot and raising the longitudinal arch. This is the so-called ‘windlass mechanism’ of the human foot, first described by Hicks (1954). The plantar aponeurosis is present in chimpanzees (Swindler and Wood, 1973), but is much thinner than that in humans (Susman, 1983; pers. obs.). Consequently, chimpanzees are not expected to exhibit a windlass mechanism during push-off.

Chimpanzees and humans possess similar pedal ligaments, but one major difference is worth noting: A long plantar ligament is present in both species, but in humans it includes a posterior portion that is absent in chimpanzees³ (Gomberg, 1985). The anterior portion that is present in both species runs between the cuboid and metatarsal bases, stabilizing the tarsometatarsal joints. The posterior portion in humans runs from the plantar surface of the calcaneus to the cuboid, and is expected to restrict motion at the calcaneocuboid joint. The absence of this portion in chimpanzees is likely to result in relatively greater overall calcaneocuboid joint mobility.

Lastly, the intrinsic foot musculature of humans and chimpanzees presents several notable distinctions. Chimpanzees typically lack a quadratus plantae (flexor accessorius) muscle (Susman, 1983), which in humans arises from the calcaneal tubercles and inserts onto the tendon

³ Lewis (1980b) suggests that the anterior portion of the long plantar ligament is actually part of the short plantar ligament in non-human primates.

of flexor digitorum longus. This muscle is believed to assist flexor digitorum longus in resisting toe dorsiflexion during push-off (Reeser et al., 1983), as well as help to regulate longitudinal arch stiffness across stance phase (Kelly et al., 2014). With regard to muscle size, humans possess a larger flexor hallucis brevis muscle than chimpanzees, presumably for resisting dorsiflexion and generating power at the first metatarsophalangeal joint during push-off (Aiello and Dean, 1990). Chimpanzees, however, possess a much larger adductor hallucis muscle than humans, which likely helps to provide a strong grasp between the hallux and the lateral digits.

1.3 Locomotion Studies

In addition to documenting differences in human and chimpanzee foot anatomy, a number of studies have investigated differences in foot function by taking experimental approaches. These studies have generally used two different techniques: video-based quantification of joint motion, and pedobarographic recordings of plantar pressure distributions. Because the first experimental analysis of chimpanzee foot mechanics used the latter approach, I will begin my discussion of these studies there.

1.3.1 Plantar Pressure Distribution

Elftman and Manter (1935b) used a specially developed apparatus to capture relative pressure distributions under the feet of humans and one chimpanzee in real time during bipedal locomotion. Subjects from both species contacted the ground with the heel first, but the chimpanzee differed from humans by placing the entire lateral edge of its foot against the ground, before rotating it to bring the medial side of the foot into contact as well. From this point forward, the chimpanzee exhibited a similar center of pressure trajectory to that of humans. Elftman and Manter recorded an increase in pressure under the base of the fifth metatarsal in the chimpanzee subject following heel lift, which they related to a midfoot dorsiflexion motion they observed during this period that resulted in the forefoot briefly maintaining contact with the ground after the heel had been lifted. This motion has since come to be called the ‘midtarsal break’, and was initially thought by Elftman and Manter to be occurring at the transverse tarsal joint complex of the foot.

Wunderlich (1999) investigated plantar pressure distributions in two chimpanzee subjects using a flexible mat with capacitor-based pressure sensors. This equipment enabled her to investigate quadrupedalism on both terrestrial and horizontal pole substrates. Her results from terrestrial quadrupedalism experiments broadly reflected the findings of Elftman and Manter, whereas the subjects in her study used considerably different pressure distribution patterns during pole walking. On the pole, they exhibited only brief, minimal heel contact, but subjected the medial midfoot and forefoot to high pressures throughout most of stance. Vereecke et al. (2003) also used pressure sensing technology to measure pressure distribution patterns in bonobos during terrestrial quadrupedalism and bipedalism. The major difference between their findings and those of Wunderlich was higher pressures on the lateral side of the foot across stance, including around push-off. From this finding, they concluded that bonobos contact the ground with a highly inverted foot, and maintain a relatively inverted foot posture across stance phase, resulting in a more laterally located center of pressure during most of stance than in humans. They also argued, on the basis of their pressure data, that the midtarsal break actually occurs at the cuboid-metatarsal joints, as opposed to the transverse tarsal joint complex.

Bates et al. (2013) quantitatively compared the bonobo plantar pressure data collected by Vereecke et al., along with data collected from a juvenile orangutan (Crompton et al., 2012), to

data from a large sample of human steps. They found a small amount of overlap between human and nonhuman data in pressure variables that they assumed to be related to the presence of a midtarsal break. Based on this result, they argued for the presence of previously unrecognized similarity in human and non-human ape midfoot mechanics.

1.3.2 Joint Kinematics

Although a number of studies have provided qualitative descriptions of differences in human and non-human great ape foot joint motion (Wood Jones, 1917; Morton, 1922, 1924; Weidenreich, 1923; Elftman and Manter, 1935b; Tuttle, 1970; Jenkins, 1972; Susman, 1983; Gebo, 1992), only recently have studies attempted to quantify these differences. Several studies have measured sagittal plane motion at the ankle during terrestrial locomotion: D’Août et al. (2002) measured two-dimensional (2-D) motion during both bipedal and quadrupedal walking in bonobos, but without using markers to track segment positions. Pontzer et al. (2014) measured 2-D marker-based kinematics in chimpanzees during both gait types, and O’Neill et al. (2015) captured 3-D hind limb joint motion with a model-based approach to kinematics during bipedal walking in humans and chimpanzees. O’Neill et al. found that chimpanzees typically use much greater ankle ranges of motion during a bipedal step than humans. DeSilva (2009) measured 2-D ankle motion in videos of wild chimpanzees climbing vertically oriented arboreal supports. He found that chimpanzees use maximum dorsiflexion angles during this behavior that are outside of the ankle range of motion typically reported for humans. However, Venkataraman et al. (2013) measured similar maximum ankle dorsiflexion angles in human Twa foragers during climbing bouts to obtain wild honey, and argued from this result that the chimpanzee ankle is *not* uniquely adapted for climbing.

In an investigation of the midtarsal break, DeSilva (2010) measured dorsiflexion angles at the midfoot joints following heel lift in apes and several Old World monkey species from videos recorded at zoos. He found that non-human primates (including chimpanzees) exhibit considerably higher peak dorsiflexion angles following heel lift than humans, with more of the midfoot break motion occurring at the cuboid-metatarsal joints than at the transverse tarsal joint complex (c.f. Vereecke et al., 2003). Several studies have subsequently quantified primate midfoot joint motion passively. Using cineradiographic techniques, Thompson et al. (2014) measured a relatively high talonavicular joint range of motion in anesthetized chimpanzee subjects, but a relatively low calcaneocuboid joint range of motion. Greiner and Ball (2014) used 3-D kinematic techniques to measure sagittal plane ranges of motion in the midfoot joints of cadaveric primate specimens using bone pin-mounted markers. They found general overlap in sagittal plane ranges of motion in humans and chimpanzees at the transverse tarsal and cuboid-metatarsal joints.

Finally, Griffin et al. (2010) used markerless kinematic techniques to measure metatarsophalangeal joint dorsiflexion angles in bonobos during terrestrial locomotion. In a small sample of steps, they found significantly lower peak dorsiflexion angles in bonobos at the first two metatarsophalangeal joints than in humans. However, they were not able to measure motion at joints 4 or 5, and their data suggested the potential for overlap between species at joints 2 and 3 given a larger sample of bonobo steps.

1.4 Early Hominin Fossils

Numerous researchers have taken the findings of these anatomical and experimental studies and used them in functional analyses of fossil hominin foot bones. These analyses are

often used to reconstruct gait and locomotor behaviors in early hominins, as well as develop narratives about human foot evolution. Here I will provide a very brief overview of the pedal material in the early hominin fossil record, and the functional interpretations of this material. I will focus on the fossil material from the Pliocene and early Pleistocene; few relevant hominin fossils dating before this time frame have been found, and the fossils found later are already quite human-like in overall morphology⁴ (Day and Napier, 1964; Trinkaus, 1983; Pontzer et al., 2010). This section will by no means be a comprehensive review of the fossil hominin pedal remains from this time period. Instead, I will touch briefly on the species and features relevant to the focus of this dissertation.

Ardipithecus ramidus. At 4.4 Ma, *Ar. ramidus* is the earliest fossil hominin for which a significant percentage of the foot skeleton has been recovered. This species is characterized by a strikingly non-human great ape-like hallux that is widely abducted and fully opposable against the lateral digits (Lovejoy et al., 2009). Torsion of the first and second metatarsals is similar to that in African apes, and confirms the use of hallucal grasping in this species. The talus presents a superior trochlear surface that slopes medially to suggest a relatively wider stance width during locomotion than in humans (White et al., 2015). The midfoot region, including the cuboid, navicular, and cuneiform bones, is intermediate in length between those of humans and chimpanzees. The cuboid presents a calcaneal process similar in morphology to that of chimpanzees and other African apes. The lateral metatarsal heads are dorsally-domed, indicating human-like dorsiflexion angles at toe-off. However, the first metatarsal head displays no such doming, suggesting a hallux that is less involved in propulsion, but helps to maintain balance during single limb-support. The proximal and intermediate phalanges are strongly curved, as in non-human great apes.

Lovejoy et al. (2009) have interpreted the foot of *Ar. ramidus* as being well-adapted for both powerful propulsion during terrestrial bipedalism, and arboreal substrate grasping during above-branch locomotion. They argue that it is not well adapted, however, for climbing large diameter supports, or for use in quadrumanous suspensory postures. So far, no independent analysis of the pedal fossil material to challenge or support this view has been published.

Australopithecus afarensis. The most extensive fossil hominin foot assemblage from the Pliocene of east Africa belongs to *Australopithecus afarensis*. Tali attributed to this species present trochlear surfaces similar to those of humans, indicating similar stance width and talocrural joint kinematics. The posterior subtalar articular surfaces of calcanei present similar radii of curvature to those measured in humans, suggesting the use of this joint in a relatively a limited range of inversion-eversion postures (Latimer and Lovejoy, 1989; Prang, 2016; but see Stern, 2000). The calcaneal tuber is very robust (Latimer and Lovejoy, 1989; Prang, 2015), and possesses a moderately developed lateral plantar process. However, the peroneal trochlea and navicular tuberosities are both large and chimpanzee-like (Stern and Susman, 1983; Harcourt-Smith and Aiello, 2004). The cuboid-metatarsal joints present flattened articular surfaces, similar

⁴ The one major exception to this statement concerns the pedal material attributed to *Homo floresiensis* from the late-Pleistocene, which presents a bewildering combination of traits that are neither human- nor chimpanzee-like in their overall morphology (Jungers et al., 2009). Due to the uncertainty concerning the phylogenetic position of this species, I will refrain from discussing it here.

to those of humans, potentially suggesting the absence of a midtarsal break in this region of the foot (DeSilva, 2010; Ward et al., 2011; Proctor, 2013). The metatarsal heads are dorsally domed, and the proximal phalanges present dorsally canted bases, indicating human-like dorsiflexion during toe-off (Stern and Susman, 1983; Latimer and Lovejoy, 1990a). The proximal and intermediate phalanges again present non-human great ape-like curvature, indicating use during arboreal support grasping. Finally, the medial cuneiform-first metatarsal articular facet is slightly curved in a manner indicative of some hallucal abductability (Stern and Susman, 1983; Berillon, 1999; Harcourt-Smith and Aiello, 2004; Proctor et al., 2008; Proctor, 2010; but see Latimer et al., 1990b).

Functional interpretations of *Au. afarensis* pedal remains are remarkably divergent. Some see the *Au. afarensis* foot as essentially human-like, suggesting human-like mechanics and a commitment to terrestrial bipedality (Latimer et al., 1987; Latimer and Lovejoy, 1989, 1990a; b; Ward et al., 2011). Others see the foot as intermediate between those of humans and non-human great apes, and therefore retaining some adaptations to arboreal substrate use (Stern and Susman, 1983; Susman et al., 1984; Deloison, 1985; Sarmiento and Marcus, 2000; Proctor et al., 2008). Divergences of opinion over the functional affinity of the *Au. afarensis* foot are based on intractable disagreements concerning certain morphological features, and are therefore unlikely to be resolved in the near future without the discovery of new fossils. Nevertheless, the *Au. afarensis* foot was almost certainly more human-like than that of *Ar. ramidus*, but at the very least appears to have retained several features that are likely adaptive for arboreal locomotion.

Laetoli footprints. The earliest non-osteological evidence for bipedal locomotion in fossil hominins comes from a 3.66 My old footprint trail found at the Laetoli site in Tanzania (Leakey and Hay, 1979). These footprints loosely resemble those of humans, and were clearly left by multiple bipedal individuals, although the overall lower limb kinematics and foot morphology of these individuals remains controversial. A number of authors have suggested that the makers of these trails possessed essentially human-like feet and bipedal walking gaits on the basis of overall shape and depth profiles of the footprints (Day and Wickens, 1980; White and Suwa, 1987; Tuttle et al., 1991; Raichlen et al., 2010; Crompton et al., 2012). These authors have pointed to such features of the footprints as their relatively deep first toe and heel impressions, and shallow medial midfoot impressions in support of their claims. Others have argued that the Laetoli print-makers possessed foot morphology and bipedal limb mechanics intermediate between those of humans and African apes (Stern and Susman, 1983; Deloison, 1991; Bennett et al., 2009), citing such features as relatively shallow medial forefoot impressions, long lateral toe impressions, and slightly abducted hallux impressions.

Controversy also exists regarding the species attribution of the Laetoli print-makers. Given their age, and the foot mechanics inferred from their depth profiles, most assume *Au. afarensis* to be responsible for the footprints (Stern and Susman, 1983; White and Suwa, 1987; Crompton et al., 2012). However, several authors have suggested that the Laetoli footprints point to a hominin with more human-like foot morphology than that indicated by pedal material attributed to *Au. afarensis* (Tuttle et al., 1991; Harcourt-Smith and Aiello, 2004). These authors therefore see the Laetoli prints as evidence of at least two contemporary hominin species with different foot biomechanics in the middle Pliocene of East Africa.

Burtele hominin foot. Haile-Selassie et al. (2012) came to a similar conclusion based on their discovery of 3.4 My old associated forefoot bones (BRT-VP-2/73) from the Burtele locality

in Ethiopia. These specimens lack a species designation, although Haile-Selassie et al. (2015, Supplementary Note 1) have suggested that they may belong to *Au. deyiremeda*. The age of these specimens places them contemporary to *Au. afarensis*, but Haile-Selassie et al. (2012) argue that they must be from a different species, primarily on the basis of preserved morphology that clearly indicates the presence of an opposable, widely abducted hallux. Several other features of these specimens are reminiscent of non-human African great apes, including relative hallux length and phalangeal curvature. However, on the basis of metatarsal head doming and certain bony proportions, Haile-Selassie et al. (2012) maintain that this foot belonged to a hominin biped with *Ar. ramidus*-like foot mechanics. Regardless of its implications for hominin foot evolution, the Burtele foot clearly belonged to some type of fossil hominoid with powerful pedal grasping capabilities.

South African hominins. Due to the general lack of associated fossil specimens from South African sites, and the difficulty in assigning precise age estimates to these specimens, I will not discuss most of the early hominin pedal material from South Africa in much detail. Briefly, what has been found consists largely of metatarsals with heads that present human-like dorsal doming, but lack mediolateral expansion of their dorsal articular surfaces (Susman and Brain, 1988; Susman and de Ruiter, 2004; DeSilva et al., 2012). Tali attributed to *Au. africanus* present talar head morphology thought to be indicative of high midfoot joint mobility (Zipfel et al., 2011), but fourth metatarsals attributed to this species indicate a relatively stiff cuboid-metatarsal joint (DeSilva, 2010; Proctor, 2013). Several first metatarsals preserve tarsometatarsal joint morphology that is intermediate between that of humans and African apes, and thus suggests some retained abductability at this joint (Clarke and Tobias, 1995; Proctor, 2010). One of these fossils belongs to the so-called ‘Little Foot’ specimen (StW 573), for which hallux abductability has been disputed (Stern, 2000; Harcourt-Smith and Aiello, 2004; Kidd and Oxnard, 2005).

The one securely dated South African fossil hominin assemblage in which significant foot material has been preserved belongs to *Australopithecus sediba*. This species preserves a remarkably chimpanzee-like calcaneus, marked by a gracile calcaneal tuber, a large peroneal trochlea, and the absence of a lateral plantar process (Zipfel et al., 2011; Prang, 2015). Additionally, it possesses subtalar, talonavicular, and cuboid-metatarsal joint articular surface morphology that is described as non-human African ape-like (Zipfel et al., 2011; DeSilva et al., 2013; Prang, 2016). These features have been interpreted as indicating that *Au. sediba* retained a significant arboreal component in its locomotor repertoire (Zipfel et al., 2011), and walked with a gait characterized by ‘hyper-pronation’ of the rearfoot (DeSilva et al., 2013).

The only other South African fossil hominin of potential relevance to this overview is the recently described *Homo naledi* (Berger et al., 2015), which preserves a complete assemblage of foot bones. The foot of this hominin is remarkably human-like in almost all aspects (Harcourt-Smith et al., 2015), but because the representative fossils remain undated, and the phylogenetic position of this species is still unresolved, it is difficult to discuss the evolutionary implications of this material in a broad context.

1.5. Study Objectives

1.5.1 Three-Dimensional Kinematics

For each of the fossil hominin species just described, reconstructions of foot mechanics, and consequently locomotor behavior, are based on comparative analyses of pedal morphology with humans and other great apes. In general, more human-like morphology is interpreted as indicating more human-like mechanics. However, interpreting less human-like morphology leads to a conundrum: What are the resulting foot mechanics, and what do they indicate about behavior? Because only a handful of quantitative studies of non-human great ape foot mechanics have been carried out, much about the actual function of the intrinsic foot joints in these species remains a mystery.

So far, precise, marker-based 3-D kinematics have only been captured for a single joint associated with the foot in a non-human great ape: the ankle joint in chimpanzees (O'Neill et al., 2015). Additionally, these data have *only* been collected during bipedal locomotion on the ground. The sole study to have measured ankle motion on an arboreal substrate involved wild subjects, and so could not use markers to accurately measure joint motion. Beyond the ankle, only two studies have attempted to quantify motion at the intrinsic joints of the foot in non-human great apes (DeSilva, 2010; Griffin et al., 2010), but these studies were on zoo animals and so were unable to use a marker-based approach to kinematics. Marker-less kinematic approaches entail large error in joint angle calculation, because joint center of rotation and relative bone position must be guessed in individual static images. This can be especially problematic for the small joints of the foot, where joint location is very difficult to determine from external views (Bates et al., 2013). Additionally, the abundant body hair and plantar soft tissue in non-human primates makes determining actual segment position from these images very difficult. Two of the studies just mentioned (DeSilva, 2009, 2010) were burdened by the additional error source of using just a single camera view to capture 2-D joint motion. Accurate 2-D kinematics require that motion occur entirely in a plane parallel to the plane of the camera view (Robertson and Caldwell, 2004). Given the opportunistic nature of data collection in zoo and wild settings, this requirement was unlikely to have been met in these studies.

Under these criteria, we still lack accurate kinematic data from most of the intrinsic foot joints that are critical to overall foot mechanics, including the subtalar joint, transverse tarsal joint complex, and tarsometatarsal joints. These joints present axes of rotation outside of the body's cardinal planes, and typically undergo relatively small ranges of motion that are difficult to quantify without a fine-scale approach to motion capture. Accurate quantification of intrinsic foot motion requires marker-based 3-D kinematics, an approach that has become common in human foot mechanics studies (see Rankine et al., 2008 and references therein).

The calculation of 3-D kinematics involves the placement of markers on known anatomical landmarks that can be used to represent segment positions. Subjects are then filmed travelling through a space using two or more stationary cameras whose internal parameters are calibrated relative to one another. A triangulation algorithm is applied to calculate the 3-D position of markers within the calibrated viewing space based on 2-D marker positions in individual camera views. Using the 3-D marker positions, joint angles can be calculated as the angle between two segments defined by the markers. Joint angles calculated in such a way will provide a single angle without reference to any of the body's cardinal planes. However, if three or more markers are placed on articulating segments, triplanar motion of one segment relative to the other can be computed using Cardan or helical angle approaches (Hamill and Selbie, 2004). The use of such techniques is ideally suited for quantification of intrinsic foot motion, as it allows for the capture of non-sagittal plane motion in joints with relatively small excursion ranges of motion.

Although the foot is modeled as a single, rigid segment in many 3-D human gait studies, researchers have developed detailed, multi-segment models of the foot over the past two decades in order to investigate specific questions about intrinsic foot joint function (see Rankine et al., 2008, and references therein). These models divide the foot into regions, or ‘segments’, which are functionally meaningful with regard to the major joints of the foot. Typically, these models consist of a rearfoot segment to represent the calcaneus, and one or more additional segments to represent the other regions of the foot, including the midfoot and forefoot. These models enable measurement of motions at joints that are otherwise difficult to capture, such as the subtalar and transverse tarsal joints. Such multisegment modeling approaches have enabled researchers to address longstanding questions about human foot mechanics, such as intrinsic joint axes, joint contributions to longitudinal arch function, and joint functional impairment in pathological conditions such as flat foot (e.g., Hunt and Smith, 2004; Levinger et al., 2010; Hösl et al., 2014).

Marker-based 3-D kinematics provide a powerful tool through which we can address longstanding questions about differences in human and non-human great ape foot function. However, no previous study has had the means by which to capture 3-D foot kinematics in non-human great apes during locomotion. For this dissertation, I was able to work with healthy chimpanzee subjects in a laboratory fully equipped for high-speed motion capture, which enabled me to collect detailed 3-D kinematic data concerning the ankle and intrinsic foot joints during locomotion on different substrates. These data allowed me to address questions about function of the intrinsic foot joints in non-human apes during locomotion that were inaccessible to previous studies.

I also had access to a pressure-sensing platform that enabled me to measure plantar pressure distributions during terrestrial locomotion in the chimpanzee subjects. Plantar pressure data have been collected and reported for non-human apes in several previous studies (Wunderlich, 1999; Vereecke et al., 2003, 2005; Crompton et al., 2010), but none of these studies have measured 3-D kinematics simultaneously. Therefore, these studies have relied on assumptions about the relationship between plantar pressure variables and intrinsic joint motion to interpret their findings in the context of foot mechanics during locomotion. By capturing both pressure and kinematic data simultaneously in this investigation, I was able to test these assumptions, and develop a more comprehensive understanding of chimpanzee foot function.

1.5.2 Questions and Objectives

The present study will be guided by three major questions, which are described below. A statement of the study objective that will be used to address the research question follows each description.

Question 1: To what extent are the chimpanzee foot and ankle joints adapted for locomotion on arboreal substrates versus locomotion on terrestrial substrates?

Because they present several obvious adaptations to arboreal locomotion (i.e., grasping hallux, long pedal digits), as well as dramatic architectural differences from the feet of humans, chimpanzee feet are often assumed to be optimally adapted for arboreal locomotion. The midtarsal break that occurs in the chimpanzee midfoot during travel on the ground is thought to be emblematic of this maladaptation to terrestrial substrates. However, the chimpanzee locomotor repertoire is dominated by terrestrial locomotion in the wild, so one might expect that a foot poorly suited to this behavior would be a major detriment to overall fitness. To explore this paradox, we need a better understanding of actual chimpanzee foot mechanics during travel

on arboreal substrates that are representative of those encountered in the wild. This includes a horizontally oriented substrate to simulate above-branch locomotion, and a vertically oriented substrate to simulate vertical climbing. Foot kinematics during travel on these supports can then be compared to those captured during terrestrial substrate walking to assess the extent to which overall foot function on the ground is compromised by adaptation to arboreal locomotion (or *vice versa*). These data can also be used to refine hypotheses concerning morphological adaptation to arboreal locomotion in the chimpanzee foot.

Objective 1: In this dissertation I will quantify chimpanzee ankle and intrinsic foot joint kinematics during locomotion on horizontally and vertically oriented arboreal substrates, and compare these to similar data collected during quadrupedal locomotion on the ground.

Question 2: Given the dramatic differences in human and chimpanzee foot anatomy, how do the foot mechanics of these species differ during terrestrial locomotion under similar conditions?

The unique anatomy of the human foot is thought to be optimally adapted for the specific mechanical challenges of bipedal locomotion. The chimpanzee foot, on the other hand, lacks many of the bipedalism-related adaptations of the human foot (e.g., adducted first metatarsal, longitudinal arch), and so overall foot mechanics during terrestrial locomotion are expected to differ markedly between species. Comparing chimpanzee and human foot joint kinematics when both species are walking bipedally will provide the most direct means of determining the relationship between the anatomical differences in the feet of these species and their consequence on function during a given task. This investigation will provide insight into the question of how human foot function is uniquely adapted for bipedal locomotion. It will also be of use in reconstructions of bipedal gait in fossil hominins preserving chimpanzee-like pedal joint morphology.

Objective 2: In this dissertation I will quantify chimpanzee and human foot joint kinematics during bipedal locomotion on a terrestrial substrate using identical experimental protocols, and assess interspecies differences in foot function.

Question 3: Are chimpanzee plantar pressure distribution patterns that are measured during locomotion actually reflective of intrinsic foot joint kinematics?

Since the pioneering work of Elftman and Manter (1935a; b) plantar pressure distributions recorded from walking steps in non-human great apes have been assumed to be reflective of the kinematics of the intrinsic foot joints. Elftman and Manter originally identified the presence of the midtarsal break from their chimpanzee pressure recordings, and the location of the joints at which this break occurs was later revised by Vereecke et al. (2003) using bonobo pressure measurements. Recently, Bates et al. (2013) argued for similarity in human and non-human great ape foot kinematics on the basis of overlap between species in midfoot plantar pressure variables. All of these studies have assumed a link between foot kinematics and plantar pressure, but no study so far has quantitatively tested the presence of such a link in non-human great apes. Establishing this link could be of critical importance to the future of great ape functional morphology studies. Detailed 3-D kinematics require experimental data collection in a controlled laboratory setting, which is unlikely to be feasible with non-human ape subjects in the foreseeable future. Plantar pressure data, however, can be collected in zoo settings (Vereecke et al., 2003, 2005; Crompton et al., 2012; Matarazzo, 2013), and so there are likely to be more opportunities to obtain these data from non-human great apes. By collecting pressure and

kinematic data simultaneously, this investigation will improve our ability to interpret ape plantar pressure data in past and future analyses, and determine whether the latter can be used to predict the former. Additionally, these data may be useful in the interpretation of fossil hominin footprints, such as those from Laetoli. Previous studies have used plantar pressure data from humans and great apes to aid functional interpretations of fossil hominin footprints (Raichlen et al., 2010; Crompton et al., 2012). By more firmly establishing the relationship between pressure and kinematic variables, this study will improve hominin gait reconstructions that are based on footprints.

Objective 3: In this dissertation I will collect both plantar pressure and 3-D foot joint kinematic data simultaneously in chimpanzees, and assess the degree to which pressure data can be used to predict intrinsic foot motion.

1.5.3 Outline of Dissertation

Chapter 2 of this dissertation will provide a detailed description of the methods used to collect the 3-D kinematic data used in Chapters 3-5. Subsequent chapters will only describe methodology specific to the analysis used in that chapter alone. I will carry out Objectives 1, 2, and 3, in Chapter 3, 4, and 5, respectively. These chapters will include background and hypotheses specific to the objective, as well as a discussion of the results of the investigation carried out in the chapter. Chapter 6 will provide a summary and synthesis of the major findings of Chapters 3-5, as well as a discussion of the implications of these findings for human evolution and the hominin fossil record. I will end Chapter 6 with rumination on future avenues of investigation for the questions raised by the research in this dissertation.

Chapter 2

Methods

This chapter will provide an overview of the data collection and analysis methods used in this study. I use slightly different statistical procedures in each individual part study, so these will be described in their corresponding chapters.

2.1 Subjects

2.1.1 Chimpanzee subjects

The Stony Brook Institutional Animal Care and Use Committee approved of all experimental procedures used in this study involving the chimpanzee subjects. I collected data from two male subadult chimpanzees (*Pan troglodytes*), who will hereafter be referred to as Chimp H and Chimp L. They were housed and maintained at the Stony Brook University Primate Locomotion Laboratory (Stony Brook, NY). This facility is equipped with three large rooms that served as the primary living space for these animals. These rooms were outfitted with ropes, hammocks, fencing, and various other objects to provide a varied and stimulating environment. The subjects interacted daily with an animal trainer in their rooms, and engaged in regular training sessions in experimental rooms equipped with wooden poles that they could walk and climb on. Based on the sizes of their enclosures, their high activity levels, and their exposure to various substrates, these animals likely received enough physical stimulation to allow for normal development of locomotor skills and postcranial morphology. Additionally, these animals were accustomed to traveling on both arboreal and terrestrial substrates prior to experimental data collection.

The chimpanzee subject data used in this study were collected over a two-year period, so subject ages and body sizes differed across experiments. A summary of subject ages and masses is provided in Table 2.1. During data collection, the average age and mass were 7.6 years and 43.6 kg for Chimp H, and 7.9 years and 43 kg for Chimp L. In the wild, chimpanzees typically do not reach full physical maturity until 15-16 years of age (Nishida, 2012). Adolescence, defined by testicle descent, is usually reached around 9 years. However, both subjects in this study had achieved testicle descent prior to the initiation of data collection, and were close to the average body mass reported for wild adult male chimpanzees throughout the duration of this study (Smith and Jungers, 1997). This is not necessarily surprising, because studies of orangutans have suggested that great apes reach physical maturity earlier in captivity than in the wild (Fooden and Izor, 1983). Therefore, I assume that the locomotor biomechanics of the subjects in this study are representative of those of adult chimpanzees. In support of this assumption, studies have documented similar center of mass mechanics (Kimura, 1996) and locomotion energetics (Taylor and Rowntree, 1973; Sockol et al., 2007) in subadult and adult chimpanzees. Personal inspection of radiographs of the feet of both subjects indicated incomplete epiphyseal fusion in several locations (metatarsal heads, phalangeal bases, calcaneal

tuber), but otherwise complete development of all foot bones. Therefore, I also expect the foot mechanics of the study subjects to be representative of those of adult chimpanzees.

2.1.2 Human subjects

The Stony Brook University Institutional Board of Review approved of all procedures involving human subjects that were implemented in this study. The human subject sample consisted of five adult males (Age = 27.8 ± 1.1 ; Body Weight = 68.2 ± 5.9) who were Stony Brook University students recruited by word-of-mouth (Table 2.2). Subjects reported no significant foot injury or pathology that would affect walking gait within one year prior to experimental data collection. I also assessed arch height to ensure subjects did not have unusually high or low arches that could indicate congenital or pathological deformity. To do so, I used the arch height index, developed by Williams and McClay (2000), which is calculated as medial foot height at midfoot length divided by medial foot length excluding the hallux. All subjects possessed longitudinal arches with arch height indices (0.35 ± 0.01 average) within one standard deviation of the mean reported for adult males (0.34 ± 0.032 ; Butler et al., 2008).

2.2 Range of motion measurements

I measured range of motion in the chimpanzee subjects at the talocrural joint, the subtalar joint, and three metatarsophalangeal joints: 1, 2, and 5. The purpose of these measurements was to provide a reference point for the amount of motion measured during experiments relative to the total range of motion at these joints. All measurements were made from photographs that were taken while the subject was fully anesthetized using isoflurane gas. For these photographs, joints were passively moved to the extremes of their ranges of motion, and then photographed such that the plane of the angle being measured was normal to the camera view. For each motion at each joint, this procedure was carried out 2-3 times. Photographs were imported into ImageJ software (Schneider et al., 2012), where I measured joint angles as the angle between points drawn on the leg and foot (see below). Repeated measurements were averaged to calculate range of motion. Below I describe in further detail how joints were positioned for range of motion measurements.

For the talocrural joint, I drew two small white dots on the lateral surface of the leg to form a line representing the long axis of the fibula, and two white dots on the skin overlying the lateral side of the calcaneus to form a line parallel to the plantar surface of the foot (Fig. 2.1). I photographed the foot in maximum dorsiflexion with the knee joint flexed roughly 45° to prevent tightening of the gastrocnemius from limiting joint excursion (Fig. 2.1a). I then photographed the foot in maximum plantarflexion (Fig. 2.1b). In these photographs, the tip of the lateral malleolus was considered to be the joint center of rotation.

For the subtalar joint, I followed the standard protocol for measuring subtalar range of motion in humans using a goniometer (Elveru et al., 1988a; b). I positioned the subject in a prone position and drew two points on the posterior surface of the leg to describe a line that divided the leg evenly into medial and lateral halves. I also drew two points on the posterior surface of the calcaneus below the insertion of the triceps surae muscles to divide the heel evenly into medial and lateral halves. Lastly I drew a point at a location where an imaginary line connecting the medial and lateral malleoli intersected the center of the posterior ankle joint. This point was used to represent the subtalar joint center of rotation. The joint was photographed in maximum inversion and eversion (Fig. 2.2).

For metatarsophalangeal joints 1 and 2, I drew points over the dorsoplantar center of the medial surfaces of the metatarsal base and proximal phalanx distal end, as determined *via* palpation. I also drew a point over the medial surface of the dorsoplantar center of the metatarsal head, which I used to represent the approximate joint center of rotation. I photographed these joints in maximum dorsiflexion and measured the supplement of the angle formed by connecting the points (Fig. 2.3). I carried out the same procedure for metatarsophalangeal joint 5, but drew points over the *lateral* surfaces of the metatarsal and proximal phalanx.

2.3 Kinematics Data Collection

Marker Set

Prior to data collection, I applied markers to the legs and feet of subjects to measure 3-D kinematics. Markers were painted onto subjects as ~ 1 cm diameter circles using non-toxic paint that was colored white or black to maximize contrast with the subject's skin. Chimpanzee subjects were fully anesthetized using isoflurane gas prior to experiments, during which time the appropriate regions of the subject's bodies were shaved and markers were applied.

To measure 3-D motion of the intrinsic foot joints, I developed a marker set that divided the foot into multiple independent 'segments'. In recent years, a number of human studies have used 'multi-segment' foot models to quantify motion of different regions of the foot relative to one another (e.g., Carson et al., 2001; MacWilliams et al., 2003; Jenkyn and Nicol, 2007; Leardini et al., 2007; Rankine et al., 2008; Saraswat et al., 2013). Typically, these models divide the foot into two to four regions, and quantify the triplanar rotation of these regions relative to one another. To measure motion in all three anatomical planes, at least three non-collinear markers must be placed on each segment (Hamill and Selbie, 2004). The three markers used to define a segment are typically called a marker 'triad'. Most investigations of foot kinematics that use multi-segment models involve motion capture systems with six to eight cameras positioned on all sides of the subject. This allows investigators to track marker position on both the medial and lateral sides of the lower limb. However, the motion capture system in the Stony Brook Primate Locomotion Laboratory uses just four cameras directed mainly at the lateral side of the subject's lower limb during locomotion trials. This arrangement made it impossible to track markers on the medial sides of the leg and foot throughout most of a step. Therefore, I had to develop a marker set based on the specifics of the motion capture system that I used, and that would address the particular hypotheses of the study.

The marker set that I developed uses marker triads to define five leg and foot 'segments': the leg (tibia and fibula), the rearfoot (calcaneus), the midfoot (cuboid, navicular, and cuneiform bones), the medial forefoot (metatarsals 2 and 3), and the lateral forefoot (metatarsals 4 and 5). The marker triads used to define these segment were designed with three goals in mind:

First, marker locations were based on readily palpable anatomical landmarks, or were positioned measurable distances from readily palpable anatomical landmarks (see below). These steps were taken to maximize the repeatability of marker application.

Second, I selected marker locations to minimize the effects of soft tissue deformation on marker position. Motion of soft tissues relative to the underlying bone can result in the misrepresentation of bone position in kinematics, and increase the error of angle calculations (Hamill and Selbie, 2004). Leardini et al. (2005) found that relative to other parts of the body, the foot is less susceptible to soft tissue-related kinematics errors because there is little intervening tissue between skin and underlying bone. Motion of surface markers relative to bone

is reported to be typically less than 5mm in the foot (Maslen and Ackland, 1994; Tranberg and Karlsson, 1998), resulting in 2-4° errors in joint angle measurements (Nester et al., 2007a). To minimize these errors, I carefully selected marker locations away from prominent skin folds and regions of substantial subcutaneous soft tissue in both humans and chimpanzees (e.g., the sub-calcaneal fat pad).

Third, I defined triads that would minimize violations of the rigid body assumption of kinematics. This is the assumption that a segment represented by multiple markers does not deform, i.e., the markers associated with a segment do not change their relative distances from one another (Hamill and Selbie, 2004). Rigid body violations frequently occur when the markers in a triad must be placed over more than one bone. This is a major problem for multi-segment foot kinematics, because the bones of the feet provide relatively little surface area for the placement of multiple markers. Lundgren et al. (2008) demonstrated that a small amount of motion occurs between all bones of the foot during normal human walking, so completely avoiding rigid body violations in a multi-segment foot model is impossible without the use of bone pin-mounted marker triads. To address this problem, a number of studies have sought to determine bone combinations that minimize the effects of rigid body violations on surface marker-based multi-segment foot kinematics (Wolf et al., 2008; Okita et al., 2009; Nester et al., 2010; Rouhani et al., 2011). I developed the marker set in this study with guidance from the findings of Nester et al. (2010) and Okita et al. (2009), who captured human foot kinematics using both surface and bone pin-mounted markers simultaneously. The implementation of their results into my marker set design will be described below.

With these goals in mind, I designed the marker triads for the five segments that I defined in this study. Below I describe each triad and how marker locations were determined. In segments requiring the placement of markers over multiple bones, I provide justification for the bone combinations selected (see Figs. 2.4 and 2.5):

1. *Leg*. These marker locations were identified by first palpating the tip of the lateral malleolus, then measuring up from this location and using a stencil to draw in marker locations.

- a. Lateral leg, inferior: 6 cm superior to the tip of the lateral malleolus.
- b. Lateral leg, posterior: 10 cm superior and 4 cm posterior to the inferior leg marker.
- c. Lateral leg, anterior: 10 cm superior and 4 cm anterior to the inferior leg marker.

2. *Rearfoot*. These marker locations were determined by first palpating the position of the peroneal trochlea, then measuring down from this location and using a stencil to draw in marker locations. Marker locations were selected to avoid underlying soft tissue motion caused by the peroneal muscle tendons and deformation of the sub-calcaneal fat pad.

- a. Lateral calcaneus, anterior: 1 cm inferior to the peroneal trochlea.
- b. Lateral calcaneus, posterior: 3 cm posterior to anterior calcaneus marker.
- c. Lateral calcaneus, inferior: 1.5 cm posterior and 2 cm inferior to anterior calcaneus marker.

3. *Midfoot*. For this segment, I placed markers over three bones: the navicular, cuboid, and lateral cuneiform. Nester et al. (2010) found that within the human midfoot, sufficiently low independent motion occurs between the cuboid and navicular such that they can reasonably be considered to represent a single functional unit for the purpose of joint kinematics calculations. These authors also suggested that incorporating the cuneiform bones into midfoot segments was

likely to increase rigid body violation-related errors. However, in order to place three non-collinear points on the midfoot, I had to incorporate the lateral cuneiform into the marker triad. No study has directly tested the motion of the lateral cuneiform relative to the navicular and cuboid during walking. However, based on its wedged articulation with these bones, I assume that its mobility relative to them is limited.

These locations were identified differently in human and chimpanzee subjects. In human subjects, bone positions were identified via palpation using standard clinical techniques (Tixa, 2003). In chimpanzee subjects, marker locations were determined based on radiographs of subjects' feet, which I obtained periodically during the duration of the study period. Briefly, plain film x-rays of subjects' feet were obtained while the subject was anesthetized using a Laseray portable x-ray machine (Xtec Inc., Miami, FL). The machine was set to 70kV with 0.08s exposure time, with an object of known size placed in the x-ray field for scale. From the x-ray images, I measured the distances from the heads of metatarsals 2, 3, and 4 to the navicular, lateral cuneiform, and cuboid, respectively (Fig. 2.6). During marker application, I palpated the metatarsal heads, and measured the distances back to the bones of the midfoot as determined from the x-rays using calipers.

- a. Cuboid: Measured distance posterior to metatarsal 4 head.
- b. Lateral cuneiform: Measured distance posterior to metatarsal 3 head.
- c. Navicular: Measured distance posterior to metatarsal 5 head.

4. *Medial Forefoot.* Okita et al. (2009) and Nester et al. (2010) demonstrated that considerable independent motion occurs between metatarsals 1-3 and metatarsals 4 and 5. Therefore, they suggested dividing the forefoot into medial and lateral segments accordingly. I followed their suggestions, although I did not include metatarsal 1 in my medial forefoot segment for the obvious reason that this bone is highly mobile relative to the other metatarsals in chimpanzees. Marker locations were determined by palpating and measuring back from the metatarsal heads.

- a. Metatarsal 2 head
- b. Metatarsal 2 base: 4 cm posterior to metatarsal 2 head.
- c. Metatarsal 3 base: 4 cm posterior to metatarsal 3 head.

5. *Lateral Forefoot.* These marker locations were determined by palpating and measuring back from the metatarsal heads.

- a. Metatarsal 4 head
- b. Metatarsal 4 base: 4 cm posterior to metatarsal 4 head.
- c. Metatarsal 5 base: 4 cm posterior to metatarsal 5 head.

In addition to the forefoot marker positions described above, I placed markers on the heads of metatarsals 3 and 5 for all experiments. To determine the optimal permutation of markers for the medial and forefoot triads, I calculated joint angles for each possible permutation in several walking trials from human subjects. Differences between triad combinations were minor, but the triads that yielded medial and lateral forefoot joint motion that most closely resembled that measured in other human foot kinematics studies (MacWilliams et al., 2003; Nester et al., 2007b; Lundgren et al., 2008) were selected for this study.

In addition to the marker set described above, I placed markers on the first metatarsal and proximal phalanges of all five digits to capture metatarsophalangeal joint motion. I was unable to

place three non-collinear markers on each digit in a configuration that would enable me to track all three markers during a step. Therefore, I could not measure tri-planar motion at the metatarsophalangeal joints. Instead, I placed markers on the proximal and distal ends of the dorsal surfaces of each proximal phalanx (Figs. 2.4-2.5), such that these markers formed a line to represent a segment for each digit. Motion at the metatarsophalangeal joints was calculated as the angle between these segments and the lines formed by the two markers on their corresponding metatarsals.

Laboratory Setup and Substrates

All locomotion experiments were carried out at the Stony Brook University Primate Locomotion Laboratory, which is equipped with a four-camera high-speed motion capture system (Xcitex Inc., Wolburn, MA). All four cameras are wall-mounted and directed towards a runway at various angles (Fig. 2.7). The runway is a level, 11 m long by 1.2 m wide surface constructed out of wood and linoleum tile. Four BP400600 force plates (AMTI, Watertown, MA) are integrated into the center of the runway, and all four cameras are directed towards these force plates. During experiments, cameras were set to record at a capture rate of 150 Hz with a 3000 ms shutter speed, and force plates were set to record at 1500 Hz. Forces and video recordings were streamed onto solid state hard drives and synchronized using ProCapture software (Xcitex). ProAnalyst was set up to save individual ‘events’ using a trigger system. This feature saves all video and force data 2 seconds prior to and following the moment that the trigger is pressed. This feature allowed me to selectively save data associated with steps that appeared to be suitable for analysis.

For arboreal substrate locomotion experiments, I used a 5 m tall, 15 cm diameter pole that was constructed out of a beech tree trunk with smooth bark. The diameter of the trunk was selected to reflect the size of an arboreal substrate that chimpanzees might travel across in the wild. At 15 cm, this trunk is between the support diameter size ranges that Susman et al. (1980) classified as branches and boughs, and is within one standard deviation of the average support diameter utilized by Mahale and Gombe chimpanzees during non-feeding arboreal locomotion bouts (Hunt, 1992). According to Doran (1992, 1993), Tai adult male chimpanzees spend the majority of their time on these support types climbing or walking quadrupedally. Additionally, travel on these support types constitutes nearly one third of all Tai adult male chimpanzee arboreal locomotor bouts (Doran, 1993). Among Mahale chimpanzees, quadrupedal walking is the most common locomotor mode on this support type, but they also use these supports for climbing (Hunt, 1992).

Square metal plates were affixed to either end of the pole using long screws, and holes were drilled into each corner of the plate for the insertion of bolts. During vertical pole climbing experiments, a portion of the runway adjacent to the force plates was removed, and the top plate of the pole was slid into a metal bracket mounted on the ceiling (Fig. 2.8). Then both top and bottom plates were bolted securely to the floor and ceiling, such that the pole was firm and completely immobile during subject climbing bouts. During horizontal pole walking experiments, the pole was situated parallel to the runway over the force plates, and cinder blocks were placed under the metal squares at either end of the pole to raise it roughly one meter off the ground.

Locomotion Experiments

During terrestrial substrate locomotion experiments, subjects walked across the runway at self-selected speeds. Human subjects were told to ‘warm-up’ by walking up and down the

runway for several minutes prior to recording, and then they were instructed to walk at a pace that felt easy and natural. Human subjects were barefoot and wore shorts so that all markers were visible. Chimpanzee subjects were encouraged to walk bipedally and quadrupedally across the runway by an animal trainer who used fruit and juice rewards. Both subjects had been trained to walk bipedally and had been doing so regularly for roughly two years prior to the initiation of data collection, and so were capable of walking bipedally in a natural and repeatable manner without assistance.

Only the chimpanzee subjects participated in arboreal substrate (horizontal and vertical pole) experiments. During vertical pole experiments, the animal trainer stood on a stepladder to one side of the pole with a fruit reward in a cup attached to the end of the pole. In this manner, the trainer was able to encourage chimpanzee subjects to climb all the way to the top of the pole while keeping their bodies (and hind limbs) in the proper orientation relative to the cameras. During horizontal pole experiments, the animal trainer encouraged subjects to climb onto the pole and walk quadrupedally from one end to the other using fruit and juice rewards. Subjects travelled at self-selected speeds during all experiments.

For analysis, I divided the data into four locomotor modes: bipedal walking on the runway, quadrupedal walking on the runway, quadrupedal walking on the horizontal pole, and climbing on the vertical pole. Because I had to use highly zoomed-in camera views to capture accurate foot kinematics, camera views were too restricted to capture full strides (stance phase and swing phase). Hip, knee, and ankle kinematics change at different walking speeds in humans (Lelas et al., 2003) and chimpanzees (Pontzer et al., 2014), so I suspect that intrinsic foot kinematics differ as a function of speed as well. Previous investigations of chimpanzee and bonobo locomotion have demonstrated a strong correlation between stance phase duration and speed of terrestrial locomotion (Demes et al., 1994; Vereecke et al., 2004; Pontzer et al., 2014). Therefore, for each individual subject in my study, I determined the relationship between stance duration and speed during terrestrial locomotor modes in recording sessions with zoomed-out cameras. From these relationships, I selected for analysis steps with stance durations that corresponded to similar dimensionless speeds across individuals. The methodology used to calculate these relationships will be explained in section 2.5. Unfortunately, I could not standardize speed between locomotor modes, because precise relationships between stance duration and speed have not yet been established for arboreal locomotion. However, I attempted to minimize speed-related effects on variation in foot kinematics during arboreal locomotion by selecting steps with similar stance durations within a given mode for each chimpanzee.

In addition to recording locomotion bouts, subjects were also recorded with their foot and ankle joints placed in a standardized posture to establish a ‘neutral position’ for all joint angles against which angular excursions could be calculated. I defined neutral position as occurring when the leg was positioned at a right angle to the foot, with the plantar surface of the foot in contact with the ground (as in normal standing) (Fig. 2.5). Additionally, for chimpanzee subjects, neutral position involved fully-extended interphalangeal joints, a moderately abducted hallux, and lateral digits that were neither abducted nor adducted with respect to the long axis of the foot. For human subjects, neutral position was recorded while the subject was standing with his foot aligned with the long axis of the runway. Several techniques were attempted to record an adequate neutral position for chimpanzee subjects: First, while still anesthetized following marker application, the subject was positioned sitting in a small chair while the foot was placed in neutral position as described above within the calibrated space. Alternatively, if the subject awoke from anesthesia before an adequate neutral position trial could be recorded, the animal

trainer directed the subject to sit in the chair, and then she placed the subject's foot and leg in neutral position following my instructions. In cases where neither of these techniques yielded an adequate neutral position shot, I used a single frame from the midst of a recorded walking bout in which the subject spontaneously placed its leg and foot into neutral position. Because I could not obtain a sitting neutral position shot in all experiments, I ultimately settled on the latter method to maintain consistency in steps used from different experiments.

During arboreal substrate experiments, in order to obtain a neutral position shot within view of the cameras, the chimpanzee subject was laid on its back on foam blocks perpendicular to the runway while still under anesthesia. The subject's foot and leg were then placed in position with a small jig constructed out of perpendicular wooden boards, which enabled me to place the leg ninety degrees to the foot, with the plantar surface of the foot flat against one of the boards, while the jig was positioned against the pole in the calibrated space.

Lastly, subjects were also recorded standing or sitting motionless on a single forceplate to measure body weight during all experiments. Vertical reaction forces were exported from these recordings and used to calculate subject body weight.

2.4 Kinematics Data Analysis

Camera Calibration

To determine 3-D marker position from recordings, I calibrated a space using a custom-built calibration fixture (Xcitex). The fixture consists of two perpendicular aluminum plates, which together describe a 50 x 60 x 50 cm space, and on each plate are 42 evenly spaced small black circular points (Fig. 2.9). Prior to experimental recording sessions, I placed the fixture at the center of the runway, and focused all four cameras on the fixture, such that each camera view was zoomed in as much as possible while maintaining a view of all of the fixture points. I captured a single-frame shot of the fixture in all camera views, and then removed the fixture from the runway. For arboreal substrate experiments, calibration images were captured before the pole was put into place. To do this, the calibration fixture was elevated to the height at which the pole was to be set when oriented horizontally, or to the height at which the subject was expected to place its foot in the second step of a climbing bout when the pole was oriented vertically. This ensured that steps on the pole substrate would be recorded within the calibrated space. Calibrated camera views were maintained during the experiment, and afterwards the fixture was returned to its original position and a second single-frame shot was taken in case of a slight shift in camera positions had occurred during the recording.

Following experiments, I used ProAnalyst software to calibrate pairs of cameras by locating all 84 fixture points in both camera views. ProAnalyst applies a direct linear transformation algorithm to triangulate the locations of each point in three-dimensional space, based on known distances of the points relative to one another. These distances are input into the program in a file that is specific to the fixture, which in this case was created by Xcitex and provided to the lab. This procedure determines the relative position, orientation, and internal parameters for each camera pair. It also provides a measure of the residual error associated with locating the 3-D position of the markers in each camera pair. Typically, the average error in point location was 0.5-1 mm for camera pairs calibrated in this manner. I assigned an arbitrary origin point for the global coordinate system to the lower left corner of the fixture where the vertical and horizontal plates meet. From this origin, the *Y*-axis was directed upward and opposite to the

force of gravity, the Z-axis was directed along the runway in line with the direction of motion (except during climbing experiments), and the X-axis was orthogonal to the other two axes (mediolateral relative to the body during movement).

Kinematic Data Processing

From recording sessions, I selected steps for analysis that met the following criteria: All markers were visible in at least two camera views throughout the duration of stance phase (defined below), and no visible soft tissue deformation that would influence marker motion was apparent. For each selected step, I cropped the recorded event to include only stance phase. I only analyzed stance phase because it is the period of a stride that is relevant to the hypotheses that I tested, and because the size of the cameras' viewing fields did not allow me to capture motion for complete strides. I defined touchdown of stance phase as occurring in the first frame that any part of the foot, other than the digits, made contact with the substrate. Touchdown, within a frame of its initiation, was easily determined by identifying deformation of plantar soft tissue. I deemed this approach superior to one where touchdown was defined based on ground reaction force recordings, because often chimpanzees brush the substrate with their foot while it is still swinging forward before coming to a stop. This slight contact elicits a reaction force signal that occurs prior to the end of swing phase, before the initiation of the joint kinematics of interest to this research. I defined liftoff as the last frame in which the hallux maintained contact with the substrate. I used this definition because it was an easy temporal landmark to assess in both human and chimpanzee subjects during locomotion on all substrate types, and because it is related to end of propulsion. I applied a radial distortion filter to all videos that I analyzed. Briefly, radial distortion filters were created by capturing single frame images of a flat board with a checkerboard pattern that was held normal to the camera view for all cameras, following the calibration shot. From these images, I was able to calculate the degree of radial distortion using ProAnalyst, which creates a set of filter coefficients that can be used to correct the distortion in a given camera view. Radial distortion filters were also applied to the camera views for the calibration shots.

After editing videos and applying image filters, I digitized all possible marker positions in all camera views in each frame of stance phase using ProAnalyst. I used calibrated camera pairs to calculate 3-D coordinates for all markers across stance, and then averaged the coordinates calculated from each camera pair using an option in ProAnalyst that applies an algorithm that weighs camera pairs with lower error more heavily in the calculation. The error values for marker coordinates were usually less than 1 mm, and always less than 2 mm, throughout stance after all camera pairs had been averaged. 3-D coordinates were exported into MATLAB software (MathWorks Inc., Natick, MA), where they were filtered using a fourth order low-pass Butterworth filter with a cut-off frequency determined *via* residual analysis (Winter, 2005). X, Y, and Z coordinates were assigned cut-off frequencies of 5, 6, and 7 Hz, respectively.

To assess the degree of soft tissue deformation and its effect on marker position, I measured the change in relative position between each marker pair in each triad. Specifically, for every frame of a step, I measured the linear distance between each marker pair in a triad using the 3-D coordinate data. In each frame, I subtracted the distance between markers in the neutral position trial. I then calculated the root-mean-squared value for this difference across the duration of stance. For each triad I calculated three such values, one for each possible pair of markers. If any of these values was over 0.1, i.e. the distance between the markers had changed

by more than 10%, I disregarded the segment represented by that triad from all subsequent analyses.

I used the KineMat software package (Reinschmidt and van den Bogert, 1997) in MATLAB to calculate 3-D joint angles from the filtered coordinate data. This software uses the marker triad positions in the previously described neutral position event to define local coordinate systems for each of the segments under investigation, and aligns them with the global coordinate system. During locomotion trials, for each frame the software computes a 3x3 rotation matrix and a 3x1 translation vector (which are combined to create a 4x4 transformation matrix) that describe the relative position of a segment within its local coordinate system based on movement of the segment's representative marker triad. To minimize the effects of soft tissue deformation on the relative positions of the markers within a triad, the software uses a singular value decomposition method described by Söderkvist and Wedin (1993). Briefly, this method calculates the transformation matrix that minimizes deviations of the markers within a triad from their positions relative to one another as defined in the neutral position event. In this manner, the software is able to reduce errors caused by both soft tissue/rigid body violations, and residual errors from 3-D marker position calculations. The software calculates 3-D joint angles by determining the relative positions of two segments in their local coordinate systems following a Cardan approach. Angles are determined as the series of rotations about axes defined by the segment coordinate systems that describe the position of one segment's coordinate system relative to that of the other. The order of these rotations is investigator-defined, but consists of one rotation in each of the standard anatomical planes. For this project, I selected an XYZ rotation sequence, following ISB recommendations⁵ for the ankle joint (Wu et al., 2002). KineMat software uses segment axes based on the joint coordinate system originally proposed by Grood and Suntay (1983). This means that for the present study, sagittal plane motion is rotation about the proximal segment's X-axis (plantarflexion [negative] and dorsiflexion [positive]), transverse plane motion is rotation about the distal segment's Y-axis (abduction [negative] and adduction [positive]), and coronal plane motion is rotation about a floating axis orthogonal to the other two axes (eversion [negative] and inversion [positive]) (Fig. 2.10).

3-D joint angles were calculated between the following segment pairs in order to quantify motion at the major intrinsic foot joints:

1. *Leg vs. Rearfoot*. Two important joints occur between these segments: the talocrural joint, and the subtalar joint. Both joints are believed to involve triplanar motion in humans (Inman, 1976; Root et al., 1977) and chimpanzees (Elftman and Manter, 1935; Lewis, 1980; Latimer et al., 1987), so assigning planar motion to one joint or the other simplifies their actual mechanics. I will assume that all sagittal plane motion between these segments occurs at the talocrural joint, and all coronal and transverse plane motion occurs at the subtalar joint.

2. *Rearfoot vs. Midfoot*. The calcaneus articulates with the cuboid anteriorly, and this joint makes up half of the 'transverse tarsal' or 'midtarsal' joint complex. The other half of this complex is the talonavicular joint. Traditionally, this complex is believed to function as a single joint in humans (Elftman and Manter, 1935; Tweed et al., 2008), but recently several studies

⁵ Note, Wu and Cavanagh (1995) and Wu et al. (2002) recommend a global coordinate system wherein the X and Z axes are reversed from what is used in this study, i.e. the X axis describes anteroposterior position, and the Z axis describes mediolateral position. Therefore, the use of an XYZ Cardan rotation sequence used in the present study is equivalent to the ZYX rotation sequence recommended by Wu et al. (2002).

have found considerably higher mobility at the talonavicular joint in both humans and chimpanzees (Greiner and Ball, 2014; Thompson et al., 2014). Because the rearfoot segment does not include markers over the talus, I assumed that the motion measured in this study will be more reflective of mobility at the calcaneocuboid joint side of the transverse tarsal joint complex. Based on passive range of motion studies, motion between the talus and midfoot segment would likely be somewhat higher than that measured here for both humans and chimpanzees.

3. *Midfoot vs. Medial Forefoot.* Metatarsals 2 and 3 articulate with the intermediate and lateral cuneiforms, respectively. The lateral cuneiform is part of the midfoot segment, and I assume that minimal motion occurs between the intermediate cuneiform and the other bones that I have defined to represent the midfoot. Therefore, I assume that motion between these segments occurs at a joint complex between these bones, and that this motion is triplanar.

4. *Midfoot vs. Lateral Forefoot.* Metatarsals 4 and 5 articulate with the cuboid, which is part of the midfoot segment. Therefore, I assume that triplanar motion between these segments occurs at the cuboid-metatarsal joints.

I calculated motion at the metatarsophalangeal joints by treating the phalanx and metatarsal segments as vectors a and b , and calculating the angle between them as:

$$\theta = \cos^{-1} \frac{a \cdot b}{\|a\| \|b\|}$$

I assumed that metatarsophalangeal joint motion occurred mainly in the sagittal plane, and that motion in other planes was negligible. In human subjects, metatarsophalangeal joint motion is mainly restricted to the sagittal plane, with a small amount of abduction-adduction possible (Briggs, 2005; Caravaggi et al., 2009). However, in passive manipulations, I found that chimpanzee metatarsophalangeal joints permit much larger ranges of abduction-adduction than those reported for humans. During locomotion on the runway, chimpanzee subjects exhibited minimal non-sagittal plane metatarsophalangeal motion. On the pole substrate, however, they occasionally exhibited considerable abduction. Therefore, I did not attempt to measure metatarsophalangeal joint motion in chimpanzee subjects during travel on the pole. However, I observed that subjects did not dorsiflex their metatarsophalangeal joints to as high a degree during pole locomotion as on the ground. Rather, subjects tended to allow their digits to slide off the pole as the foot was being carried forward or upward, similar to the manner described by Meldrum (1991) for digit postures in cercopithecines during arboreal locomotion.

2.5 Joint motion statistics

For each of the segment pairs, I calculated the instantaneous joint angle in all three planes of motion throughout the duration of stance. These data were used to calculate maximum, minimum, and total range of motion in each plane at each joint. I compared these values among groups statistically by pooling steps between subjects within each group. Specific statistical tests used in analyses will be described in subsequent chapters.

To qualitatively compare patterns of motion between locomotor modes, data from each step were normalized to 51 time points to represent 0% to 100% of stance by 2% increments using a linear interpolation algorithm (the ‘normalfu’ function in the KineMat package). Within each locomotor mode I calculated means and standard deviations for joint angles at each time point. Slight variations in marker placement and neutral position angles between experimental sessions can lead to offsets in absolute joint angle between experiments, which can lead to artificially high variance in mean angles calculated from multiple subjects and/or recording sessions (Kadaba et al., 1989). To deal with this problem I followed the approach taken by

Kadaba et al. (1989), and for each step, within each plane of motion of each joint, I subtracted the average joint angle over the entire stance duration from each time point. I then calculated the average joint angle at each time point from all steps following this ‘de-averaging’ procedure. I also calculated the standard deviation from these ‘de-averaged’ values. I then added back the average starting angle from the first time point of all steps to the group mean at all time points in order to recover the average absolute angle over stance relative to neutral position. Normalized data adjusted in this manner were plotted for all groups to assess differences in patterns of motion across joints.

Aside from its use by Kadaba et al. (1989), this is not a standard procedure in kinematics investigations. However, I felt that it would be an appropriate way to deal with added variance due to differences in chimpanzee neutral positions in this study, as it was more difficult for me to precisely standardize neutral position in my chimpanzee subjects than it is to standardize neutral position in typical human studies. This measure helps to avoid the impression that chimpanzee foot kinematics are more variable than they really are, although I only used this procedure for graphing my results and qualitative comparison. Standardized data were *not* used for statistical analyses (except for coefficient of multiple correlation calculations; see Section 3.2), because this procedure deflates the variance that would be obtained from absolute values.

2.6 Speed Estimation

As previously described, I was unable to measure speed for the steps that I analyzed. To achieve estimates of relative speeds for between-group comparisons, I determined the relationship between speed and stance duration during terrestrial locomotion for each subject in my study. The relationship between these variables has been previously demonstrated for humans (Vilensky and Gehlsen, 1984) and chimpanzees (Demes et al., 1994; Pontzer et al., 2014). To determine this relationship, I had to carry out separate locomotion experiments for each subject with zoomed out camera views that would allow me to capture motion throughout complete strides. This required calibrating camera pairs with a larger calibration fixture than that previously described. The fixture used for these experiments was 1.9 x 1.1 x 0.6 m, with 36 points. Camera pairs were calibrated in an identical manner as previously described, using a direct linear transformation algorithm.

Prior to these experiments markers were placed/applied on subjects on the following locations: greater trochanter, anterior superior iliac spine, posterior superior iliac spine, and ischial tuberosity. The markers used with human subjects were small spherical balls placed over tight-fitting spandex shorts. Markers were painted onto chimpanzee subjects while they were under full anesthesia using the methods previously described. During experiments, human subjects were directed to walk at a wide variety speeds, and chimpanzee subjects walked at self-selected speeds. Subjects were recorded using the previously described motion capture system. From these recordings, I selected 15 steps for each subject based on stance phase duration, targeting a sample of steps that provided a wide range of stance durations. Using ProAnalyst software, I tracked the position of a single pelvis marker (depending on which markers were visible in multiple camera views) at the first and last frames of a stride. Strides were defined as beginning at touchdown of a foot and ending at touchdown of the same foot. From these marker positions, I calculated the total horizontal distance traveled by the subject during the stride, and divided this by the duration of the stride to calculate velocity of locomotion. I also digitized the greater trochanter position at midstance to calculate the functional lower limb length during the stride. I accounted for the effects of body size on speed by non-dimensionalizing velocity during

locomotion. I used velocity (v_d) and lower limb length (L) to calculate dimensionless velocity (v) using the following equation:

$$v = v_d / (g * L)^{1/2}$$

where g is the gravitational constant 9.81 ms^{-2} . I calculated a least-squares linear regression for the relationship between natural logs of the inverse of stance duration and dimensionless velocity for each subject in my study. I calculated separate regression equations for bipedal and quadrupedal locomotion in chimpanzee subjects. The equations and R-squared values for these regressions are provided in Table 2.3. These equations were used to estimate velocity in the steps where I analyzed foot kinematics.

2.7 Limitations

The methodology used to collect the data in this study, and the dataset that I analyzed, were characterized by several notable limitations. I will discuss these limitations, and their expected effects on my results below.

Subjects

The most obvious and major limitation of this study is the small, homogenous chimpanzee subject sample. Because I only had access to two individuals, of the same sex, with similar ages and body sizes, I cannot claim to have captured even a small percentage of the probable diversity in chimpanzee foot biomechanics. Inspection of foot motion in videos of other chimpanzees has led me to conclude that the subjects in this study should not be assumed to represent the ‘average’ chimpanzee condition (see Chapter 3, Section 3.4.2). However, I have no reason to suspect that the individuals in this study were unusual, and I do not believe that captivity has affected their foot function in any significant way. What I hope to have captured in this study is how chimpanzees use their feet differently in different, common locomotor behaviors. The extent to which these postures vary across chimpanzees would be a much larger project, but what I have measured can be assumed to represent chimpanzee foot kinematics within the normal range of variation.

Marker Placement

In addition to these issues, a number of studies have demonstrated that the repeatability of marker placement can be a major source of error in kinematics studies (Kadaba et al., 1989; Ferber et al., 2002; McGinley et al., 2009). Repeatability studies of multi-segment foot kinematics protocols have demonstrated that between-researcher marker placement is a greater source of error than within-researcher marker placement (Leardini et al., 1999; Carson et al., 2001; Caravaggi et al., 2011). I was solely responsible for marker placement for my experiments, and I tried to minimize the effects of within-researcher marker placement by drawing the steps in my analysis from as few experiments possible.

Talonavicular Joint

Passive manipulation studies have revealed the talonavicular joint to be a site of substantial midfoot mobility in chimpanzees. It has been found to yield a 1.5 to 3 times greater range of motion than the calcaneocuboid joint in studies of both anesthetized animals (Thompson et al., 2014) and cadaveric limbs (Greiner and Ball, 2014). Because I cannot place markers on the talus, I cannot directly assess talonavicular joint motion in this study. Rather, I am limited to measuring motion between the calcaneus and the midfoot segment, which includes the navicular

bone. Therefore, the rearfoot-midfoot motion that I capture in this study is likely to more closely represent motion at the calcaneocuboid joint than at the talonavicular joint. It is plausible to assume that motion occurring strictly at the talonavicular joint will be somewhat greater than that which I am measuring between the rearfoot and midfoot segments. The orientation of the axis about which the chimpanzee talonavicular joint rotates *in vivo* is unknown, but Thompson et al. (2014) suggested that it may include a substantial coronal plane component. This notion is somewhat supported by the results of Greiner and Ball (2014), who measured only a small sagittal plane range of motion ($\sim 4^\circ$) at this joint, indicating that its greatest mobility lies in other planes. Therefore, in this investigation I will assume that chimpanzee talonavicular joint motion is slightly greater than the motion that I capture between the midfoot and rearfoot segments, and that this difference in motion mainly occurs in the transverse and coronal planes.

Chapter 2: Tables

Table 2.1. Chimpanzee subject body mass and age by experiment.

Subject	Experiment Date	Data Collected ^a	Chapter ^b	Age (years)	Body Mass (kg)
Chimp H	Aug 2013	Ground	3	6.8	34.9
	Jan 2014	Climb	4	7.2	38.5
	May 2014	Pole	4	7.4	40.9
	Aug 2014	Ground	3, 4	7.8	45.2
	Nov 2014	Pressure	5	8	47.7
	May 2015	Pressure	5	8.5	54.2
<i>Average ± S. D.</i>				<i>7.6 ± 0.6</i>	<i>43.6 ± 6.9</i>
Chimp L	Aug 2013	Ground	3, 4	7	39.9
	Jan 2014	Climb	4	7.3	37.5
	June 2014	Pole	4	7.5	41.5
	July 2014	Ground	3	7.8	42.3
	Sep 2014	Ground	4	8	42.2
	June 2015	Pressure	5	8.8	48.1
	June 2015	Pressure	5	8.8	49.5
<i>Average ± S. D.</i>				<i>7.9 ± 0.7</i>	<i>43 ± 4.3</i>

^a Specifies the type of locomotion data collected. Climb = climbing on vertically oriented pole; Ground = quadrupedal and bipedal walking on flat runway substrate; Pole = quadrupedal walking on horizontally oriented pole substrate; Pressure = quadrupedal and bipedal walking on flat runway substrate over pressure pad.

^b Indicates dissertation chapter where data from experiment are used.

Table 2.2. Human subject information.

Subject	Age (years)	Body Mass (kg)	Arch Height Index ^a
Human A	28	69.5	0.35
Human B	26	62.6	0.35
Human C	28	64.1	0.36
Human D	28	77.5	0.37
Human E	29	67.3	0.33
<i>Average ± S. D.</i>		<i>68.2 ± 5.9</i>	<i>0.35 ± 0.01</i>

^a Arch height index is described in Williams and McClay (2000). Briefly, it is the medial height of the foot at midfoot, divided by the medial length of the foot not including the first toe.

Table 2.3. Least-squares linear regression equations describing the relationship between dimensionless velocity (v) and the inverse of stance phase duration (t_s^{-1}).

Subject	Equation	SEE ^a	R ²
Chimp H			
<i>Bipedal</i>	$\ln(v) = 0.76 * \ln(t_s^{-1}) - 1.25$	0.034	0.78
<i>Quadrupedal</i>	$\ln(v) = 1.41 * \ln(t_s^{-1}) - 1.39$	0.11	0.73
Chimp L			
<i>Bipedal</i>	$\ln(v) = 0.79 * \ln(t_s^{-1}) - 1.17$	0.03	0.72
<i>Quadrupedal</i>	$\ln(v) = 1.37 * \ln(t_s^{-1}) - 1.34$	0.071	0.91
Human A	$\ln(v) = 1.54 * \ln(t_s^{-1}) - 1.59$	0.033	0.98
Human B	$\ln(v) = 2.07 * \ln(t_s^{-1}) - 1.73$	0.039	0.95
Human C	$\ln(v) = 1.63 * \ln(t_s^{-1}) - 1.42$	0.027	0.98
Human D	$\ln(v) = 1.47 * \ln(t_s^{-1}) - 1.36$	0.046	0.96
Human E	$\ln(v) = 1.85 * \ln(t_s^{-1}) - 1.47$	0.053	0.96

^a $\ln(v)$ must be exponentiated to obtain an estimate of v .

^b Standard error of estimate.

Chapter 2: Figures

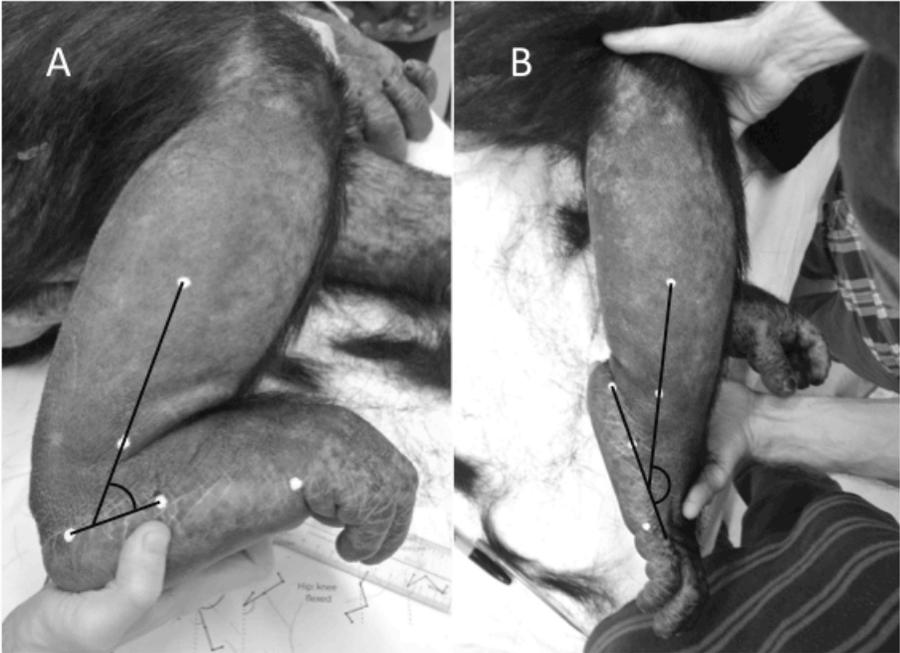


Fig. 2.1. Passive talocrural joint range of motion measurements. A) dorsiflexion; B) plantarflexion.

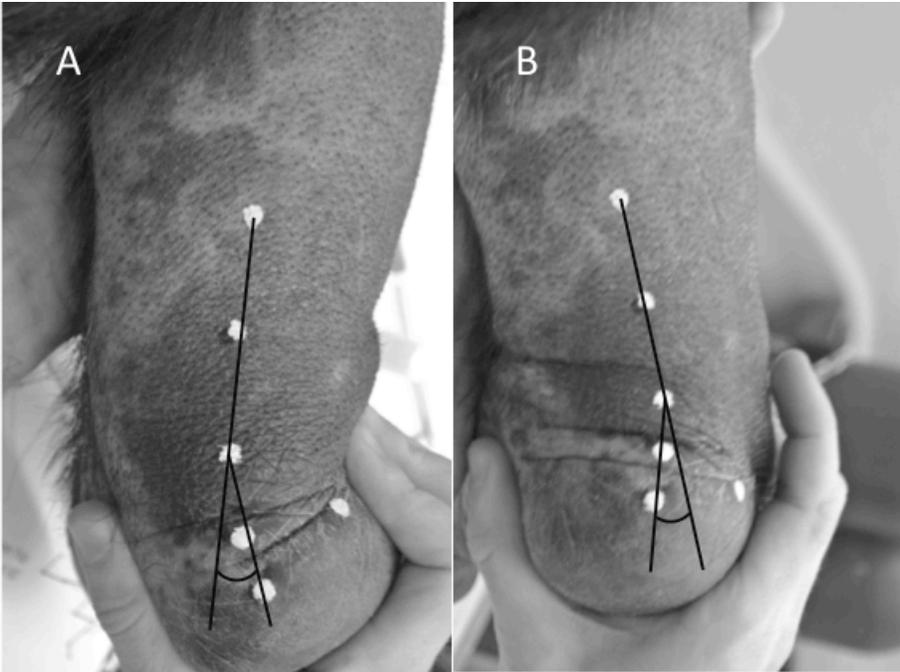


Fig. 2.2. Passive subtalar joint range of motion measurements. A) eversion; B) inversion.

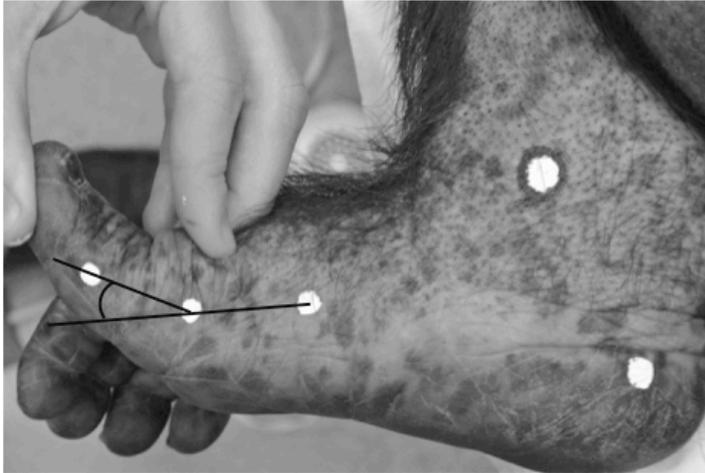


Fig. 2.3. Passive metatarsophalangeal joint range of motion measurement for digit 1. Digit 2 and 5 were measured in a similar fashion.

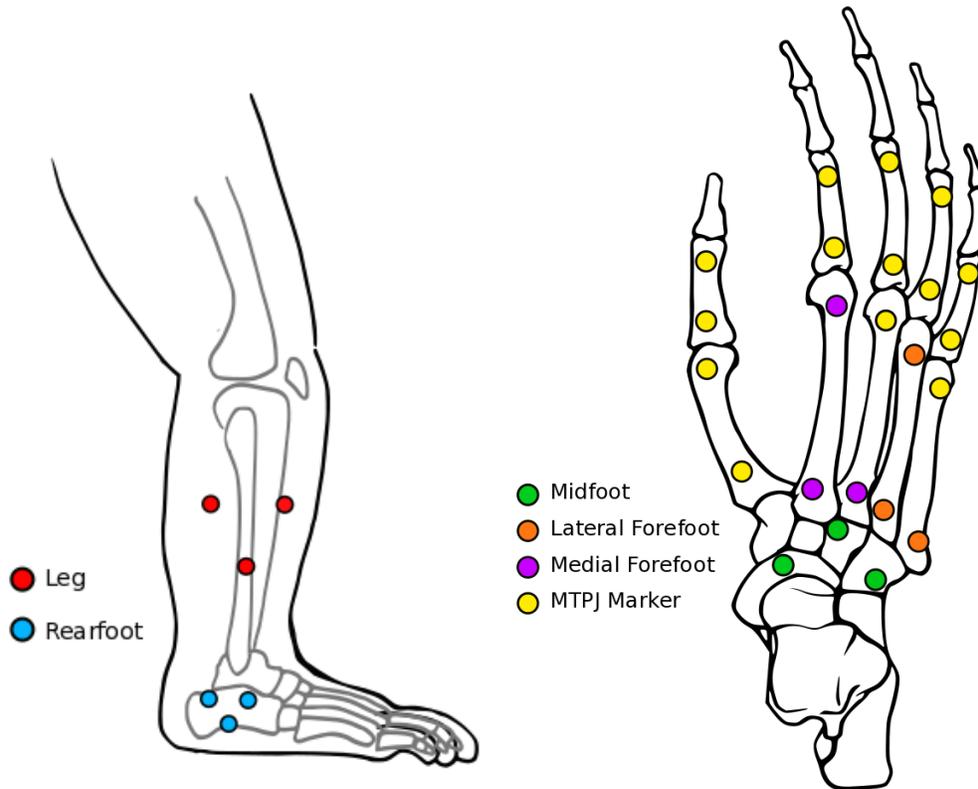


Fig 2.4. Marker locations relative to bones of the leg and foot of a chimpanzee. Colors are used to denote segment triads to which markers belong. ‘MTPJ Marker’ refers to markers used strictly to measure motion at the metatarsophalangeal joints.



Fig. 2.5. Example of foot and leg postures used to define 'neutral position'. The leg is 90° to foot, and the foot is flat against the substrate. In chimpanzee subjects (left) the interphalangeal joints are extended and the hallux is moderately abducted.

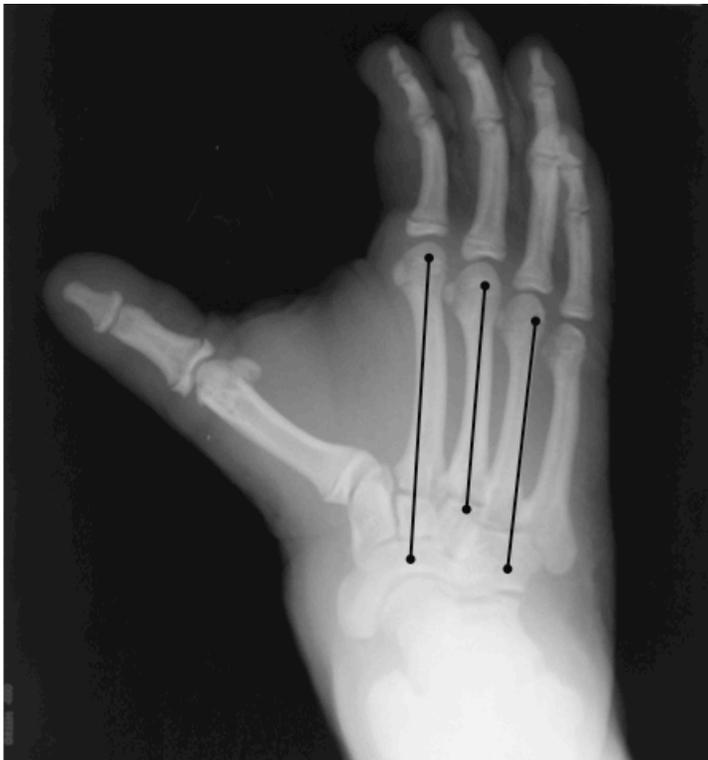


Fig 2.6. X-ray image of subject foot depicting measurements used to determine marker positions for midfoot triad.

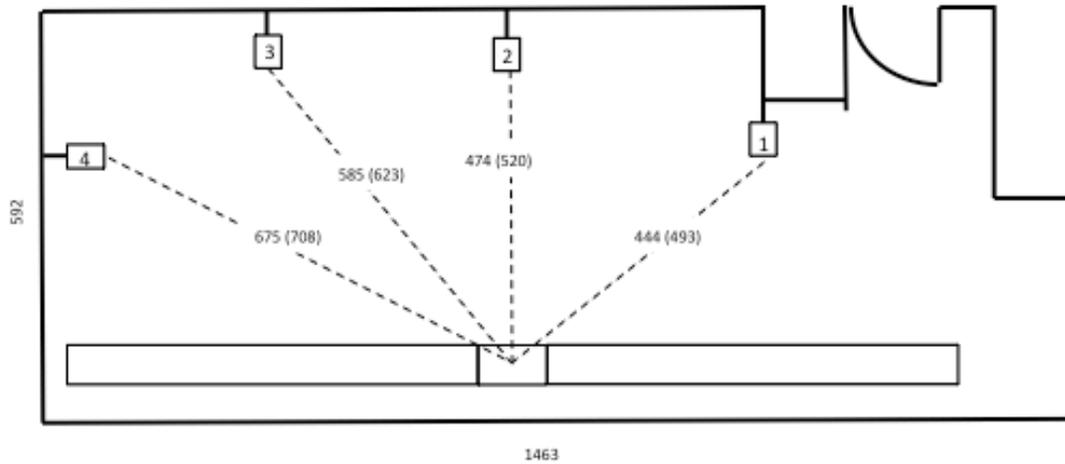


Fig. 2.7. Floor plan of room used to collect kinematic data with runway substrate in place. The four cameras used to record subject motion are labeled. Numbers represent distances in cm. All cameras are mounted at a height of 215 cm. Dashed lines indicate distance from camera to force plates, with numbers out of parentheses indicating distance on the ground, and numbers in parentheses indicating absolute distance.

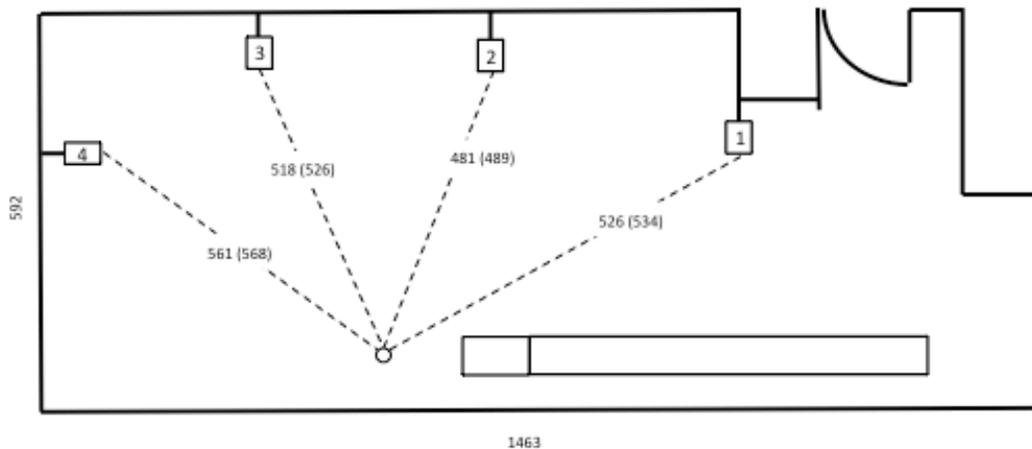


Fig. 2.8. Floor plan of room used to collect kinematic data with vertical pole substrate in place. The four cameras used to record subject motion are labeled. Numbers represent distances in cm. All cameras are mounted at a height of 215 cm. Dashed lines indicate distance from camera to climbing pole, with numbers out of parentheses indicating distance on the ground, and numbers in parentheses indicating absolute distance.

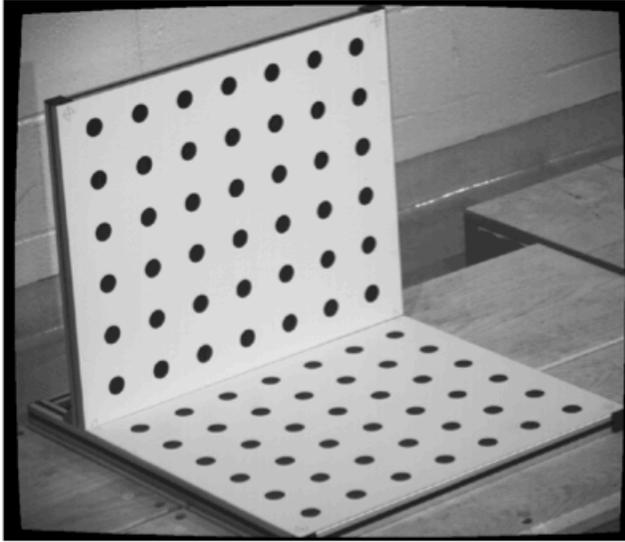


Fig. 2.9. Fixture used to calibrate camera pairs.

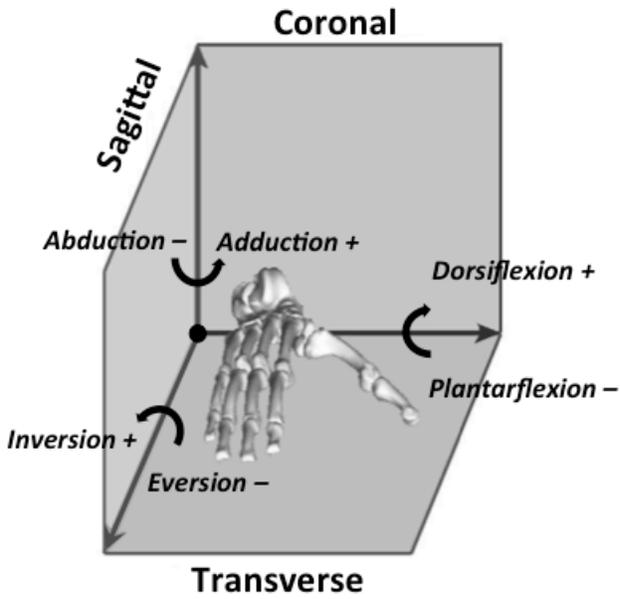


Fig. 2.10. Planes of motion relative to the foot, and polarity of the motions in each plane. All terms apply to each joint measured in this study.

Chapter 3

Chimpanzee Foot Kinematics During Locomotion on Arboreal and Terrestrial Substrates

3.1 Introduction

3.1.1 Background

In comparison to the feet of humans, anatomists have long interpreted chimpanzee feet to be primarily adapted for arboreal locomotion. In early anatomical investigations, the chimpanzee foot was characterized as a ‘prehensile’ structure, based on skeletal features such as digit length proportions, metatarsal torsion, and hallucal opposability (Wood Jones, 1917; Morton, 1922; Keith, 1929). In several studies, authors described midfoot ‘flexibility’ among the suite of arboreal adaptations in the chimpanzee foot (Weidenreich, 1923; Morton, 1924), but did not provide an anatomical basis for this characteristic. Elftman and Manter (1935b) were the first to formally describe midfoot motion in chimpanzees during locomotion. In an investigation of plantar pressure distributions during bipedal walking, they observed the chimpanzee subject in their study to briefly maintain forefoot contact with the ground following heel lift *via* dorsiflexion at the midfoot, a motion which has since come to be called the ‘midtarsal break’ (Susman, 1983). Elftman and Manter (1935a) suggested that a mediolateral axis at the transverse tarsal joint provided the mechanism for this motion. Their argument was later taken up by Bojsen-Møller (1979), who contended that calcaneocuboid joint morphology was a major determinant of midtarsal mobility. Lewis (1980a) further argued that this morphology enables chimpanzees and other primates to rotate the joints of their feet into close-packed positions during the inverted foot postures used in arboreal locomotion.

More recently, based on their study of bonobo plantar pressure distributions, Vereecke et al. (2003) suggested that the midtarsal break motion is more likely to occur at the cuboid-metatarsal joints. In videos of captive chimpanzees, DeSilva (2010) measured greater midfoot dorsiflexion at these joints than at the calcaneocuboid joint, a result that was confirmed by Greiner and Ball (2014) in a study of passive motion in cadaveric specimens. Regardless of the site of motion, these studies all suggested that midfoot joint mobility contributes to the use of the foot as a prehensile grasping organ during arboreal locomotion. Consequently, a number of authors have suggested that chimpanzee foot function is compromised during locomotion on terrestrial substrates (Tuttle, 1970; Langdon, 1986; Lovejoy et al., 2009; DeSilva, 2010). They argue that midfoot dorsiflexion during the propulsive phase of a step prevents the foot from functioning as a rigid lever during push-off, and mechanical power produced at the ankle joint is consequently used less efficiently for propulsion (Bojsen-Møller, 1979).

Several studies have also suggested that the chimpanzee ankle, including the talocrural and subtalar joints, is specially adapted for arboreal locomotion, particularly climbing on vertically oriented supports. Chimpanzee climbing is thought to involve the use of ankle postures that are both highly dorsiflexed (DeSilva, 2009) and inverted (Wood Jones, 1917; Weidenreich, 1923). Lewis (1980b) and Latimer et al. (1987) argued that chimpanzee talocrural joint geometry

causes the foot to abduct and invert when it is highly dorsiflexed, placing it in an ideal position to oppose an arboreal substrate while climbing. At the subtalar joint, Deloison (1985) and Latimer and Lovejoy (1989) used measures of joint curvature to suggest that chimpanzees are capable of loading this joint in a greater range of inversion-eversion postures than humans, which would be advantageous for arboreal locomotion. Lewis (1980a) contended that orientation of the subtalar joint articular surfaces causes the chimpanzee midfoot joints to reach their close-packed positions when inverted during arboreal locomotion, leaving them more mobile during terrestrial weight-bearing.

That so many aspects of foot joint morphology have been cited as arboreal adaptations seems paradoxical when one considers the fact that most of chimpanzee locomotion occurs on the ground (Tuttle, 1986). Although chimpanzees forage and sleep in the trees, travel between sites is almost exclusively terrestrial (Doran and Hunt, 1994). During infancy, chimpanzee locomotion occurs mainly on arboreal substrates, but by adolescence terrestrial quadrupedalism is the primary locomotor behavior (Doran, 1992b; Sarringhaus et al., 2014). Across different field sites, 70 to 90% of adult chimpanzee locomotion consists of terrestrial quadrupedalism (Doran, 1992a; b; Hunt, 1992; Sarringhaus et al., 2014). Climbing is the most common arboreal locomotor mode used by adult chimpanzees, followed by arboreal quadrupedal walking and suspensory locomotion (Doran, 1992b, 1993; Doran and Hunt, 1994). The degree to which these behaviors, as opposed to terrestrial locomotion, have influenced chimpanzee foot evolution is difficult to determine based on current kinematic evidence. As terrestrial quadrupedalism is the dominant locomotor mode, one might expect that the chimpanzee foot shows adaptations that are advantageous for travel on the ground. Nevertheless, many features of the chimpanzee trunk and upper limb represent adaptations for arboreal locomotion while using orthograde body postures (Larson and Stern, 1987; Hunt, 1991; Larson, 1998), so it is reasonable to hypothesize that foot anatomy might have been driven by such selective pressures as well.

A thorough understanding of chimpanzee foot mechanics *in vivo* is necessary to address the potential tradeoffs of pedal joint adaptations for arboreal versus terrestrial locomotion. However, to date, the vast majority of chimpanzee foot joint functional morphology studies have been anatomical and osteological investigations (e.g., Bojsen-Møller, 1979; Lewis, 1980a; b; Gomberg, 1985; Langdon, 1986; Latimer et al., 1987; Latimer and Lovejoy, 1989; Sarmiento and Marcus, 2000; Berillon, 2003). Relatively few studies have actually attempted to quantify chimpanzee foot joint motion, either passively in cadaveric feet or anesthetized animals (Holowka and O'Neill, 2013; Greiner and Ball, 2014; Thompson et al., 2014), or during locomotion *in vivo* (DeSilva, 2009, 2010; Pontzer et al., 2014; O'Neill et al., 2015). Such data are necessary to determine which joints are mobile during chimpanzee locomotion, their relative mobility, and how this mobility differs across locomotor behaviors.

These data are also of critical importance for improving our understanding of the evolution of the human foot and reconstructing the gait of early hominins. Most studies of hominin pedal remains assess joint morphology on a spectrum from monkey-like, to great ape-like, to modern human-like, and then try to derive functional interpretations depending upon where on this spectrum the morphology falls. However, without a solid understanding of nonhuman primate foot mechanics, such interpretations are necessarily speculative. The pedal remains of numerous early hominins preserve chimpanzee-like joint morphology (e.g., Stern and Susman, 1983; Sarmiento and Marcus, 2000; Lovejoy et al., 2009; Zipfel et al., 2011; Haile-Selassie et al., 2012), so improving our knowledge of chimpanzee foot joint motion *in vivo* will help us to better understand the locomotion of these species.

To this end, I measured 3-D kinematics of the chimpanzee foot joints during locomotion on arboreal and terrestrial substrates. Specifically, I measured motion at the ankle and midfoot joints while chimpanzee subjects were walking on a flat runway and a horizontal pole, and climbing a vertical pole. During these behaviors I captured motion at the talocrural, subtalar, transverse tarsal, and tarsometatarsal joints. These data were used to address several hypotheses about chimpanzee joint function that have been derived from anatomical and observational studies.

3.1.2 Hypotheses

I tested four different hypotheses in this study; the first three hypotheses concern motion at specific joints, and the last hypothesis concerns foot mobility across locomotor modes.

H1: Chimpanzees use different ankle postures during arboreal and terrestrial locomotion.

Hereafter I will use the term ‘ankle’ to refer to both the talocrural and subtalar joints, which are sometimes referred to as the upper and lower ankle joints, respectively (Elftman and Manter, 1935a). I will use this terminology because my measurement methodology does not allow me to precisely distinguish between motions at these joints (see Chapter 2). I expect chimpanzees to exhibit high ankle dorsiflexion angles during both climbing and walking on arboreal supports. DeSilva (2009) has already measured high ankle dorsiflexion in chimpanzees during climbing, and I expect chimpanzees to use relatively dorsiflexed ankles while walking on horizontal arboreal supports as well for the following reasons: First, flexed limb joints can potentially increase arboreal stability by lowering the body’s center of mass, which will reduce gravitational overturning moments (Cartmill, 1985). Joint flexion can also increase limb compliance (Larney and Larson, 2004), which may reduce peak vertical gravitational forces (Schmitt, 1999). If the ankle is highly dorsiflexed, then the foot should also be inverted and abducted relative to the leg, based on analyses of chimpanzee talocrural joint geometry (Lewis, 1980b; Latimer et al., 1987).

Chimpanzees are also expected to use inverted subtalar joint postures to augment foot inversion during arboreal locomotion (Morton, 1924; Elftman and Manter, 1935a). In contrast, during terrestrial locomotion, Elftman and Manter (1935a; b) observed that chimpanzees evert their feet to place the entire plantar surface against the ground. Also, Pontzer et al. (2014) found that chimpanzees typically dorsiflex their ankles $<15^\circ$ during quadrupedal walking on the ground, which is far below the climbing dorsiflexion angles measured by DeSilva (2009). Therefore, I make the following predictions:

P1: Chimpanzees will use more dorsiflexed ankle postures during arboreal locomotion than during terrestrial locomotion.

P2: Chimpanzees will use more inverted ankle postures during arboreal locomotion than during terrestrial locomotion.

H2: The midtarsal break involves motion at both the transverse tarsal and cuboid-metatarsal joint complexes in chimpanzees.

The midtarsal break observed in previous studies of chimpanzee and bonobo locomotion is believed to result from dorsiflexion of the transverse tarsal and/or cuboid-metatarsal joints following heel lift (Elftman and Manter, 1935b; Susman, 1983; Vereecke et al., 2003; DeSilva, 2010). DeSilva (2010) measured midfoot dorsiflexion at both joint complexes in captive chimpanzees during locomotion, but more recently Greiner and Ball (2014) found considerable

mobility differences between them in a cadaver study. They found the cuboid-metatarsal joints to be highly mobile, but the calcaneocuboid joint to be virtually motionless during passive dorsiflexion. However, Thompson et al. (2014) measured a small amount of passive calcaneocuboid mobility in anesthetized chimpanzees using cineradiography. Therefore I expect both joints to contribute to this motion.

Determining the location of the midtarsal break is important for understanding pedal adaptations to arboreal locomotion. Because the break is thought to compromise locomotor efficiency, it is expected that joints that exhibit a break during terrestrial locomotion are adapted for hyper-mobility during arboreal substrate grasping. Based on previous investigations of the midtarsal break, I make the following predictions:

P1: Chimpanzees will dorsiflex their calcaneocuboid joints following heel lift during terrestrial locomotion.

P2: Chimpanzees will dorsiflex their cuboid-metatarsal joints following heel lift during terrestrial locomotion.

H3: The joints between the lateral and intermediate cuneiforms and their respective metatarsals are less mobile than the cuboid-metatarsal joints in chimpanzees during locomotion.

No previous study has reported or suggested that dorsiflexion occurs at the lateral and intermediate tarsometatarsal joints in chimpanzees following heel lift. This may be because the morphologies of the articulating surfaces of these joints are more complex than those of the cuboid-metatarsal joints (Lewis, 1980a). My own observation of the relative mobility at these joints in passive manipulations of a cadaveric foot specimen supports this assumption. However, there are two reasons that they may actually be more mobile *in vivo* than passive manipulation suggests: First, plantar pressure data indicate that chimpanzees tend to load the medial sides of their feet at the end of stance during push-off (Elftman and Manter, 1935b; Wunderlich, 1999), which could cause a high dorsiflexion moment at the intermediate and lateral tarsometatarsal joints following heel lift. Second, as the cuneiform-metatarsal joints and the cuboid-metatarsals joints form a nearly straight mediolateral axis across the foot, one might expect all tarsometatarsal joints to dorsiflex simultaneously following heel lift during a midtarsal break. I make the following prediction about motion at these joints:

P: Chimpanzees will exhibit greater ranges of motion at the cuboid-metatarsal joints than at the lateral and intermediate cuneiform-metatarsal joints in all locomotor modes.

H4: Overall chimpanzee foot mobility differs between substrates and locomotor modes.

Most previous studies of chimpanzee foot morphology have assumed that greater joint ranges of motion represent adaptations to arboreal locomotion (Elftman and Manter, 1935a; Stern and Susman, 1983; Latimer and Lovejoy, 1989; DeSilva, 2009, 2010; Lovejoy et al., 2009; Zipfel et al., 2011; Prang, 2016). The presence of a midtarsal break at the cuboid-metatarsal and/or transverse tarsal joint complexes is thought to be a consequence of this adaptation for arboreal locomotion. Greater ankle mobility is also thought to allow chimpanzees to position the foot at greater excursion angles, and to allow the foot to conform better to arboreal supports. Some authors have suggested that foot joint mobility is particularly important during vertical climbing. They argue that midfoot mobility is important for optimally positioning the foot during pedal grasping, but negatively affects foot function during propulsion in quadrupedal walking (Langdon, 1986; Lovejoy et al., 2009; DeSilva, 2010). Based on these arguments, I make the following predictions:

P1: Chimpanzees will use greater foot joint ranges of motion during travel on arboreal substrates than on terrestrial substrates.

P2: Chimpanzees will use greater foot joint ranges of motion during climbing than during walking on a horizontally oriented arboreal substrate.

3.2 Methods

Most of the methodology used in this chapter is described in Chapter 2, including the subject information and data collection/processing protocols. What follows is a description of the statistical tests performed in this chapter. All tests were carried out using MATLAB software. Alpha significance levels were set at 0.05 for all tests.

I compared maximum and minimum joint angles, as well as joint ranges of motion in the three locomotor modes statistically by pooling steps between subjects within each mode. I pooled steps between subjects due to low sample sizes. Pooling data in this manner resulted in data that were not normally distributed for some variables, violating the normality assumption of parametric statistics. Therefore, I used non-parametric Kruskal-Wallis tests to test for differences among locomotor modes (Sokal and Rohlf, 2005). For these tests, locomotor mode was the single factor being considered, with individual steps serving as the data points. The alpha significance level was set to 0.05. When significant differences among modes were detected, I conducted post-hoc Kruskal-Wallis pairwise comparisons between locomotor modes using MATLAB's 'multcompare' function. A sequential Bonferroni correction was used to adjust the alpha significance levels (0.05) for these tests (Abdi, 2010).

Finally, I also calculated coefficients of multiple correlation (CMC) for each locomotor mode to assess variability in kinematic waveforms. CMC values provide a measure of the overall similarity between gait data over the entire duration of a specified time interval, e.g., stance phase or a whole stride. This statistic was originally developed by Kadaba et al. (1989), and has since been used to measure variation in kinetic, kinematic, and electromyographic data in numerous human gait studies (see McGinley et al., 2009 and references therein). For this study, I calculated overall CMC values for each joint after pooling steps from both subjects to assess overall similarity of kinematic waveforms within locomotor modes. I used the following equation⁶ to calculate this CMC values:

$$CMC = \sqrt{\frac{\sum_{i=1}^M \sum_{j=1}^N \sum_{t=1}^T (Y_{ijt} - \bar{Y}_t)^2 / T(MN - 1)}{\sum_{i=1}^M \sum_{j=1}^N \sum_{t=1}^T (Y_{ijt} - \bar{Y})^2 / (TMN - 1)}}$$

In this equation, M represents the number of subjects, N represents the number of steps per subject, and T represents the number of time points in each step. Following Kadaba et al. (1989), I used time normalized, 'de-averaged' steps to calculate CMC values (see Section 2.6). This measure decreases variance, and so increases CMC values. However, the effect of this procedure

⁶ This equation is identical to that used by Kadaba et al. (1989) to calculate 'between day' variation when comparing waveforms collected from a single subject from multiple steps over multiple experimental days. My use of this equation replaces the 'between day' calculation with a 'between subject' calculation. This means that I compare variation in waveforms over all steps used for a given locomotor mode, regardless of subject identity of the step. This metric is most relevant to the present study, because I statistically compare joint kinematics between locomotor modes, but not between subjects.

should be similar across locomotor modes. I compared CMC values between locomotor modes to qualitatively assess the relative variability in joint kinematics between modes.

3.3 Results

3.3.1 Passive Range of Motion

Passive range of motion results for the talocrural and subtalar joints are presented in Table 3.1. Together, the subjects averaged 103° of total talocrural joint motion, which is similar to measurements reported for cadaveric chimpanzee specimens (Thorpe et al., 1999; Holowka and O'Neill, 2013). Subjects averaged a maximum of $42^\circ \pm 1^\circ$ of dorsiflexion and $60^\circ \pm 5^\circ$ of plantarflexion at this joint. These ranges are nearly identical to those obtained using cineradiography techniques to measure talocrural joint range of motion in the subjects included in this study (Thompson et al., 2014; N. Thompson, unpublished data). At the subtalar joint, subjects averaged $48^\circ \pm 4^\circ$ of total motion, which is considerably lower than the 68° measured by Holowka and O'Neill (2013) in cadaveric specimens. The probable reason for this difference is that in the present study I made an effort to isolate subtalar joint motion, whereas in the previous study I measured whole foot inversion and eversion. Thus, the tarsometatarsal and transverse tarsal joints are likely to be capable of at least 20° of inversion-eversion beyond that at the subtalar joint. Subjects in this study averaged nearly 50% greater eversion ($28.5^\circ \pm 0.5^\circ$) than inversion ($19.5^\circ \pm 4.5^\circ$) ranges of motion.

3.3.2 Description of Foot Joint Kinematics

For each locomotor mode, I analyzed five steps per subject. I was limited in the number of steps that I could analyze due to the difficulty of capturing steps suitable for analysis, as well as the considerable amount of time required to process each step. After inspecting the data, I decided that adding more steps to the sample would be unlikely to substantially alter my results, as within-subject variation was reasonably low. Stance phase durations for the steps included in the analysis differed greatly between locomotor modes, but were similar within them. Stance phase durations were 0.71 ± 0.06 s for ground walking steps (corresponds to 0.42 ± 0.04 dimensionless velocity based on equations in Table 2.3), 1.0 ± 0.08 s for pole walking steps, and 1.09 ± 0.11 s for climbing steps. For some steps, intra-triad marker motion index at the forefoot or midfoot segments was above the threshold that I defined to indicate significant marker triad deformation (see Chapter 2, Section 2.4). In these cases, I removed the data points for the joints involving these segments from the steps used in analysis. This included all midfoot-lateral forefoot angles from Chimp L during pole walking, because in all selected steps the lateral forefoot segment deformation index was above the established threshold. See Table 3.2 for the number of steps included in analysis for all joint angles and all locomotor modes. Images of foot and lower limb postures during stance phase in all three locomotor modes are depicted in Figures 3.1-3.3. Patterns of motion at each joint for each locomotor mode are presented in Figures 3.4-7. Patterns of motion for each subject individually are presented in Figures 3.8-11.

Below I provide general descriptions of limb postures during each locomotor mode, followed by more detailed qualitative descriptions of foot and ankle joint kinematics that are pertinent to the hypotheses. I also highlight major differences in motion patterns between subjects. For the sake of simplicity, in these descriptions I will refer to motion between the

segment pairs as occurring at ‘joints’, without specifying the actual anatomical joint at which I believe motion to be occurring.

Ground walking. See Fig. 3.1. Chimp H contacted the ground with the heel first, whereas Chimp L contacted with the entire lateral side of his foot. Otherwise, both subjects exhibited very similar foot postures across stance. They both landed with an inverted foot, which they rapidly everted to bring the entire plantar surface into contact with the ground. During stance, their halluces were moderately abducted, and their interphalangeal joints were extended (i.e., toes were not flexed). Neither subject exhibited a pronounced midtarsal break motion following heel lift. Towards liftoff, both subjects appeared to push-off with the medial side of the foot, and the hallux and second digit were usually the last parts of the foot to leave the substrate. In all of the steps that I analyzed, subjects placed the foot that was being measured lateral to the ipsilateral hand at touchdown. Hind limb ground reaction forces are different between feet placed medial or lateral to the ipsilateral hand (Demes et al., 1994), so I would expect somewhat different foot joint kinematics in these postures. However, because markers were obstructed when the foot was placed medial to hand, I was limited to analysis of laterally placed feet.

In keeping with my qualitative observations of ankle posture, kinematic data indicate that subjects contacted the ground with plantarflexed and inverted leg-rearfoot joints, which they rapidly everted to bring the foot into contact with the substrate (Fig. 3.4a). They inverted and dorsiflexed these joints from 25% to 75% of stance. Simultaneously, they dorsiflexed their rearfoot-midfoot and midfoot-forefoot joints as the heel was lifted from the substrate (Figs. 3.5a-7a). Dorsiflexion of all joints peaked around 75% of support phase, after which they were rapidly plantarflexed prior to liftoff. The primary difference between subjects was the degree to which they dorsiflexed their midfoot joints; Chimp L displayed considerable midfoot-rearfoot dorsiflexion from 25% of stance onward, whereas in Chimp H this motion was virtually absent (Fig. 3.9a). Conversely, Chimp H displayed dramatic midfoot-forefoot joint dorsiflexion during this period, while Chimp L only displayed a small spike in medial midfoot-forefoot dorsiflexion around 80% of stance (Figs. 3.10a-11a).

Pole walking. See Fig. 3.2. The subjects exhibited somewhat different limb postures from one another when walking across the pole substrate. Overall, Chimp L used postures that appeared to indicate a more cautious style of locomotion than Chimp H. Whereas Chimp H used knuckle-walking hand postures, Chimp L used palmigrade hand postures, effectively grasping the pole with his hands as he traveled forward. Both styles have been observed in chimpanzees in the wild, although knuckle-walking is far more common (Hunt, 1992; Doran, 1993). As a consequence of his palmigrade hand posture, Chimp L’s body was positioned closer to the pole, resulting in increased hip flexion, abduction, and external rotation. He also positioned the long axis of his foot at a wide angle to the long axis of the pole during most of stance. Chimp H, on the other hand, maintained a more extended hip joint and positioned his foot at a more acute angle to the pole. Surprisingly, Chimp L used a lateral sequence gait on the pole, whereas Chimp H tended to use diagonal sequence gaits, which is far more common for primates during arboreal locomotion (Young, 2012). Nevertheless, both subjects contacted the substrate in a similar manner at touchdown, bringing the lateral side of the foot down first, followed by the medial side. In both subjects, the medial side of the foot appeared to bear weight throughout stance phase, and liftoff usually occurred between the hallux and second digit.

Subjects displayed similar leg-rearfoot motion patterns to those described for ground walking, except with more exaggerated angular excursions. Unlike ground walking, however, they rapidly abducted the leg-rearfoot joint following touchdown, and then adducted it across the

remainder of stance (Fig. 3.4b). Subjects adopted an everted rearfoot-midfoot joint at touchdown, which they gradually inverted as stance progressed (Fig. 3.5b). Subjects also displayed progressive dorsiflexion of the midfoot-forefoot joints throughout most of stance (Figs. 3.6b-7b). Among subjects, Chimp L displayed marked abduction at the rearfoot-midfoot joint throughout stance, followed by rapid adduction prior to liftoff (Fig. 3.9b). Chimp H displayed progressive eversion and abduction of the midfoot-forefoot joints, whereas Chimp L maintained relatively inverted and adducted postures at these joints throughout most of stance (Figs. 3.10b-11b).

Climbing. See Fig. 3.3. Both subjects exhibited similar limb postures during climbing. They placed their hands on either side of the pole with their upper limbs in tension, while placing their feet against the side of the pole facing them. The hind limb joints were maintained in highly flexed postures during most of stance, and then extended at the initiation of swing phase. Both subjects made touchdown with the medial side of the forefoot first, before bringing the lateral side of the forefoot into contact with the pole. The heel was never brought into contact with the pole. Subjects grasped the pole between the hallux and lateral digits during most of stance. At liftoff, the hallux lost contact with the pole first, and the lateral digit were then carried off by the upward swinging limb.

Foot motion patterns differed during pole climbing from the other two locomotor modes in several respects. Subjects rapidly dorsiflexed the leg-rearfoot joint following touchdown, and then maintained this dorsiflexed posture throughout most of stance (Fig. 3.4c). They exhibited relatively little motion at this joint, and maintained a relatively static rearfoot-midfoot joint, until the final 25% of stance. Then, they rapidly supinated (inverted, adducted, and plantarflexed) the leg-rearfoot joint and pronated (everted, abducted, and dorsiflexed) the rearfoot-midfoot joint (Figs. 3.4c-5c). They progressively dorsiflexed the midfoot-forefoot joints across the first 75% of stance phase, then rapidly pronated these joints prior to liftoff (Figs. 3.6c-7c). There were no major differences in the pattern of motion between subjects during pole climbing.

3.3.3 Minimum and Maximum Joint Angles and Ranges of Motion

Minimum and maximum angles and joint ranges of motion in all three planes for all joints during stance are presented in Tables 3.3-6. Results of Kruskal-Wallis and post-hoc tests are presented in Tables 3.7-9. Note, lower minimum angles indicate a greater magnitude of joint excursion in the direction defined here as negative; i.e., greater plantarflexion, eversion, or abduction. Conversely, greater maximum joint angles indicate greater magnitudes of excursion in motions defined as positive: dorsiflexion, inversion, and adduction.

There were significant differences between locomotor modes in range of motion for all three planes at the leg-rearfoot joint, for the coronal plane at the rearfoot-midfoot joint, and for the transverse plane at the midfoot-forefoot joints (Table 3.7). In every case of significant difference, range of motion was always greatest during pole walking, and was usually lowest during ground walking. Post-hoc tests indicate that range of motion was greater during pole walking than ground walking in each case mentioned above, except for coronal plane motion at the leg-rearfoot joint. Pole walking range of motion was also greater than climbing range of motion in each case except for coronal plane motion at the rearfoot-midfoot joint, and transverse plane motion at the medial midfoot-forefoot joint. Coronal plane range of motion at the leg-rearfoot joint was higher during ground walking than during climbing.

Differences in minimum joint angles between locomotor modes generally reflected the differences in overall joint ranges of motion. Significant differences among locomotor modes occurred in all three planes of motion at the leg-rearfoot joint, and in two planes of motion for

the other three joints (Table 3.8). In pairwise comparisons, subjects tended to exhibit significantly lower minimum angles during pole walking than during the other locomotor modes, and significantly lower minimum angles during ground walking than during climbing. Subjects exhibited a somewhat opposite pattern among locomotor modes in maximum joint angles (Table 3.9). Significant differences occurred in the sagittal plane at the leg-rearfoot joint, in all three planes at the midfoot-lateral forefoot joint, and in two planes at the midfoot-medial forefoot joint. In pairwise comparisons, significantly greater maximum angles tended to occur during climbing. Overall, these results indicate that chimpanzees tend to use more dorsiflexed postures during climbing, and more plantarflexed and everted postures during pole walking, with ground walking generally falling between these extremes.

3.3.4 Coefficients of Multiple Correlation

CMC values are presented in Table 3.10. Because even sample sizes for all treatments are necessary to calculate CMC values, I did not remove joint angle data points calculated from segments that violated the soft tissue deformation index criterion, as I did in previous analyses. Generally, the highest CMC values were calculated for the leg-rearfoot joint, followed by the midfoot-forefoot joints, with the lowest CMC values usually calculated for the rearfoot-midfoot joint. This means that across locomotor modes, the leg-rearfoot joint yielded the most consistent kinematic waveform patterns, and that the rearfoot-midfoot joint yielded the most variable patterns. Sagittal plane motion tended to yield the highest CMC values. Pole walking yielded the highest CMC values most frequently (eight out of 12 cases), followed by ground walking (three out of 12 cases). Climbing usually yielded the lowest CMC values (seven out of 12 cases). This means that kinematics waveform patterns were least variable during pole walking, and most variable during climbing. These results can be interpreted as indicating the use of relatively consistent foot postures during pole walking, and relatively variable foot postures during climbing. The CMC value calculated for coronal plane motion at the rearfoot-midfoot joint during ground walking was actually expressed as an imaginary number. This can happen in cases of extreme difference between waveforms (Ferrari et al., 2010), and in this case simply indicates that coronal plane motion at this joint during ground walking showed very different patterns between subjects. In other words, this result is equivalent to a very low CMC value.

3.4 Discussion

For this chapter I collected quantitative data of chimpanzee foot joint kinematics in order to provide an accurate characterization of joint motion during different locomotor modes, and to test hypotheses about relative foot mobility during these modes. I will begin the discussion of these data by considering the major joint complexes individually, and then I will discuss differences in overall foot mobility among the locomotor modes. As previously mentioned, I assume that motion between the leg and rearfoot segments occurred at the talocrural (plantarflexion-dorsiflexion) and subtalar (inversion-eversion) joints of the ankle complex, motion between the rearfoot and midfoot segments occurred primarily at the calcaneocuboid joint, motion between the midfoot and lateral forefoot segments occurred at the cuboid-metatarsal joints, and motion between the midfoot and medial forefoot segments occurred at the lateral and intermediate cuneiform-metatarsal joints.

3.4.1 Ankle Kinematics

The first hypothesis of this chapter states that chimpanzees use different ankle postures during locomotion on arboreal substrates than during locomotion on terrestrial substrates. The first prediction of this hypothesis, that chimpanzees will use more dorsiflexed ankle joints during arboreal locomotion, was supported. Subjects used significantly greater maximum dorsiflexion angles during both pole walking and climbing than during ground walking. The difference between terrestrial and arboreal locomotor modes for this variable was greater than 10° on average, suggesting that the relatively high range of passive dorsiflexion motion measured in chimpanzees (Thorpe et al., 1999; Holowka and O'Neill, 2013; Thompson et al., 2014; present study) is adaptive for arboreal locomotion.

DeSilva (2009) argued that this high range is particularly adaptive for climbing, although Venkataraman et al. (2013) found that human foragers use dorsiflexion postures similar to chimpanzees when climbing to obtain wild honey. Overall joint range of motion, they suggested, may be related to muscle fiber length, and hence highly variable among modern humans. However, osteological features of the chimpanzee ankle joint suggest that the bony morphology of chimpanzees may be better adapted than that of humans to accommodate high dorsiflexion angles (Latimer et al., 1987; DeSilva, 2009). In this study I measured average maximum dorsiflexion angles of 26° during climbing, which is far below the average of 45° measured by DeSilva (2009) for wild chimpanzees. The discrepancy between our results is likely due to methodological differences in angle measurement, rather than differences between captive versus wild individuals. I measured angles using a marker-based 3-D kinematic technique, whereas DeSilva measured angles directly from 2-D videos recorded in the wild under less controlled conditions. The subjects in the present study were healthy and highly active, and did not use the full range of ankle dorsiflexion motion that I measured in passive manipulations when they were climbing. Therefore, the lower angular excursions measured in the present study are not likely to be due to captivity-related inflexibility. The climbing dorsiflexion angles measured in this study are similar to those reported for gibbons (Yamazaki and Ishida, 1984) and spider monkeys (Hirasaki et al., 1993), but above those measured for Japanese macaques (Hirasaki et al., 1993). This supports the idea that these climbing postures are shared by more plantigrade primates (Schmitt and Larson, 1995), including humans (Venkataraman et al., 2013), but that more digitigrade primates use a different climbing style. As noted by DeSilva (2009), this difference may be related to the high midfoot mobility of some monkeys, which obviates the need for highly dorsiflexed ankle postures during climbing.

Chimpanzees use similar maximum dorsiflexion angles during climbing and pole walking, which indicates that chimpanzee talocrural joint features associated with high dorsiflexion angles are not solely climbing adaptations *per se*. High dorsiflexion during pole walking is likely part of an overall kinematic strategy to improve stability during arboreal locomotion. Primates adopt flexed, compliant limbs when travelling on arboreal supports to reduce peak limb forces and lateral toppling moments (Cartmill, 1985; Schmitt, 1998, 1999; Larney and Larson, 2004; Chadwell and Young, 2015). Accordingly, the chimpanzees in this study dorsiflexed their ankles to a much higher degree during pole walking than when walking on the ground. To my knowledge, no other study has reported quantitative anthropoid ankle joint motion data during arboreal support walking, but Meldrum (1991) described ankle and foot motion during arboreal travel in cercopithecines. In his descriptions and depictions, these animals do not use high talocrural dorsiflexion angles, but instead exhibit substantial midfoot dorsiflexion as the hip extends and the knee flexes during stance. Cercopithecines possess highly mobile midfeet that dorsiflex following heel lift during walking (Meldrum, 1991; Berillon et al., 2010; DeSilva,

2010; Hirasaki et al., 2010; Greiner and Ball, 2014). Chimpanzees possess less mobile midfeet than cercopithecines (DeSilva, 2010; Greiner and Ball, 2014), so they may need a greater range of talocrural joint motion to facilitate limb compliance when walking on arboreal substrates.

The second prediction of the first hypothesis states that chimpanzees will use greater ankle inversion angles during arboreal locomotion than during terrestrial locomotion. This prediction was partially supported; inversion angles are not significantly different between locomotor modes, but chimpanzees only use highly inverted ankle joints at touchdown during ground walking. During climbing, chimpanzees maintain inverted ankle joints throughout stance, whereas during ground walking, chimpanzees maintain everted postures after ~10% of stance. Therefore, chimpanzees use more inverted postures during climbing than during ground walking when considering the periods where the hind limb is expected to face the greatest substrate reaction forces during these behaviors (Hirasaki et al., 1992; Pontzer et al., 2014). Chimpanzees use similar inversion angles during ground walking and pole walking.

The majority of both coronal and transverse plane motion at the chimpanzee ankle is expected to occur at the subtalar joint (Elftman and Manter, 1935a; Lewis, 1980a; b; Latimer et al., 1987). Several studies have used measurements of articular surface curvature to suggest that chimpanzees are capable of loading their subtalar joints in a greater range of postures than humans (Deloison, 1985; Latimer and Lovejoy, 1989; Zipfel et al., 2011; Prang, 2016). The passive ranges of motion measured for the subjects in this study support this notion, with chimpanzees exhibiting roughly twice the range of motion reported in human studies (49° vs. 20-30°) that used similar measurement methods⁷ (Root et al., 1977; Kapandji, 1987; Grimston et al., 1993; Menadue et al., 2006). Chimpanzees are thought to need high subtalar mobility to adopt inverted foot postures during arboreal locomotion (Lewis, 1980a; DeSilva, 2009; Zipfel et al., 2011). Therefore, it is somewhat surprising that what actually distinguishes chimpanzees from humans is their high *eversion* range of motion. Chimpanzee passive inversion ranges overlap with some of those reported for humans (20° vs. 10-20°) (Grimston et al., 1993; Menadue et al., 2006), but their passive eversion ranges are roughly twice as high (29° vs. 10-15°). These results suggest that the chimpanzee subtalar joint may actually be adapted to allow more everted foot postures during arboreal locomotion.

During arboreal and terrestrial walking, chimpanzees contact the substrate with relatively inverted subtalar joint postures, fitting previous qualitative descriptions of chimpanzee and bonobo foot strikes (Elftman and Manter, 1935b; Vereecke et al., 2003). During ground walking, chimpanzees rapidly evert the subtalar joint following touchdown to bring the medial side of the foot into full contact with the underlying substrate, in contrast to several previous descriptions of chimpanzee foot motion (Weidenreich, 1923; Tuttle, 1970; Gebo, 1992), but in accordance with Elftman and Manter (1935b). Subtalar eversion is even more dramatic during arboreal support walking, possibly because chimpanzees are forced to place their feet closer to the body's midline

⁷ Subtalar joint range of motion is notoriously difficult to measure due to the oblique position of its axis relative to other standard hind limb reference points. Consequently, measurements of subtalar range of motion in humans vary dramatically between studies, from 10 to 60°, due largely to different measurement methods (Jastifer and Gustafson, 2014). To ensure an accurate comparison between my measurements on chimpanzee subjects and those from previous studies on human subjects, I only compare my results to studies where the coronal plane component of subtalar joint motion was measured specifically. This discrimination allows for the most reliable interspecies comparisons possible.

than during terrestrial locomotion. The subjects in this study placed their feet atop the pole in a manner similar to that described by Meldrum (1991) for semi-terrestrial cercopithecines. Chimpanzees possess a relatively varus neutral position of the talocrural joint (Latimer et al., 1987), so a high subtalar eversion range may be necessary to place the foot below the body on top of the support.

In contrast to walking locomotor modes, the subjects in this study maintained a relatively static, slightly inverted foot posture during climbing stance phase. This inversion could be occurring at the subtalar joint, but it could also be occurring at the talocrural joint as a consequence of joint articular surface geometry. Specifically, the tall lateral margin of the chimpanzee talar trochlea (relative to medial margin) places the chimpanzee foot in an inverted neutral position relative to the leg (Latimer et al., 1987). Chimpanzees maintain highly dorsiflexed ankles during climbing, which should also result in inverted foot postures based on Lewis' (1980b) reconstruction of talocrural joint motion. A similar phenomenon occurs during pole walking, where the ankle dorsiflexion between 25% and 75% of stance is accompanied by steady inversion. Together, these results support the notion that talocrural dorsiflexion and inversion are coupled in chimpanzees (Lewis, 1980b). However, contrary to the expectations of Lewis (1980b) and Latimer et al. (1987), these motions do not coincide with ankle abduction; instead, adduction of the rearfoot coincides with inversion during all locomotor modes. This result is likely due to the fact that subtalar inversion and adduction coincide (Elftman and Manter, 1935a; Lewis, 1980a), and this motion may overwhelm any opposing abduction at the talocrural joint.

3.4.2 Midtarsal Break Kinematics

The second hypothesis states that both the transverse tarsal and cuboid-metatarsal joint complexes participate in the midtarsal break. My first prediction was that chimpanzees would dorsiflex their calcaneocuboid joints following heel lift during ground walking. In this study, I measured motion of the calcaneus relative to a midfoot segment that included the cuboid and navicular bones, but because I was unable to measure talus motion, I assume that rearfoot-midfoot motion captured in this study is mainly representative of motion at the calcaneocuboid joint. Under this assumption, the two subjects in this study exhibited somewhat different calcaneocuboid joint kinematics across the different locomotor modes investigated. During ground walking, Chimp L exhibited progressive joint dorsiflexion after the first 25% of stance, which peaked just prior to liftoff. The precise initiation of heel lift is not easy to distinguish without plantar pressure measurements, but appeared to occur around 50% of stance phase based on inspection of videos. Active dorsiflexion of the rearfoot relative to the forefoot during heel lift indicates the presence of a midtarsal break at the calcaneocuboid joint in Chimp L. Chimp H, on the other hand, exhibited progressive abduction of this joint during heel lift, but very little sagittal plane motion, indicating the absence of a midtarsal break at the calcaneocuboid joint. These results provide partial support for the first prediction; one subject showed a midtarsal break at the calcaneocuboid joint, but this joint does not appear to be a universal midtarsal break site in chimpanzees.

Chimp L was further distinguished from Chimp H by using more dorsiflexed and abducted calcaneocuboid joint postures during pole walking, and more inverted postures during climbing. The greater active mobility of this joint in Chimp L ran contrary to expectations based on its lower passive range of motion measured in cineradiography (Thompson et al., 2014). In that study, Chimp H exhibited over twice as much calcaneocuboid joint motion as Chimp L

during passive foot flexion. A number of factors could account for these conflicting results, but one likely explanation is that Chimp H actively limited calcaneocuboid joint motion during locomotion *via* contraction of foot muscles. This finding suggests that caution is warranted when making conclusions about joint function based solely on passive manipulation.

The second prediction of the second hypothesis states that chimpanzees will dorsiflex their cuboid-metatarsal joints following heel lift during ground walking. In the converse of their respective calcaneocuboid joint motions, Chimp H exhibited progressive cuboid-metatarsal joint dorsiflexion during heel lift, whereas this joint complex was relatively static throughout stance in Chimp L. These results again provide partial support for my prediction: the cuboid-metatarsal joint complex can be a site of midtarsal break motion in chimpanzees, but is not so in all individuals. Therefore, overall, the second hypothesis of this chapter is supported: the calcaneocuboid and cuboid-metatarsal joints are both sites of the midtarsal break in chimpanzees. However, in neither subject did both joints contribute to this motion, so the individual roles of these joints in the midtarsal break appear to be variable among individuals. This result is in-line with the intersubject variability measured at these joints in passive range of motion studies (Greiner and Ball, 2014; Thompson et al., 2014).

It must be pointed out that the total midfoot dorsiflexion following heel lift that was measured in this study was only about 10° for both subjects. This magnitude is small relative to what has been previously reported and depicted for the midtarsal break in chimpanzees and bonobos (Vereecke et al., 2003; DeSilva, 2010). From careful inspection of video recordings of seven other chimpanzees from past projects carried out at the Stony Brook Primate Locomotion Laboratory, I observed that the degree of midfoot dorsiflexion following heel lift is somewhat variable across chimpanzee individuals. This is consistent with plantar pressure studies that have indicated variability in midtarsal break magnitude among bonobos (Griffin et al., 2010; Bates et al., 2013). In that sense, the subjects in this study by no means display the full range of variation present in chimpanzees. Across the spectrum of the individuals I observed, Chimp H and Chimp L show relatively limited midfoot dorsiflexion following heel lift. However, they were certainly not outliers among the individuals I observed, so they should be assumed to fall within the normal range of variation of chimpanzees with respect to midtarsal break magnitude.

3.4.3 Tarsometatarsal Joint Kinematics

The third hypothesis of this chapter states that the lateral and intermediate cuneiform-metatarsal joints are less mobile than the cuboid-metatarsal joints in chimpanzees during locomotion. I predicted that the former joints would exhibit lower overall ranges of motion across locomotor modes than the latter. Inspection of joint ranges of motion in Tables 3.5 and 3.6 clearly refute this prediction. The cuneiform-metatarsal joints show similar or higher ranges of motion than the cuboid-metatarsal joints in all locomotor modes, except in the coronal plane. Interestingly, both joint complexes show similar patterns of motion across all locomotor modes. This result was surprising when considering the relatively complex articular surface morphology of these joints (Lewis, 1980a) but chimpanzee plantar pressure data may explain this paradox. Elftman and Manter (1935b) and Wunderlich (1999) found that chimpanzees push-off on the medial sides of their feet following heel lift during ground walking, likely exposing their medial tarsometatarsal joints to relatively high torques. Wunderlich also found that chimpanzees primarily load the medial sides of their feet during pole walking. Although she does not present results for climbing steps, pressure distributions during this behavior are likely to be similar to those of pole walking, based on my inspection of videos from the present study. Therefore, I

expect the cuneiform-metatarsal joints to experience higher joint torques than the cuboid-metatarsal joints during all three locomotor modes investigated here, which could explain the relative amounts of motion at these joint complexes. The differences in range of motion suggest that the articular surface morphologies of these joints may not reflect their actual relative mobility *in vivo*.

3.4.4 Overall Foot Mobility

The fourth hypothesis states that overall foot joint mobility will differ across locomotor modes. I predicted that chimpanzees would use greater ranges of motion during arboreal locomotion than during ground walking. This prediction received partial support; subjects exhibited significantly higher ranges of motion in at least one plane at all four joint complexes during pole walking compared to ground walking. This result indicates that chimpanzees require mobile ankle and midfoot joints to adjust to the challenges of maintaining balance and stability while walking on arboreal substrates. In particular, the high coronal plane motion at the calcaneocuboid joint during pole walking suggests that this joint is adapted to allow the rearfoot to pivot while the forefoot is maintained in a stable grasping position on the pole. High transverse plane tarsometatarsal joint mobility also appears to allow the foot to better conform to the substrate during pole walking. However, the subjects in this study did not exhibit significant differences in ranges of motion between ground walking and climbing, except at the subtalar joint, where they used a greater range of coronal plane motion during ground walking. Furthermore, they exhibited significantly greater ranges of motion during pole walking than they did during climbing at the talocrural, subtalar, and cuboid-metatarsal joints. Therefore, my second prediction, that chimpanzees would exhibit the highest overall foot mobility during climbing, was clearly refuted.

This result is surprising in light of arguments that overall foot mobility in chimpanzees is adaptive for climbing (Langdon, 1986; DeSilva, 2009, 2010; Lovejoy et al., 2009; White et al., 2015). During climbing, chimpanzees use their digits to grasp the substrate, but the rest of the foot is held relatively stationary. The heel never touches the substrate, likely due in part to the high dorsiflexion angles at the midfoot joints. Chimpanzees also maintain relatively high subtalar and calcaneocuboid joint inversion angles, as well as abducted tarsometatarsal joint angles during climbing. Therefore, although the foot joints generally do not exhibit large ranges of motion during a climbing step, high joint mobility may enable chimpanzees to position their feet into optimal postures during climbing. Interestingly, climbing tended to yield the lowest CMC values, meaning that foot motion patterns were more variable in this locomotor mode than in either of the other two modes investigated. The use of less stereotypical foot postures during climbing could be taken to indicate that chimpanzees use whatever posture is sufficient to achieve a good grip on the substrate and avoid falling. Chimpanzees may need high foot joint mobility to utilize these more variable foot postures during climbing, even if they do not use high joint ranges of motion.

The subjects in this study used notably different lower limb postures during pole walking, so one might question the extent to which foot kinematics in these individuals was consistent enough to make general statements about this locomotor mode. Surprisingly, for 75% of the joint planes of motion measured in this study, I calculated the highest between-subject CMC values for pole walking. This result indicates that subjects exhibited greater similarity in foot joint kinematics between steps during pole walking than during any other locomotor mode. *A priori*, I would have expected to calculate the highest CMC values during ground walking, considering

the simplicity of the substrate when compared to an arboreal support. However, the higher CMC values in pole walking are not surprising when considering the kinematic data, which reveal differences in midfoot motion between the subjects during ground walking. Based on these results, we can conclude that the marked differences in overall lower limb posture between subjects during pole walking did not translate into great between subject differences in foot kinematics. Therefore, the pole walking results from this study should be generally representative for chimpanzees.

3.4.5 Overall Foot Kinematics

Here I provide a general description of foot kinematics in chimpanzees that highlights the differences between the locomotor modes and summarizes the major points of the preceding discussion. During ground walking, chimpanzees touchdown with a plantarflexed and highly inverted foot, which they rapidly evert to bring the full plantar surface into contact with the substrate. From 25 to 75% of stance phase, chimpanzees dorsiflex the talocrural joint, and progressively dorsiflex the midfoot joints (transverse tarsal and/or tarsometatarsal) as the heel is being lifted from the substrate. In the final 25% of stance they plantarflex the foot at the talocrural joint to push off of the substrate, and dorsiflex the rearfoot relative to the planted forefoot at the midfoot joints.

During pole walking, chimpanzees also touchdown with a relatively inverted and plantarflexed foot. Following touchdown, they evert (and abduct) the foot at the subtalar joint to an even greater degree than in ground walking, likely to position the foot atop the pole near the body's median sagittal plane. From 25-75% of stance, they dramatically dorsiflex the talocrural joint, and supinate (invert and adduct) the foot at the subtalar joint under the forward-moving leg. This motion is accompanied by eversion of the rearfoot relative to the midfoot at the transverse tarsal joints as the heel is being lifted from the pole. Simultaneously, the rising midfoot supinates at the tarsometatarsal joints relative to the forefoot. This series of rotations likely enables the forefoot to maintain a strong grasp on the pole while the foot is being lifted and the leg is moving forward.

During climbing, chimpanzees again touchdown with a foot that is relatively inverted at the subtalar joint, but unlike in the other locomotor modes they maintain this joint position throughout the remainder of stance. This position likely improves climbing stability by allowing a greater percentage of the forefoot to contact the pole, thereby increasing friction and preventing slippage. Following touchdown chimpanzees invert the foot further at the transverse tarsal joints, and dorsiflex the midfoot at the tarsometatarsal joints. Due in part to the latter motion, the heel fails to make contact with the pole at any time in stance. Chimpanzees dorsiflex the foot at the talocrural joint at the beginning of stance, but then maintain the ankle and midfoot joints in a relatively static position throughout the majority of stance. At the end of stance they plantarflex the foot at the talocrural joint and and slightly supinate the midfoot joints to lift the foot from the substrate.

These descriptions reveal the major differences in intrinsic foot motion between the three locomotor modes described here. Most notably, pole walking requires marked rotatory mobility at the subtalar, transverse tarsal, and tarsometatarsal joints throughout stance phase to facilitate a stable pedal grasp on the substrate while the leg is moving forward. Climbing requires some midfoot and subtalar mobility to properly position the foot following touchdown, but otherwise the foot is maintained in a relatively static posture throughout most of stance in this locomotor mode. During ground walking the foot utilizes only a subset of the joint mobility exhibited

during the arboreal locomotor modes, functioning as a relatively rigid lever during push-off, albeit with some midfoot dorsiflexion occurring during heel lift.

3.4.6 Limitations

In addition to the study limitations discussed in Chapter 2, Section 2.6, several other limitations that characterize the data collected in this chapter must be acknowledged.

Foot Posture. Both subjects in this study consistently walked with fully extended interphalangeal joints and an abducted hallux. However, some chimpanzees walk with flexed digits and adducted halluces (Tuttle, 1970; Susman, 1983), and these postures have been found to influence plantar pressure distributions in bonobos (Vereecke et al., 2003), so they could influence foot kinematics as well. Due to the small subject sample and great time required for data processing, I could not capture the full breadth of variation in chimpanzee foot postures in this study. However, these data present chimpanzee foot function under standardized conditions during locomotion *in vivo*. Therefore, they can still be used to draw broad conclusions about chimpanzee foot functional morphology.

Substrates. The substrates I chose for this study represented highly simplified versions of the substrates chimpanzees actually encounter in the wild. Chimpanzee foot kinematics may differ on more natural, uneven surfaces, which should be taken into account in interpreting the results of this study. However, changing the substrates in a manner to simulate these conditions would likely have yielded wildly inconsistent results that would have provided little useful insight into chimpanzee foot function. Therefore, it was necessary to use simplified substrate types.

As previously described, the pole substrate used in this study was designed with the purpose of mimicking an arboreal support that an adolescent male chimpanzee would actually climb or walk on in the wild (see Chapter 2, Section 2.3). That said, chimpanzees travel on a wide variety of different support sizes and shapes in the wild (Doran, 1992a, 1993; Hunt, 1992), and it is quite likely that foot kinematics differ markedly across these supports. Therefore, it must be acknowledged that foot joint kinematics could reveal much different patterns and ranges of motion during travel on substrates of different sizes, so I do not claim to have captured the full variety of arboreal foot postures. However, what I have captured is how travel on substrate orientations that present different mechanical challenges, but are both common to normal chimpanzee locomotion, affect foot kinematics in different ways.

Speed. Unfortunately, I could not measure speed of locomotion, so I selected steps for analysis with consistent stance phase durations within each locomotor mode. Previous studies have demonstrated the relationship between stance duration and speed during ground walking chimpanzees and bonobos (Demes et al., 1994; Vereecke et al., 2004; Pontzer et al., 2014); however, the relationship between these variables is unknown during locomotion on arboreal substrates. I suspect that some variation in speed of locomotion across locomotor modes would have a relatively minor effect on joint kinematics relative to differences caused by substrate types, but this remains to be demonstrated.

3.4.7 Conclusions

The results of this study reveal that chimpanzee foot joints are adapted for arboreal locomotion in several unexpected ways. Chimpanzees possess a high talocrural joint range of dorsiflexion that they utilize to a similar degree during both climbing and walking on arboreal supports. They also possess a high range of subtalar eversion, which they use to place their feet

close to the body's midline when travelling atop arboreal supports. Surprisingly, the passive chimpanzee subtalar joint inversion range of motion is similar to that of humans, and chimpanzees only use moderately inverted ankle postures during climbing. Both the calcaneocuboid and cuboid-metatarsal joints can contribute to the midtarsal break, but the magnitude and site of this motion is variable between individuals. Additionally, motion at the cuneiform-metatarsal joints tended to be slightly greater than motion at the cuboid-metatarsal joints across locomotor modes, likely reflecting the patterns of forefoot loading at push-off. The intrinsic foot joints of chimpanzees generally exhibit greater ranges of motion during pole walking than either of the other locomotor modes examined here, which suggests that high foot joint mobility is particularly advantageous for maintaining balance atop arboreal supports. Climbing, on the other hand, involves high ankle and midfoot dorsiflexion angles, but relatively stationary foot joints otherwise.

These results have important overall implications for our understanding of chimpanzee foot functional morphology, as well as hominin foot evolution. The chimpanzee foot has often been characterized as a highly mobile prehensile organ, and as such is placed in dichotomy to the human foot. However, the chimpanzee midfoot joint motion measured here is dramatically less than that depicted and described for cercopithecines (Meldrum, 1991; Berillon et al., 2010; DeSilva, 2010; Hirasaki et al., 2010; Greiner and Ball, 2014) and Asian apes (Tuttle, 1970; Gebo, 1992; Vereecke et al., 2005). Therefore, the chimpanzee foot should be characterized as stiff relative to that of all other anthropoids except humans (and perhaps gorillas). It is probable that chimpanzees have evolved (or retained) a relatively stiff midfoot in order to provide joint stability during push-off from terrestrial substrates. This would allow the foot to function as a more efficient lever during terrestrial locomotion, which takes up the greatest percentage of the chimpanzee locomotor repertoire in the wild (Doran, 1992a; b; Hunt, 1992; Sarringhaus et al., 2014). The reduced midfoot mobility, however, likely requires chimpanzees to use more dorsiflexed ankle joint postures during horizontal and vertical arboreal substrate locomotion than those previously described for cercopithecines (Meldrum, 1991; Hirasaki et al., 1993).

Chimpanzees do, however, exhibit several interesting intrinsic foot joint motion patterns that may indicate bony adaptation to locomotion on arboreal supports. The high subtalar eversion exhibited during pole-walking, coupled with the high passive eversion range of motion measured in this study, may be reflected in the highly curved articular surface morphology reported for the chimpanzee subtalar joint posterior facet (Deloison, 1985; Latimer and Lovejoy, 1989; Zipfel et al., 2011; Prang, 2016). Motion at the calcaneocuboid joint, which is used to evert and invert the midfoot to a high degree while walking and climbing on pole substrates, may be related to the articular surface morphology of this joint, which is characterized by a relatively centrally located flange on the cuboid and a corresponding concavity on the calcaneus (Bojsen-Møller, 1979; Lewis, 1980a; Susman, 1983). The cuneiform- and cuboid-metatarsal joints in chimpanzees also appear to be adapted for relatively high sagittal and transverse plane mobility during arboreal locomotion. The chimpanzee fourth metatarsal presents a relatively convex base (DeSilva, 2010; Proctor, 2013), which may be indicative of this cuboid-metatarsal joint mobility. However, no morphological correlates of chimpanzee cuneiform-metatarsal mobility have yet been investigated. The talonavicular joint, at which I was not able to capture motion in this study, is also likely to be a site of considerable mobility during chimpanzee locomotion. This joint has been shown to be more mobile than the calcaneocuboid joint in passive manipulation studies (Greiner and Ball, 2014; Thompson et al., 2014), and could also be a major site of motion during arboreal locomotion.

As has been previously suggested (Stern and Susman, 1983; Deloison, 1985; Latimer et al., 1987; Latimer and Lovejoy, 1989; DeSilva, 2009), chimpanzees need exceptional talocrural and subtalar joint mobility to position the foot at high excursion angles during arboreal locomotion. Of the joints investigated in this study, these appear to be the most critical for enabling chimpanzees to travel on arboreal supports in the manner that they do. However, none of the joints in this study exhibits any particularly extreme motion patterns during climbing alone. Therefore, it is likely that the chimpanzee foot joints are adapted to meet the general demands of travel on arboreal supports, but are not specifically adapted for climbing *per se*. As such, chimpanzee pedal morphology should not be taken to represent an extreme climbing adaptation in comparative studies focused on hominin foot evolution. Rather, chimpanzees possess feet that are versatile structures adapted to both extensive travel on the ground, and generalized locomotion on arboreal substrates.

Chapter 3: Tables

Table 3.1. Passive ranges of motion in chimpanzee subjects.

Joint	Motion	Chimp H (8.5 years)	Chimp L (8.5 years)	Average
Talocrural	Plantarflexion	65°	55°	50°
	Dorsiflexion	43°	41°	42°
	Total	108°	96°	102°
Subtalar	Inversion	24°	15°	19.5°
	Eversion	28°	29°	28.5°
	Total	52°	44°	48°

Table 3.2. Number of steps used in analysis for each joint and each locomotor mode.

Mode	Leg-Rearfoot	Rearfoot- Midfoot	Midfoot-Lat. Forefoot	Midfoot-Med. Forefoot
Ground Walking				
<i>Chimp H</i>	5	5	5	5
<i>Chimp L</i>	5	4	4	4
<i>Total</i>	10	9	9	9
Pole Walking				
<i>Chimp H</i>	5	5	5	5
<i>Chimp L</i>	5	5	0	5
<i>Total</i>	10	10	5	10
Climbing				
<i>Chimp H</i>	5	4	4	4
<i>Chimp L</i>	5	5	5	5
<i>Total</i>	10	9	9	9

Table 3.3. Average maximum and minimum angles and ranges of motion between the *leg* and *rearfoot* for all locomotor modes.

Plane	Motion	Ground Walking	Pole Walking	Climbing
Sagittal	Plantarflexion	-11.4 ± 3.9°	-11.6 ± 7.4°	-1 ± 5.4°
	Dorsiflexion	13 ± 5.2°	26.2 ± 5.5°	26.3 ± 3.7°
	<i>Range</i>	24.4 ± 3.5°	37.8 ± 4.8°	27.3 ± 4.1°
Coronal	Eversion	-5.6 ± 5.9°	-11.4 ± 9.4°	1.7 ± 6.9°
	Inversion	12.5 ± 8.2	10 ± 3.3°	11.8 ± 5.7°
	<i>Range</i>	18.1 ± 5.3	21.3 ± 9.2°	10.1 ± 5°
Transverse	Abduction	-3.3 ± 2.1°	-8.8 ± 2.7°	-3.9 ± 1.9°
	Adduction	4.8 ± 2.5°	4 ± 3.9°	4.3 ± 3.4°
	<i>Range</i>	8.1 ± 2.1°	12.8 ± 3.8°	8.2 ± 2.7°

Table 3.4. Average maximum and minimum angles and ranges of motion between the *rearfoot* and *midfoot* for all locomotor modes.

Plane	Motion	Ground Walking	Pole Walking	Climbing
Sagittal	Plantarflexion	$0 \pm 3.4^\circ$	$-6.2 \pm 4.7^\circ$	$-4.5 \pm 3.2^\circ$
	Dorsiflexion	$7.9 \pm 4.4^\circ$	$3.8 \pm 3.2^\circ$	$3.5 \pm 2.7^\circ$
	<i>Range</i>	$7.9 \pm 2.3^\circ$	$9.9 \pm 2.8^\circ$	$8 \pm 3.7^\circ$
Coronal	Eversion	$-3.3 \pm 3.5^\circ$	$-7 \pm 2.3^\circ$	$-1.0 \pm 4.9^\circ$
	Inversion	$2.9 \pm 3.5^\circ$	$3.8 \pm 3.4^\circ$	$7.5 \pm 5.9^\circ$
	<i>Range</i>	$6.2 \pm 2.1^\circ$	$10.8 \pm 3.2^\circ$	$8.5 \pm 2.6^\circ$
Transverse	Abduction	$-5.8 \pm 2.2^\circ$	$-3.1 \pm 7.4^\circ$	$-4.7 \pm 1.3^\circ$
	Adduction	$1.6 \pm 1.1^\circ$	$5.5 \pm 4.5^\circ$	$1.8 \pm 2.5^\circ$
	<i>Range</i>	$7.5 \pm 1.9^\circ$	$8.7 \pm 3.7^\circ$	$6.5 \pm 2^\circ$

Table 3.5. Average maximum and minimum angles and ranges of motion between the *midfoot* and *lateral forefoot* for all locomotor modes.

Plane	Motion	Ground Walking	Pole Walking	Climbing
Sagittal	Plantarflexion	$-5.6 \pm 2.7^\circ$	$1.7 \pm 1.4^\circ$	$-0.7 \pm 1.6^\circ$
	Dorsiflexion	$3.8 \pm 3.5^\circ$	$8.9 \pm 1.5^\circ$	$7 \pm 2.9^\circ$
	<i>Range</i>	$9.3 \pm 2^\circ$	$7.2 \pm 2^\circ$	$7.7 \pm 2.9^\circ$
Coronal	Eversion	$-3.4 \pm 2^\circ$	$-12.5 \pm 2.3^\circ$	$-4.4 \pm 2.6^\circ$
	Inversion	$5.3 \pm 2.5^\circ$	$-0.8 \pm 1.4^\circ$	$6.1 \pm 2^\circ$
	<i>Range</i>	$8.7 \pm 2.8^\circ$	$11.7 \pm 3.3^\circ$	$10.5 \pm 2.3^\circ$
Transverse	Abduction	$-3.5 \pm 0.5^\circ$	$-2.8 \pm 0.6^\circ$	$-4.1 \pm 4.2^\circ$
	Adduction	$1.2 \pm 1.2^\circ$	$6.2 \pm 2.9^\circ$	$1.4 \pm 4.4^\circ$
	<i>Range</i>	$4.7 \pm 1.4^\circ$	$9 \pm 2.5^\circ$	$5.6 \pm 1.9^\circ$

Table 3.6. Average maximum and minimum angles and ranges of motion between the *midfoot* and *medial forefoot* for all locomotor modes.

Plane	Motion	Ground Walking	Pole Walking	Climbing
Sagittal	Plantarflexion	$-5.1 \pm 1.8^\circ$	$-3.2 \pm 4.2^\circ$	$3.1 \pm 2.7^\circ$
	Dorsiflexion	$5.4 \pm 2.4^\circ$	$7.2 \pm 3.5^\circ$	$12.7 \pm 3.6^\circ$
	<i>Range</i>	$10.5 \pm 4^\circ$	$10.5 \pm 1.5^\circ$	$9.6 \pm 1.9^\circ$
Coronal	Eversion	$-1.8 \pm 2.7^\circ$	$-5.7 \pm 4.8^\circ$	$-2.1 \pm 2.3^\circ$
	Inversion	$5.6 \pm 4.3^\circ$	$3.8 \pm 4.2^\circ$	$7 \pm 2.6^\circ$
	<i>Range</i>	$7.3 \pm 2.4^\circ$	$9.5 \pm 2.1^\circ$	$9.1 \pm 2.1^\circ$
Transverse	Abduction	$-4.8 \pm 2.5^\circ$	$-1.9 \pm 3.1^\circ$	$-6.7 \pm 2.3^\circ$
	Adduction	$1.1 \pm 1^\circ$	$10.6 \pm 6.7^\circ$	$0.3 \pm 2.3^\circ$
	<i>Range</i>	$5.9 \pm 2.5^\circ$	$12.4 \pm 5.1^\circ$	$7 \pm 2.2^\circ$

Table 3.7. *P*-values for Kruskal-Wallis and post-hoc tests for differences between groups in range of motion. Bold indicates *P*-value below alpha significance level for Kruskal-Wallis tests (0.05) and post-hoc tests with a sequential Bonferroni adjustment.

Joint	Plane	Kruskal-Wallis	Post-Hoc Tests		
			GW vs. PW	GW vs. C	PW vs. C
Leg-Rearfoot	Sagittal	4 E -5	PW > GW 1 E -5	0.5	PW > C 4 E -3
	Coronal	3 E -3	0.9	GW > C 0.02	PW > C 5 E -3
	Transverse	6 E -3	PW > GW 0.01	0.9	PW > C 0.02
Rearfoot-Midfoot	Sagittal	0.27	-	-	-
	Coronal	7 E -3	PW > GW 5 E -3	0.2	0.4
	Transverse	0.36	-	-	-
Midfoot-Lateral Forefoot	Sagittal	0.2	-	-	-
	Coronal	0.1	-	-	-
	Transverse	0.01	PW > GW 0.01	0.8	PW > C 0.04
Midfoot-Medial Forefoot	Sagittal	0.6	-	-	-
	Coronal	0.1	-	-	-
	Transverse	4 E -3	PW > GW 4 E -3	0.7	0.05

Abbreviations: GW, ground walking; PW, pole walking; C, climbing.

Table 3.8. *P*-values for Kruskal-Wallis and post-hoc tests for differences between groups in *minimum* joint angle. Bold indicates *P*-value below alpha significance level for Kruskal-Wallis tests (0.05) and post-hoc tests with a sequential Bonferroni adjustment. Note, greater sign (>) here is used to indicate which locomotor mode had greater plantarflexion, eversion, or abduction angles.

Joint	Plane	Kruskal-Wallis	Post-Hoc Tests		
			GW vs. PW	GW vs. C	PW vs. C
Leg-Rearfoot	Sagittal	2 E -3	0.9	GW > C 5 E -3	PW > C 8 E -3
	Coronal	0.01	0.4	0.2	PW > C 8 E -3
	Transverse	7 E -4	PW > GW 1 E -3	0.9	PW > C 7 E -3
Rearfoot-Midfoot	Sagittal	9 E -3	PW > GW 0.01	0.05	0.9
	Coronal	0.01	0.1	0.6	PW > C 8 E -3
	Transverse	0.53	-	-	-
Midfoot-Lateral Forefoot	Sagittal	2 E -4	GW > PW 2 E -4	GW > C 0.01	0.3
	Coronal	3 E -3	PW > GW 3 E -3	0.9	PW > C 0.01
	Transverse	0.41	-	-	-
Midfoot-Medial Forefoot	Sagittal	7 E -4	0.8	GW > C 9 E -4	PW > C 7 E -3
	Coronal	0.13	-	-	-
	Transverse	7 E -3	0.3	0.2	C > PW 4 E -3

Abbreviations: GW, ground walking; PW, pole walking; C, climbing.

Table 3.9. *P*-values for Kruskal-Wallis and post-hoc tests for differences between groups in *maximum* joint angle. Bold indicates *P*-value below alpha significance level for Kruskal-Wallis tests (0.05) and post-hoc tests with a sequential Bonferroni adjustment. Note, greater sign (>) here is used to indicate which locomotor mode had greater dorsiflexion, inversion or abduction angles.

Joint	Plane	Kruskal-Wallis	Post-Hoc Tests		
			GW vs. PW	GW vs. C	PW vs. C
Leg-Rearfoot	Sagittal	2 E -4	PW > GW 7 E -4	C > GW 2 E -3	0.9
	Coronal	0.5	-	-	-
	Transverse	0.7	-	-	-
Rearfoot-Midfoot	Sagittal	0.08	-	-	-
	Coronal	0.2	-	-	-
	Transverse	0.2	-	-	-
Lateral Midfoot-Forefoot	Sagittal	0.02	0.02	0.4	0.2
	Coronal	3 E -3	GW > PW 0.01	0.8	C > PW 3 E -3
	Transverse	0.02	0.02	0.8	0.08
Medial Midfoot-Forefoot	Sagittal	1 E -3	0.5	C > GW 1 E -3	0.03
	Coronal	0.23	-	-	-
	Transverse	1 E -4	GW > PW 3 E -3	0.8	C > PW 2 E -4

Abbreviations: GW, ground walking; PW, pole walking; C, climbing.

Table 3.10. Coefficients of multiple correlation (CMC) for each locomotor mode. Bold numbers indicate highest CMC value (smallest variation) across locomotor modes for a given joint and plane.

Mode	Leg-Rearfoot			Rearfoot-Midfoot			Lateral Midfoot-Forefoot			Medial Midfoot-Forefoot		
	Sag.	Cor.	Tran.	Sag.	Cor.	Tran.	Sag.	Cor.	Tran.	Sag.	Cor.	Tran.
Ground Walk	0.959	0.753	0.293	0.476	0.174i	0.742	0.645	0.669	0.704	0.795	0.238	0.731
Pole Walk	0.964	0.670	0.793	0.533	0.655	0.574	0.808	0.495	0.655	0.824	0.595	0.736
Climb	0.949	0.495	0.788	0.498	0.574	0.509	0.606	0.755	0.478	0.762	0.415	0.706

Chapter 3: Figures



Fig. 3.1. Foot postures across stance phase in Chimp L during ground walking. Images represent roughly 0%, 25%, 50%, 75% and 98% of stance.



Fig. 3.2. Foot postures across stance phase in Chimp H during pole walking. Images represent roughly 0%, 25%, 50%, 75% and 98% of stance.



Fig. 3.3. Foot postures across stance phase in Chimp H during climbing. Images represent roughly 0%, 25%, 50%, 75% and 98% of stance.

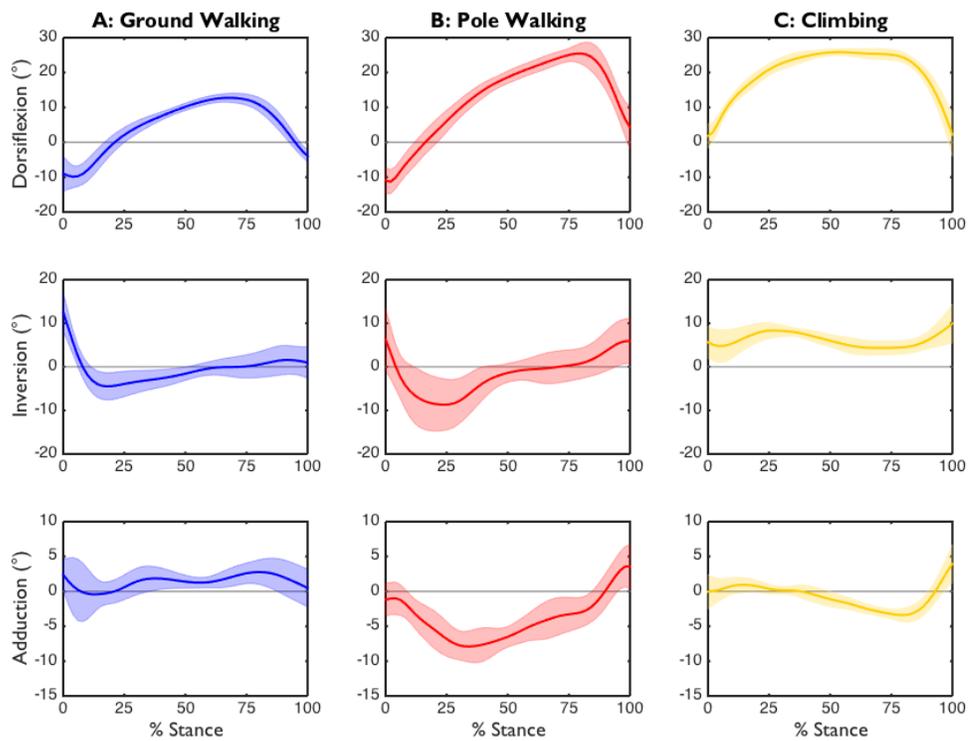


Fig. 3.4. Average motion between the leg and rearfoot segments in all three planes for all locomotor modes. Solid lines represent average angle at each % of stance, and shaded regions represent \pm one standard deviation from the mean. Rows: top = sagittal plane motion, middle = coronal plane motion, bottom = transverse plane motion. Y-axis labels indicate positive motion (see Figure 2.10). Touchdown is at 0% of stance, and liftoff is at 100% of stance.

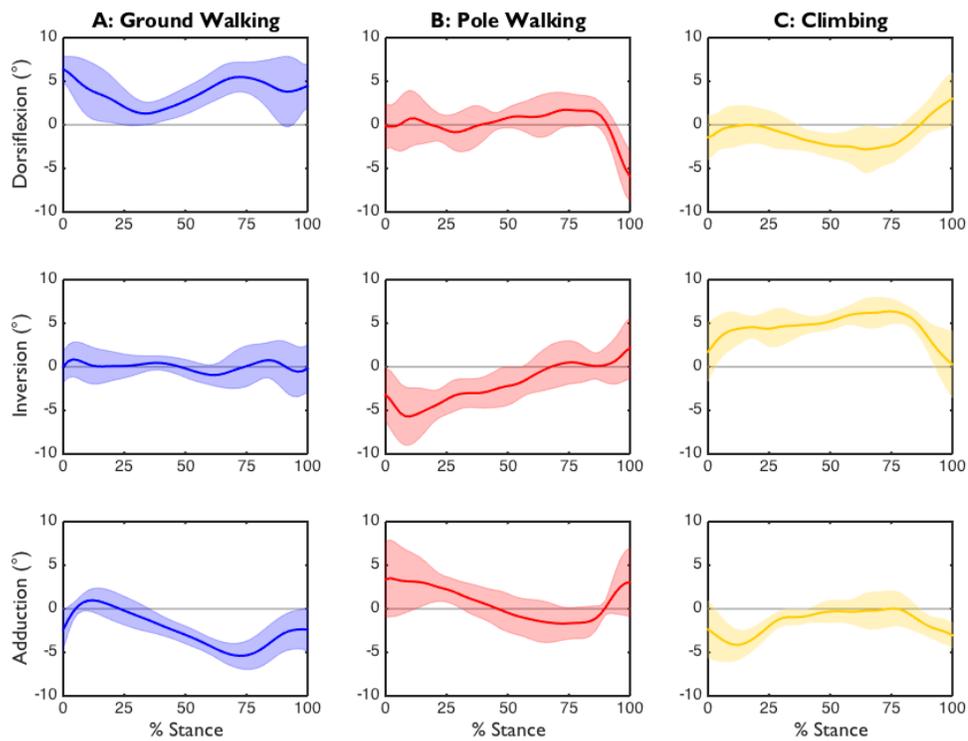


Fig. 3.5. Average motion between the rearfoot and midfoot segments in all three planes for all locomotor modes. Solid lines represent average angle at each % of stance, and shaded regions represent \pm one standard deviation from the mean. Rows: top = sagittal plane motion, middle = coronal plane motion, bottom = transverse plane motion. Y-axis labels indicate positive motion (see Figure 2.10). Touchdown is at 0% of stance, and liftoff is at 100% of stance.

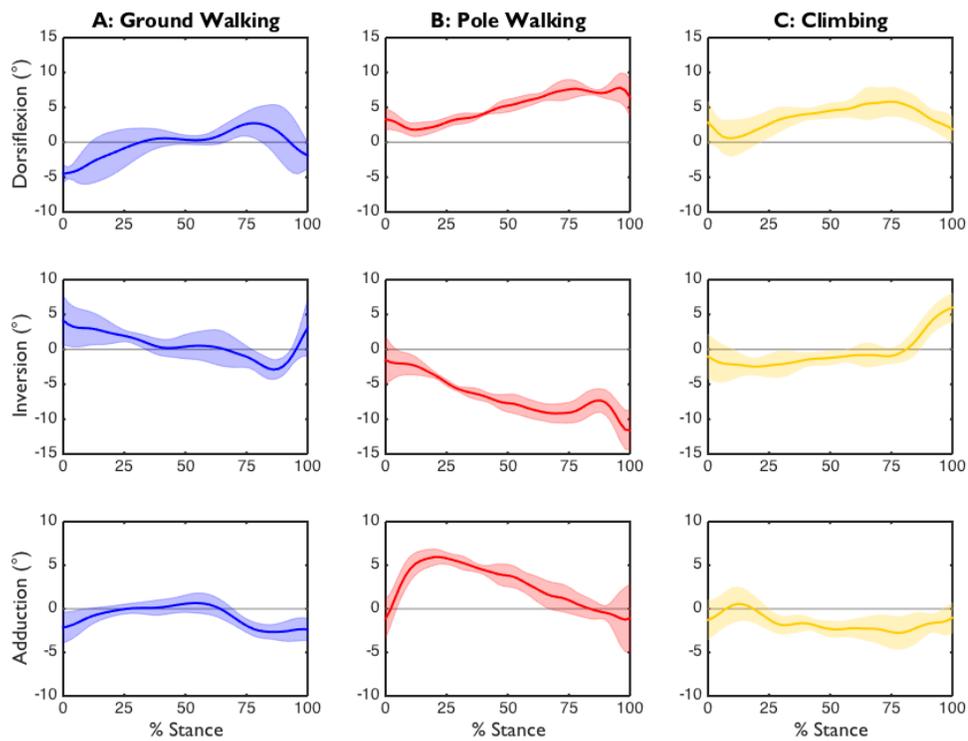


Fig. 3.6. Average motion between the midfoot and lateral forefoot segments in all three planes for all locomotor modes. Solid lines represent average angle at each % of stance, and shaded regions represent \pm one standard deviation from the mean. Rows: top = sagittal plane motion, middle = coronal plane motion, bottom = transverse plane motion. Y-axis labels indicate positive motion (see Figure 2.10). Touchdown is at 0% of stance, and liftoff is at 100% of stance.

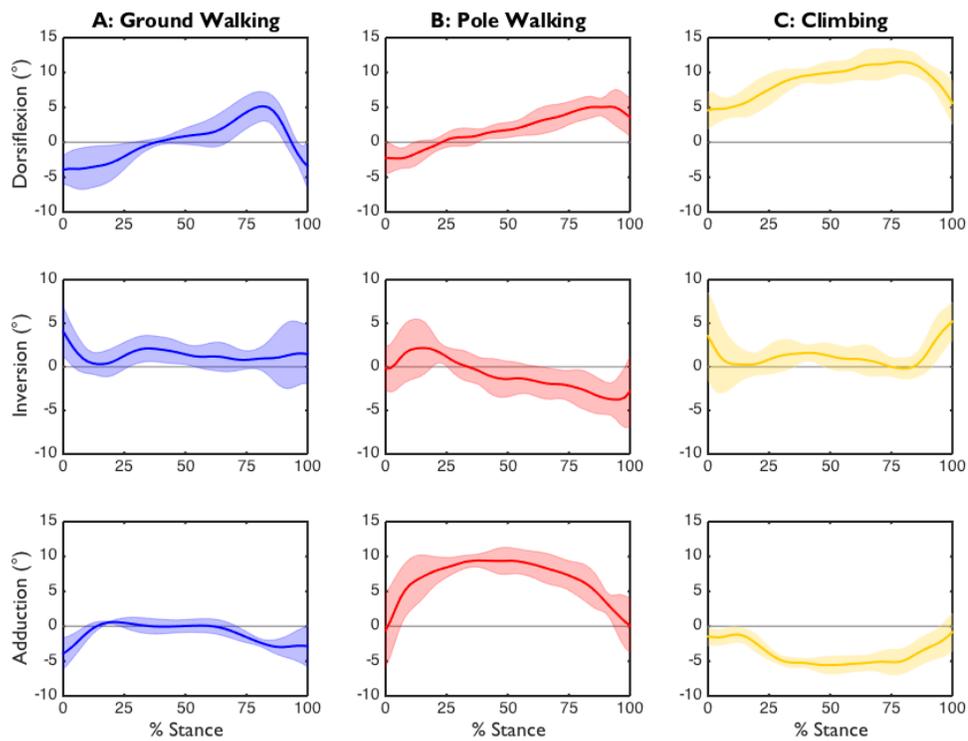


Fig. 3.7. Average motion between the midfoot and medial forefoot segments in all three planes for all locomotor modes. Solid lines represent average angle at each % of stance, and shaded regions represent \pm one standard deviation from the mean. Rows: top = sagittal plane motion, middle = coronal plane motion, bottom = transverse plane motion. Y-axis labels indicate positive motion (see Figure 2.10). Touchdown is at 0% of stance, and liftoff is at 100% of stance.

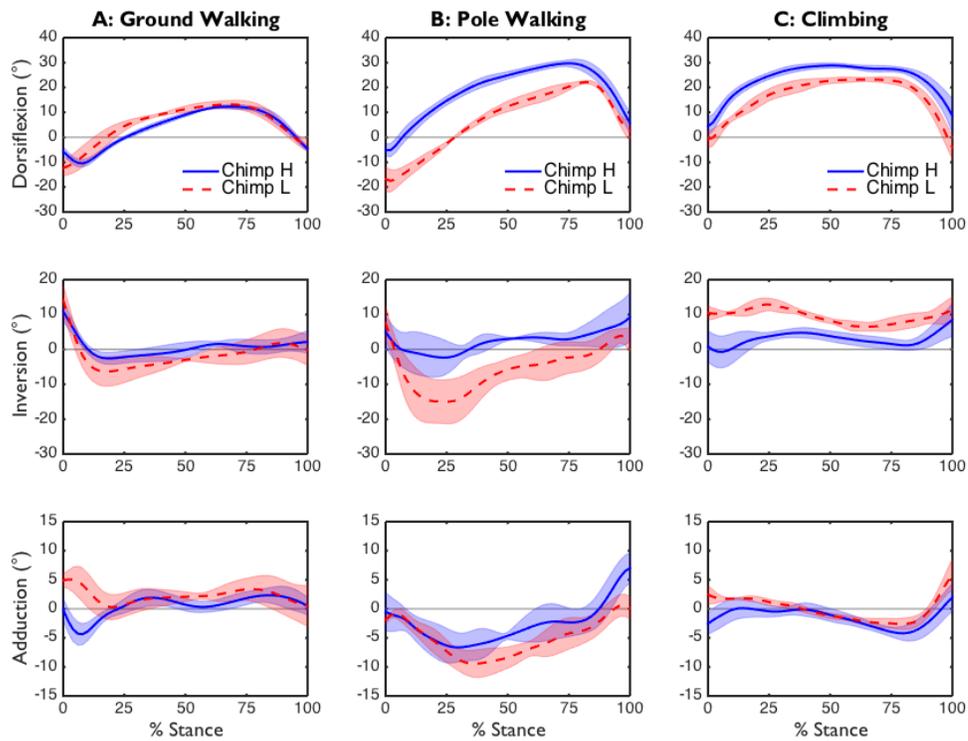


Fig. 3.8. Individual subject motion between the leg and rearfoot segments in all three planes for all locomotor modes. Solid lines represent average angle at each % of stance, and shaded regions represent \pm one standard deviation from the mean. Rows: top = sagittal plane motion, middle = coronal plane motion, bottom = transverse plane motion. Y-axis labels indicate positive motion (see Figure 2.10). Touchdown is at 0% of stance, and liftoff is at 100% of stance.

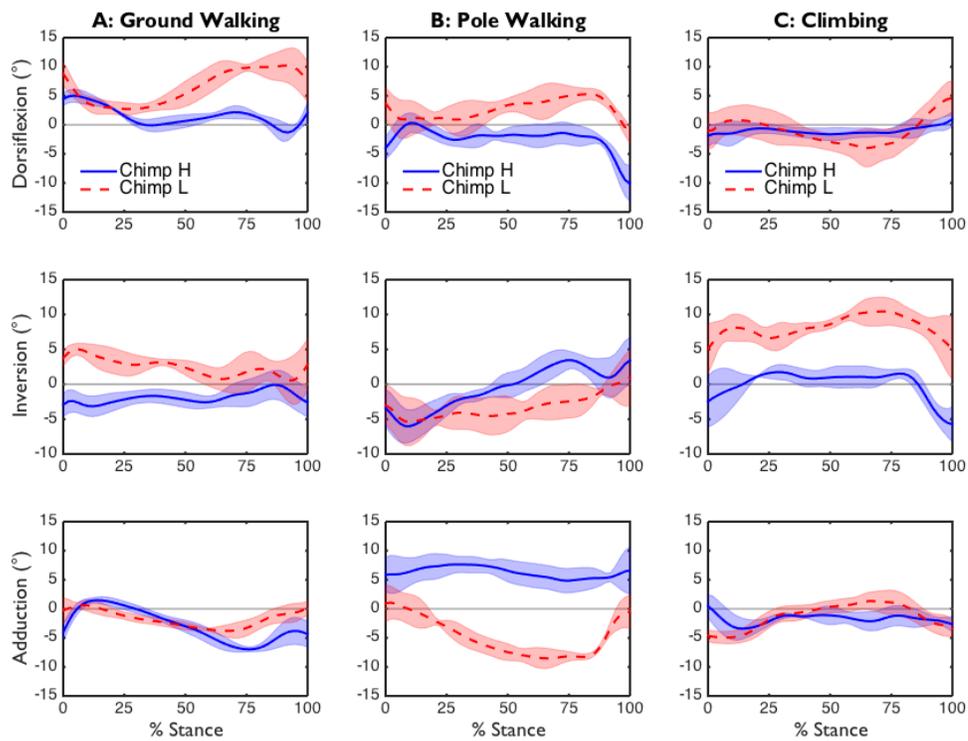


Fig. 3.9. Individual subject motion between the rearfoot and midfoot segments in all three planes for all locomotor modes. Solid lines represent average angle at each % of stance, and shaded regions represent \pm one standard deviation from the mean. Rows: top = sagittal plane motion, middle = coronal plane motion, bottom = transverse plane motion. Y-axis labels indicate positive motion (see Figure 2.10). Touchdown is at 0% of stance, and liftoff is at 100% of stance.

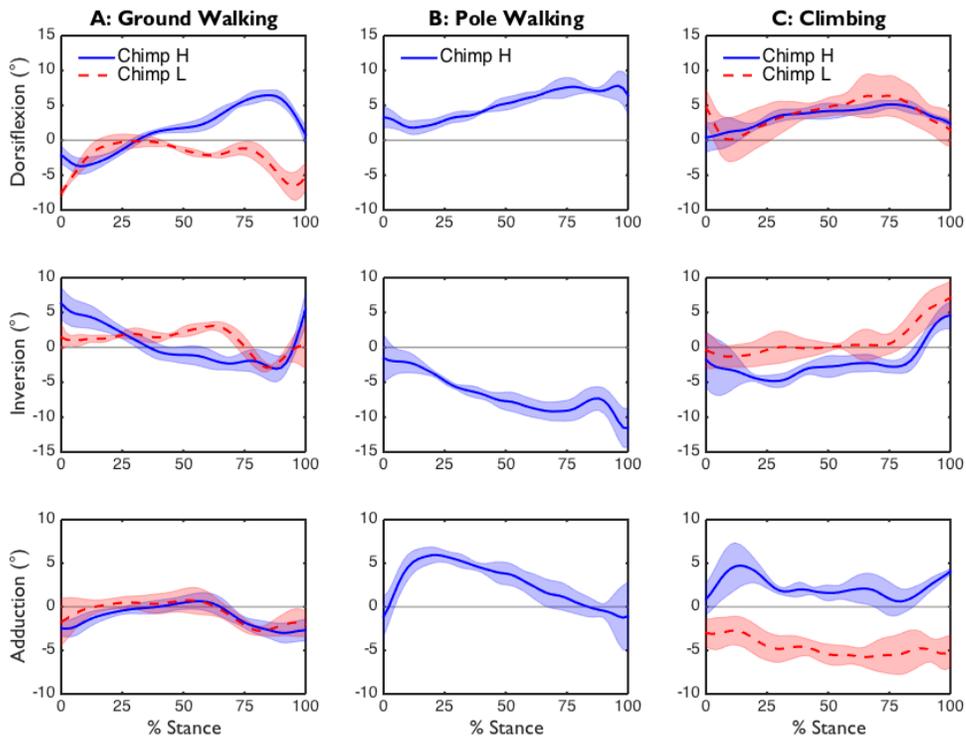


Fig. 3.10. Individual subject motion between the midfoot and lateral forefoot segments in all three planes for all locomotor modes. Solid lines represent average angle at each % of stance, and shaded regions represent \pm one standard deviation from the mean. Rows: top = sagittal plane motion, middle = coronal plane motion, bottom = transverse plane motion. Y-axis labels indicate positive motion (see Figure 2.10). Touchdown is at 0% of stance, and liftoff is at 100% of stance.

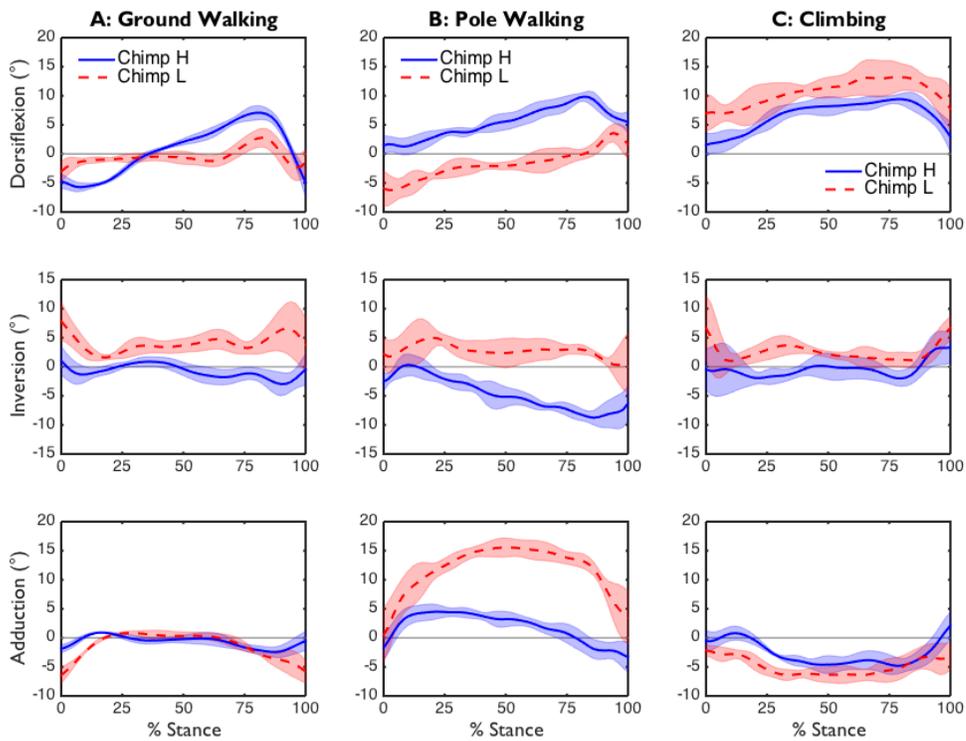


Fig. 3.11. Individual subject motion between the midfoot and medial forefoot segments in all three planes for all locomotor modes. Solid lines represent average angle at each % of stance, and shaded regions represent \pm one standard deviation from the mean. Rows: top = sagittal plane motion, middle = coronal plane motion, bottom = transverse plane motion. Y-axis labels indicate positive motion (see Figure 2.10). Touchdown is at 0% of stance, and liftoff is at 100% of stance.

Chapter 4

Human and Chimpanzee Foot Kinematics During Bipedal Walking

4.1 Introduction

4.1.1 Background

Anatomists have long recognized the foot as a site of major adaptive divergence between humans and chimpanzees (see Susman, 1983 and references therein). Most obviously, chimpanzees possess an abducted, fully opposable hallux, whereas the human hallux is adducted in line with the other digits, and lacks significant mobility. Additionally, chimpanzees possess long, powerful lateral digits for arboreal substrate grasping, while these digits are remarkably shortened and have lost most of their prehensile capability in humans (Preuschoft, 1970). Human and chimpanzee feet are also distinguished by a number of soft tissue differences; humans possess a broad, thick plantar aponeurosis and other strong plantar ligaments that are reduced or absent in chimpanzees (Swindler and Wood, 1973; Lewis, 1980a; Gomberg, 1985). Along with these distinctions, differences in tarsal articular surface morphology (Elftman and Manter, 1935b; Bojsen-Møller, 1979; Lewis, 1980a; Rose, 1986), result in an architectural dichotomy between human and chimpanzee feet; whereas the feet of chimpanzees are longitudinally flat and possess only an incipient transverse arch (Elftman and Manter, 1935b), human feet are characterized by a pronounced longitudinal arch. The functional differences resulting from this dichotomy have long been the subject of scientific inquiry by physical anthropologists and biomechanists.

The study of the chimpanzee foot has informed our understanding of both modern human foot mechanics and hominin foot evolution. Comparative anatomists working in the early twentieth century recognized the importance of studying the feet of great apes as a means of understanding the unique pedal anatomy of humans (Wood Jones, 1917; Morton, 1922, 1924; Weidenreich, 1923; Keith, 1929). Elftman and Manter (1935a; b) studied chimpanzee locomotion *in vivo* as a means of investigating intrinsic foot joint function, and discovered that certain features of the human transverse tarsal joint complex prevent arch collapse and midfoot dorsiflexion following heel lift. This latter phenomenon they observed in chimpanzees, and it has since come to be referred to as the ‘midtarsal break.’

Later investigators took up the findings of Elftman and Manter in order to explain the function of the human arch (e.g. Hicks, 1953; Close et al., 1967; Root et al., 1977; Phillips and Phillips, 1983; Blackwood et al., 2005). In particular, Bojsen-Møller (1979) described how the calcaneocuboid joint morphology of humans enables proper function of the foot’s ‘windlass mechanism.’ The windlass mechanism, originally described by Hicks (1954), takes effect at the end of stance phase of a step, when the toes passively dorsiflex as the heel rises from the ground. This motion tightens the plantar aponeurosis, raising the longitudinal arch and supinating the forefoot relative to the rearfoot (Sarrafian, 1987). According to Bojsen-Møller (1979), African

apes lack the bony morphology necessary to close-pack the midfoot, negating the utility of a windlass mechanism in their feet.

Not only were these studies critical to the development of models of human foot function (Tweed et al., 2008; Jastifer and Gustafson, 2014), but they also influenced some of the initial efforts to reconstruct fossil hominin foot mechanics. Investigators used joint articular surface morphology in fossils attributed to *Homo habilis* (Lewis, 1980b; Susman and Stern, 1982) and *Australopithecus afarensis* (Langdon et al., 1991), as well as pressure distribution patterns inferred from the Laetoli footprints (Stern and Susman, 1983; White and Suwa, 1987), to determine the extent to which these early hominins were capable of human-like foot mechanics. Recent discoveries of associated pedal remains from multiple fossil hominin sites have revived interest in this approach to foot functional morphology (Jungers et al., 2009; Lovejoy et al., 2009; Pontzer et al., 2010; Zipfel et al., 2011; Haile-Selassie et al., 2012; Harcourt-Smith et al., 2015). Additionally, a number of recent studies have provided new experimental data concerning differences in human and African ape foot function. These studies include measurements of ankle and foot joint kinematics in wild (DeSilva, 2009) and captive (D'Août et al., 2002; DeSilva, 2010; Griffin et al., 2010; Pontzer et al., 2014; Thompson et al., 2014; O'Neill et al., 2015) animals, as well as cadaveric specimens (Holowka and O'Neill, 2013; Greiner and Ball, 2014). Additionally, several studies have provided new, and more detailed African ape plantar pressure distribution data (Wunderlich, 1999; Vereecke et al., 2003; Crompton et al., 2012; Bates et al., 2013).

Thanks to these studies, our understanding of African ape foot mechanics has improved considerably over the last decade and a half. However, no study so far has been able to directly quantify 3-D foot motion of these species *in vivo*. These data are necessary because many of the differences in human and African ape foot joint kinematics are likely to occur outside of the sagittal plane. For instance, both the subtalar joint and the transverse tarsal joint complex are thought to yield significant coronal and transverse plane motion in these species, based on their reconstructed rotational axes (Elftman and Manter, 1935a; Lewis, 1980a; Rose, 1986). Non-sagittal plane motions of the intrinsic foot joints are critical to the function of the human longitudinal arch (Sarraffian, 1987; Leardini et al., 2007a), but these motions have gone virtually undocumented in African apes *in vivo*, and could be a major source of distinction between these species and humans.

Detailed 3-D kinematic data from great apes are also needed to evaluate recent experimental studies that have reported unexpected similarities in human and *Pan* (chimpanzees and bonobos) midfoot mobility. Several studies have found that some humans exhibit midfoot pressure distribution patterns that overlap with those of bonobos, suggesting similar degrees of midfoot dorsiflexion during push-off (Crompton et al., 2012; Bates et al., 2013; DeSilva and Gill, 2013; DeSilva et al., 2015). Additionally, Greiner and Ball (2014) demonstrated that humans and chimpanzees display similar levels of passive mobility of their midfoot joints, which runs contrary to expectations derived from the mid-tarsal break observed in chimpanzees.

These studies point towards a breakdown of the traditional mobile *versus* rigid dichotomy used to characterize chimpanzee and human midfoot joints, respectively. However, kinematic data collected from humans and chimpanzees during locomotion are necessary to fully evaluate the conclusions of these studies. Comparing human and chimpanzee foot kinematics during bipedal locomotion provides the best means of directly assessing similarities and differences between species in overall foot function. By standardizing the gait under investigation, we can determine how differences in pedal anatomy result in differences in foot mechanics under similar

conditions. Foot kinematic data collected from chimpanzees during bipedalism will also aid functional analyses of fossil hominin pedal remains. By improving our understanding of chimpanzee foot mechanics during bipedal locomotion, we can develop more accurate reconstructions of gait in early hominins that preserve great ape-like pedal joint morphology.

4.1.2 Hypotheses

In this study, I compare 3-D kinematic data collected from human and chimpanzee subjects during bipedal locomotion. Specifically, I measured triplanar motion between the leg and rearfoot segments, and between the rearfoot and forefoot (medial and lateral) segments. These measurements allowed me to quantify motion occurring at the talocrural, subtalar, and midfoot (transverse tarsal and tarsometatarsal) joints during stance phase of bipedal steps. I also measured 3-D joint motion at all five metatarsophalangeal joints. I compared joint kinematics during bipedal walking in order to assess interspecies differences in foot function when both species were walking under similar conditions. However, to determine normal chimpanzee foot function, and the extent to which it might be altered during bipedalism, I also compared chimpanzee joint kinematics during bipedal and quadrupedal locomotion. I used the data collected in this study to address the following hypotheses:

H1: The chimpanzee subtalar joint is more mobile than the human subtalar joint during bipedal walking.

Chimpanzees possess greater passive subtalar joint ranges of motion than humans (Holowka and O'Neill, 2013; see Chapter 3), which is reflected in their subtalar joint articular surface morphology (Deloison, 1985; Latimer and Lovejoy, 1989; Prang, 2016). This greater range of motion may come at the cost of lower joint stability during a biomechanically challenging behavior like bipedal walking. In particular, Elftman and Manter (1935a) argued that the chimpanzee subtalar joint lacks the osteological constraints that limit eversion during weight bearing in humans. As a consequence, they contended, chimpanzee subtalar joint motion is unrestrained during stance, resulting in heightened transverse tarsal joint mobility. Several fossil hominin studies have made similar arguments based on subtalar joint morphology: Gebo and Schwartz (2006) reported chimpanzee-like posterior subtalar facet morphology in specimens attributed to *Au. afarensis* (AL 333-8, -55, -75, -97), which they argued would have resulted in reduced joint stability and greater susceptibility to leg muscle fatigue during bipedal walking. DeSilva et al. (2013) measured chimpanzee-like subtalar joint articular surface curvature in *Au. sediba* (MH2), and they argued this would have resulted in a 'hyper-pronating' gait. They also suggested that such hyperpronation would result in greater internal rotation of the tibia relative to the foot, as these motions are thought to be coupled at the subtalar joint (Close et al., 1967). Therefore, greater subtalar mobility in chimpanzees could yield greater coronal and transverse plane ranges of motion at this joint during walking when compared to humans.

Several studies have also reported that *Pan* species use more inverted foot postures at touchdown than humans (Elftman and Manter, 1935b; Susman, 1983; Vereecke et al., 2003). Chapter 3 analyses revealed that this motion occurs at the subtalar joint during quadrupedalism, and that the foot is rapidly everted following touchdown to bring it into full contact with the underlying substrate. This additional difference in human and chimpanzee joint kinematics is expected to contribute to the interspecies disparity in subtalar mobility during bipedal walking.

In this study, I assume that subtalar joint motion is represented by coronal and transverse plane motion between the leg and rearfoot segments (see Chapter 2, Section 2.4). Therefore, I make the following predictions:

P1: Chimpanzees will use a greater coronal plane range of motion (inversion-eversion) between their leg and rearfoot segments than humans.

P2: Chimpanzees will use a greater transverse plane range of motion (abduction-adduction) between their leg and rearfoot segments than humans.

H2: The chimpanzee midfoot joints are more mobile than the human midfoot joints during bipedal walking.

This hypothesis follows from studies that have documented the occurrence of a substantial midtarsal break in chimpanzees and other great apes during terrestrial locomotion. This motion is far less pronounced in humans (DeSilva, 2010), so it is commonly assumed that the chimpanzee midfoot joints use a greater range of motion than those of humans during walking. This assumption has been extended to functional interpretations of midfoot joint morphology, with more chimpanzee-like transverse tarsal (Elftman and Manter, 1935a; Bojsen-Møller, 1979; Jungers et al., 2009; Zipfel et al., 2011) and tarsometatarsal (DeSilva, 2010; Zipfel et al., 2011; Proctor, 2013; DeSilva et al., 2015) joint morphology being taken as evidence of greater joint mobility. In opposition to this assumption, several recent studies have suggested significant overlap between great ape and human midfoot mobility (Crompton et al., 2012; Bates et al., 2013; DeSilva and Gill, 2013; Greiner and Ball, 2014; DeSilva et al., 2015), warranting a quantitative comparison of joint motion *in vivo*.

Motions at the transverse tarsal and tarsometatarsal joints are believed to contribute to the midtarsal break (Elftman and Manter, 1935a; Vereecke et al., 2003; DeSilva, 2010; Greiner and Ball, 2014). Both of these joints occur between the rearfoot and forefoot segments defined in this study, so the motion between these segments should provide an adequate description of overall midfoot joint motion. The transverse tarsal joint complex permits significant sagittal and coronal plane motion in humans and chimpanzees (Elftman and Manter, 1935a; Lewis, 1980a; Tweed et al., 2008; Thompson et al., 2014), whereas the tarsometatarsal joints are expected to move mainly in the sagittal plane (DeSilva, 2010). Previous studies have implicated the cuboid-metatarsal joints in significant midfoot motion in *Pan* species (Vereecke et al., 2003; DeSilva, 2010), but in Chapter 3 I found that the intermediate and lateral cuneiform-metatarsal joints are at least as mobile as the cuboid-metatarsal joints in chimpanzees across different locomotor modes. Therefore, I expect both tarsometatarsal joint complexes to be relatively mobile in chimpanzees during bipedal walking, and make the following predictions:

P1: Chimpanzees will use a greater sagittal plane range of motion (plantarflexion-dorsiflexion) between their rearfoot and forefoot segments than humans.

P2: Chimpanzees will use a greater coronal plane range of motion (inversion-eversion) between their rearfoot and forefoot segments than humans.

H3: Humans use higher peak dorsiflexion angles at their metatarsophalangeal joints than chimpanzees during the push-off phase of bipedal walking.

The human metatarsophalangeal joints (MTPJs) are passively dorsiflexed to a high degree following heel lift, tightening the plantar aponeurosis, and driving the windlass mechanism of the arch (Hicks, 1954; Erdemir et al., 2004; Caravaggi et al., 2009). The other great apes are believed to lack a windlass mechanism (Bojsen-Møller, 1979; Stern and Susman,

1983; Griffin et al., 2010), and therefore have no need to passively dorsiflex their MTPJs to as high degree as humans. Additionally, the MTPJs of great apes are thought to be adapted for high stability in grasping postures, but low stability at high dorsiflexion angles (Susman et al., 1984; Latimer and Lovejoy, 1990a; Fernández et al., 2015). This morphology is believed to prevent great apes from using highly dorsiflexed joint angles during push-off, when the joints must accommodate high loads. Griffin et al. (2010) confirmed these assumptions in their investigation of MTPJ kinematics in humans and bonobos. They measured significantly higher peak dorsiflexion angles in humans at the first two MTPJs. However, they were only able to capture joint motion for a small sample of bonobo steps from joints two and three, and their results suggested the potential for overlap with humans given a larger sample size. Therefore, a larger sample of steps with motion from all five joints is necessary to thoroughly test for differences in human and great ape MTPJ motion.

I will measure peak dorsiflexion angles at push-off at all five MTPJs in humans and chimpanzees during bipedal walking. I make the following prediction:

P: Humans will exhibit higher peak dorsiflexion angles than chimpanzees at all metatarsophalangeal joints during bipedal walking.

H4: Chimpanzees use similar foot kinematics during bipedal and quadrupedal locomotion.

In the wild, chimpanzees only occasionally use bipedal gaits on the ground (Hunt, 1992; Doran, 1993), so we might expect them to use highly variable foot joint positions while walking bipedally. Along these lines, Vereecke et al. (2003) found that bonobos displayed more variable plantar pressure distribution patterns during bipedal walking compared to quadrupedal walking. However, the subjects in my study were encouraged to walk bipedally from a young age, and had been doing so for almost two years prior to the initiation of data collection. Therefore, I expect that they will show more consistent bipedal kinematics than the bonobos in Vereecke et al.'s study, which were not trained to walk bipedally.

One might also expect foot kinematics to differ between bipedal and quadrupedal gaits because bipedalism requires the use of only a single limb for support throughout much of stance, unlike quadrupedalism. This condition might lead to challenges in maintaining balance that are not encountered during quadrupedalism, resulting in altered foot kinematics. Indeed, Pontzer et al. (2014) measured higher mediolateral ground reaction forces during bipedal walking in chimpanzees, which they attributed to the difficulties of maintaining balance without the ability to use the lesser gluteals as hip abductors as humans do. Nevertheless, they measured nearly identical ankle joint kinematics in both gaits when subjects were walking at moderate speeds. Based on these results, and the fact that no study has yet reported any observed difference in foot motions between gaits, I make the following predictions:

P1: Chimpanzees will use similar subtalar joint kinematics in both gait types.

P2: Chimpanzees will use similar midfoot joint kinematics in both gait types.

P3: Chimpanzees will exhibit similar peak metatarsophalangeal joint angles at push-off in both gait types.

4.2 Methods

Most of the methodology used in this chapter is described in Chapter 2, including the subject information and data collection/processing protocols. What follows is a description of the dataset composition and statistical tests used in this chapter. All tests were carried out using

MATLAB software. Statistical comparisons were performed among the following groups: human bipedal steps, chimpanzee bipedal steps, and chimpanzee quadrupedal steps. Within these groups, steps were pooled among subjects. Alpha significance levels were set at 0.05 for all tests.

4.2.1 Triplanar joint motion

A majority (12/20) of the chimpanzee bipedal steps selected for analysis exhibited within-triad marker motion in the midfoot segment that was above the threshold that I defined to indicate significant triad deformation (see Chapter 2, Section 2.4). This motion appeared to be caused by high ankle dorsiflexion angles occurring near midstance when the foot was placed in a relatively everted position. This appeared to cause bunching of the skin near the midfoot, resulting in some independent motion of the markers within the triads relative to one another. Because such a large number of the chimpanzee bipedal steps selected for analysis showed these errors, I decided to exclude the midfoot segments from all comparisons involving chimpanzee bipedal locomotion, limiting my analyses to motion between three segment pairs: leg-rearfoot, rearfoot-lateral forefoot, and rearfoot-medial forefoot. Because I could not accurately capture midfoot segment motion, I will assume that motion between rearfoot and forefoot segments occurs at the both the transverse tarsal and tarsometatarsal joints combined. This assumption is similar to that made in a number of human 3-D foot kinematics studies that investigate motion between the rearfoot and forefoot without using a midfoot segment (e.g., Kidder et al., 1996; Carson et al., 2001; Hunt and Smith, 2004). Measuring motion between rearfoot and forefoot segments will still allow me to capture motion at the midfoot joints, but at a coarser level than in Chapter 3.

I carried out two sets of statistical tests: chimpanzee *versus* human kinematics during bipedal walking, and chimpanzee joint kinematics during bipedal *versus* quadrupedal walking. In each comparison, I tested for differences between groups in maximum joint excursions, and joint ranges of motion. Because my data sometimes violated the normality assumption of parametric statistics (see Chapter 3, Section 3.2), I used non-parametric Wilcoxon Rank-Sum tests. I set an alpha significance level of 0.05 for all tests.

4.2.2 Metatarsophalangeal joint motion

For the metatarsophalangeal joints, I calculated the maximum joint dorsiflexion angles that occurred at the end of stance just prior to toe-off, after the data had been filtered following the same procedure as that carried out for triplanar joint angle calculation (Fig. 4.1). I tested for differences in maximum dorsiflexion angles at all five digits between humans and chimpanzees during bipedal locomotion, and in chimpanzees between bipedal and quadrupedal locomotion. The maximum angles used in these tests occurred just prior to liftoff, in the final 20% of stance. I used Wilcoxon Rank-Sum tests for these comparisons. I also tested for differences in metatarsophalangeal joint dorsiflexion angles among the five digits within groups. I used non-parametric Kruskal-Wallis tests to test for overall differences among the MTPJs, and I used post-hoc Kruskal-Wallis tests for pairwise comparisons between joint pairs (using MATLAB's 'multcompare' function). A sequential Bonferroni correction was used to adjust the alpha significance levels (0.05) for these tests (Abdi, 2010).

4.3 Results

4.3.1 Chimpanzee and human bipedalism

For each chimpanzee subject, I selected 10 bipedal steps for analysis (total N=20); for each human subject, I selected 5 bipedal steps for analysis (total N=25). Using the linear regression equations described in Chapter 2, I estimated dimensionless velocity for each step that I selected. Average stance phase durations and dimensionless velocities estimated for each subject and each group overall are presented in Table 4.1. Chimp L walked slightly faster than Chimp H (0.48 and 0.42, respectively), but the average dimensionless velocity estimated for all chimpanzee steps was very close to that estimated for all human steps (0.46 and 0.45, respectively). Patterns of motion at each joint for both species, and both chimpanzees individually, are presented in Figs. 4.2a,b-4.4a,b. Ranges of motion, and maximum joint angles, are presented in Tables 4.2-4, and results of significance tests are presented in Table 4.5.

Here I provide a general description of chimpanzee foot joint kinematics during bipedal locomotion. I highlight major differences between humans and chimpanzees, as well as differences between the chimpanzee subjects. As in Chapter 3, I will refer to motion between the segment pairs as occurring at segment ‘joints’, without specifying the actual anatomical joint at which motion may be occurring. I will also describe the relative timing of kinematic events in terms of double- and single-support phases: ‘First double-support phase’ refers to the period of time following touchdown during which the contralateral foot is still in contact with the ground, ‘single-support phase’ refers to the period of stance in which only a single foot is in contact with the ground, and ‘second double-support phase’ begins when the contralateral foot touches down. Double-support phases were longer in chimpanzee subjects than in humans; in humans they took up roughly the first and last 18% of stance, whereas in chimpanzees they took up the first and last 25% of stance.

Leg-Rearfoot. Chimpanzee subjects contacted the ground with a plantarflexed and highly inverted leg-rearfoot joint, which they rapidly everted following touchdown (Fig. 4.2a). This contrasts with humans, who contacted with only a slightly inverted joint that was neutrally positioned in the sagittal plane. Both species abducted their joints rapidly in the first double-support phase to a similar degree, indicating internal rotation of the leg relative to the planted, stationary foot. During single-support phase, both species dorsiflexed and adducted their joints, but chimpanzees reached much higher peak dorsiflexion angles. Both species maintained slightly everted joints throughout single-support phase. During double-support phase, humans rapidly inverted their joints to a high peak near liftoff, but chimpanzee maintained a relatively everted posture. Both species displayed rapid plantarflexion in the second double-support phase just prior to liftoff.

Chimpanzees displayed significantly greater ranges of motion in all three planes at the leg-rearfoot joint than humans (Tables 4.2 and 4.5). In the coronal plane, this difference was driven by the significantly greater peak inversion angles achieved by chimpanzees at touchdown, as well as their significantly greater peak eversion angles, which they reached at the end of the first double-support phase. Chimpanzees also displayed significantly greater peak adduction angles than humans, which occurred at the beginning of the second double-support phase. In the sagittal plane, range of motion differences were driven by the significantly higher peak dorsiflexion angles achieved by chimpanzees at the end of single-support phase. Humans, however, exhibited significantly higher peak plantarflexion angles, which occurred at the end of stance when the ankle is plantarflexed to generate the propulsive power for push-off.

Patterns of motion between the leg and rearfoot were similar between the two chimpanzee subjects (Fig. 4.2b). However, there were two notable differences in the magnitude

of joint angles: Chimp L achieved and maintained a more everted joint posture following the first double-support phase, whereas Chimp H displayed a more abducted joint posture until the beginning of the second double support phase.

Rearfoot-Lateral Forefoot. Chimpanzee and human rearfoot-lateral forefoot motion patterns differed considerably from one another (Fig. 4.3a). In the first double-support phase, humans rapidly pronated (dorsiflexed, abducted and everted) this joint, a motion related to lowering of the longitudinal arch under weight support. In contrast, chimpanzees touched down with a highly abducted joint posture, which they swiftly adducted, but they did not exhibit any dramatic motions in the sagittal or coronal planes during the first double-support phase. During single-support, humans progressively everted and abducted their joints, corresponding to further arch depression. Chimpanzees also abducted their joints, but also progressively dorsiflexed across midstance, reaching a peak dorsiflexion angle at the beginning of the second double-support phase. This motion likely corresponds to the presence of a midtarsal break. Humans and chimpanzees both supinated (plantarflexed, inverted, and adducted) their joints in the second double-support phase, but these motions were generally greater in magnitude in humans than in chimpanzees.

Humans exhibited greater ranges of motion at the rearfoot-lateral forefoot joint than chimpanzees in both the sagittal and transverse planes (Tables 4.3 and 4.5). These differences were driven by humans' use of significantly greater maximum plantarflexion and adduction angles than chimpanzees, both of which occurred at liftoff. Humans also used significantly greater maximum inversion angles than chimpanzees at liftoff as well. Chimpanzees did, however, use significantly greater abduction angles than humans, with peaks at touchdown and the end of single support phase.

Between subjects, chimpanzees displayed similar motion patterns at the rearfoot-lateral forefoot joint (Fig. 4.3b). Slight differences occurred during the second double-support phase, where Chimp H used a greater degree of inversion, but Chimp L plantarflexed his joint more. Chimp L also maintained a slightly more abducted joint posture throughout most of stance.

Rearfoot-Medial Forefoot. Motion of the medial forefoot segment relative to the rearfoot was generally similar to that described for the rearfoot-lateral forefoot joint for both species, with several notable differences (Fig. 4.4a). Humans displayed relatively static joint postures in coronal and transverse planes through the first two phases of stance, although they exhibited the sagittal plane motions characteristic of arch depression described previously. Chimpanzees showed similar patterns to those described for the rearfoot-lateral forefoot joint, but with greater eversion in the coronal plane and reduced abduction in the transverse plane. During the second double-support phase, both species rapidly plantarflexed their joints, although this motion was again more dramatic in humans. Humans also displayed rapid adduction of this joint during this phase, whereas chimpanzees maintained a static posture in the transverse plane. Both species slightly inverted their joints prior to liftoff as well.

As on the lateral side, humans displayed significantly greater sagittal and transverse plane ranges of motion at the rearfoot-medial forefoot joint than chimpanzees (Tables 4.4 and 4.5). Once again, this difference was driven by the human subjects' use of significantly greater maximum plantarflexion and adduction angles at liftoff. Chimpanzees again displayed significantly greater maximum abduction angles than humans, which occurred at touchdown. However, chimpanzees also displayed a significantly greater coronal plane range of motion than humans, although the difference between species was $< 3^\circ$. Chimpanzees displayed significantly

greater maximum dorsiflexion angles than humans, which occurred at the beginning of the second double support phase, corresponding to a midtarsal break.

Chimpanzee subjects displayed similar motion patterns at the rearfoot-medial forefoot joint, except in the coronal plane (Fig. 4.4b). Chimp H maintained a relatively static joint posture in this plane, whereas Chimp L displayed a large range of motion across stance. Chimp L contacted with an inverted joint, which he everted throughout the first half of stance. Following midstance, Chimp L progressively inverted the joint until liftoff.

4.3.2 Chimpanzee Bipedalism and Quadrupedalism

For this comparison, I used the same chimpanzee bipedal steps as those selected for the chimpanzee-human comparison, and the same quadrupedal steps as those selected to represent ‘ground walking’ in Chapter 3. The dimensionless velocities estimated for the quadrupedal steps are presented in Table 4.1. The average dimensionless velocity estimated for Chimp H’s quadrupedal steps was slightly faster than that estimated for Chimp L’s (0.43 *versus* 0.41, respectively). The average dimensionless velocity estimated for the quadrupedal steps of both chimpanzees was lower than that estimated for the bipedal steps, but not dramatically so (0.42 *versus* 0.46, respectively). Patterns of motion at each joint for both species, and both chimpanzees individually, are presented in Figs. 4.2c-4c. Ranges of motion, and maximum joint angles, are presented in Tables 4.2-4, and results of significance tests are presented in Table 4.3. Here I describe differences in patterns, ranges, and maximum joint angles between gait types.

Leg-Rearfoot. The subjects exhibited similar patterns of motion at the leg-rearfoot joint in the sagittal and coronal planes during both gaits, but used significantly larger ranges of motion in both planes during bipedalism (Fig. 4.2c; Tables 4.2 and 4.3). This difference was due their use of significantly higher maximum inversion angles at touchdown, and significantly higher maximum dorsiflexion angles at the end of single-support phase, during bipedalism. In the transverse plane, during quadrupedalism the subjects did not exhibit the rapid abduction following touchdown that occurred during bipedalism. This resulted in significantly higher maximum abduction angles and transverse plane ranges of motion during bipedalism. This indicates that chimpanzees internally rotate the leg more during bipedal *versus* quadrupedal walking.

Rearfoot-Medial Forefoot. Patterns and ranges of motion were generally similar at the rearfoot-medial forefoot joint during both gaits (Fig. 4.3c; Tables 4.3 and 4.5). In the sagittal plane, chimpanzees used significantly greater maximum plantarflexion angles during bipedal walking, which occurred just following touchdown. However, the difference between gaits was < 4° on average.

Rearfoot- Lateral Forefoot. Patterns and ranges of motion were also very similar at the rearfoot-lateral forefoot joint during both gaits (Fig. 4.4c; Tables 4.4 and 4.5). The only significant difference between gaits occurred in the sagittal plane, where subjects used greater maximum dorsiflexion angles at the beginning of the second double support phase. However, the actual magnitude of this difference between gaits was < 3° on average.

4.3.3 Metatarsophalangeal Joint Motion

Passive Range of Motion. Chimpanzee MTPJ passive dorsiflexion ranges are presented in Table 4.6. Among the joints measured, both subjects possessed the greatest ranges for MTPJ 2 (both 55°). Both subjects possessed similar ranges for MTPJ 1 (36 and 41°), which were

considerably lower than those measured for MTPJ 2. Subjects differed markedly in MTPJ 5 ranges: Chimp H possessed a much greater range (54°) than Chimp L (31°).

Active Range of Motion. For most of the chimpanzee steps included in analysis, I could not measure peak dorsiflexion angles for the first MTPJ, because the markers on the hallux were not in view of the cameras during liftoff. To measure motion at this joint, I had to select separate steps in which the medial side of the foot was in view of the cameras. Therefore, the data for the chimpanzee MTPJ 1 that was included in this study is mostly from different steps than those used for other joint angles. However, I was still able analyze a matching number of steps for MTPJ 1 and the other MTPJs for both bipedal (N=20) and quadrupedal (N=10) locomotion. The dimensionless speeds estimated for steps used to calculate MTPJ 1 dorsiflexion angles were generally similar to those used for the other MTPJs: 0.45 ± 0.04 for bipedal steps (compared to 0.46 ± 0.05 for steps used for MTPJs II-V), 0.43 ± 0.08 for quadrupedal steps (compared to 0.42 ± 0.04 for steps used for MTPJs II-V).

Typical MTPJ motion patterns for human and chimpanzee subjects are depicted in Fig. 4.1. Peak dorsiflexion angles tended to occur around 90% of stance in both species, although MTPJ 5 tended to achieve a slightly earlier peak in chimpanzees. Peak MTPJ dorsiflexion angles for humans and chimpanzees are reported in Table 4.7 and depicted in Fig. 4.5. Humans exhibited significantly greater dorsiflexion angles at all five joints ($P < 1 \text{ E-}6$ at all joints). The greatest disparity in joint angles occurred at MTPJ 1, where humans dorsiflexed their joints 36° more than chimpanzees, on average. Moving laterally across MTPJs 2-5, humans and chimpanzees exhibited a similar decrease in peak joint angles, although the gradient was steeper in chimpanzees. Chimpanzees exhibited similar peak dorsiflexion angles in bipedal and quadrupedal locomotion (Fig. 4.5). They used significantly greater peak dorsiflexion angles at MTPJs 3 and 4 during quadrupedal locomotion ($P = 1 \text{ E-}3$, $P = 0.02$, respectively), although the differences between gaits for these joints were only 5° and 3° on average, respectively.

For humans and chimpanzees (both gait types), Kruskal-Wallis tests indicated that peak dorsiflexion angles were significantly different among the MTPJs ($P < 1 \text{ E-}7$ for all tests). The results of the post-hoc tests are presented in Table 4.8. Among the human steps, MTPJ dorsiflexion angles were statistically indistinguishable between the first four joints. MTPJ 5 had significantly lower dorsiflexion angles than all other digits. Within the chimpanzee bipedal steps, MTPJ 1 dorsiflexion was statistically indistinguishable from that of MTPJs 4 and 5, but MTPJs 2 and 3 exhibited greater dorsiflexion peaks. MTPJ 2 dorsiflexion was significantly greater than that of all other joints except MTPJ 3. MTPJ 3 dorsiflexion was significantly greater than that of MTPJs 4 and 5. MTPJ 4 and 5 dorsiflexion angles were statistically indistinguishable. Chimpanzee MTPJs showed similar difference patterns during quadrupedal steps, except that peak dorsiflexion angles were not significantly different between MTPJs 3 and 4.

4.4 Discussion

4.4.1 Human versus Chimpanzee Bipedalism

Subtalar Joint. The first hypothesis of this chapter states that the chimpanzee subtalar joint is more mobile than the human subtalar joint during bipedal walking. I assume that motion between the leg and rearfoot segments defined in this study occurs at two joints: the talocrural joint, which should be the site of most sagittal plane motion between these segments, and the subtalar joint, which should be the site of most coronal and transverse plane motion. Under this assumption, chimpanzees use significantly greater talocrural joint motion than humans, which

agrees with the findings of O'Neill et al. (2015). At the subtalar joint, chimpanzees also exhibit significantly greater coronal and transverse plane ranges of motion than humans, supporting both predictions of my first hypothesis. In the coronal plane, this difference is mainly driven by chimpanzee subtalar joint motion at the beginning of stance, when the highly inverted joint is rapidly everted following touchdown (Fig. 4.2a). After reaching an everted joint position, the chimpanzee subtalar joint remains relatively static in the coronal plane for the remainder of stance. This result contradicts the notion that African apes maintain inverted foot postures throughout stance (Weidenreich, 1923; Tuttle, 1970; Gebo, 1992; DeSilva et al., 2013), as well as the idea that the peroneal trochlea serves to support weight in these species (Lewis, 1983; Deloison, 1985; Latimer and Lovejoy, 1989; Gill et al., 2014). In fact, the peroneal trochlea is never in contact with the substrate, including at touchdown when the foot is in its most inverted position, as indicated in Fig. 4.6. DeSilva et al. (2013) suggested that African apes rely on inverted subtalar joint postures during bipedal walking because they swing their centers of mass laterally over their ankles, producing an inverting torque. However, Demes et al. (2015) found that the chimpanzee center of mass only travels 3.5 ± 1.1 cm mediolaterally during a bipedal stride, on average. This distance is far below the normal stance width of chimpanzees during bipedal walking, which is typically 15-25 cm (N. Thompson, unpublished data), so there is no way that the center of mass could produce an inverting torque at the subtalar joint. Rather, these results agree with the initial observations of Elftman and Manter (1935a; b), who reported that chimpanzees evert their subtalar joints to bring the medial side of the foot into full contact with the ground when walking bipedally.

One expected correlate of high rearfoot eversion during weight support is increased internal rotation of the tibia with respect to the fixed foot (Close et al., 1967; Inman, 1976; Piazza, 2005). Following the touchdown, the foot becomes firmly planted on the substrate, setting up a closed kinematic chain (Donatelli, 1985). However, the leg continues to rotate internally relative to the stationary foot. Because the talocrural joint is not designed to accommodate this rotation, it must be transferred to the subtalar joint, where it drives simultaneous eversion and abduction motions. While I did find significantly greater ranges of motion and maximum adduction in angles at the subtalar joint in chimpanzees compared to humans, I did not find a difference in maximum abduction angles between species. This means that the relatively high eversion angles exhibited by chimpanzees at the end of the first double-support phase do not result in greater internal rotation of the leg relative to the foot when compared to humans. Although this result seems to contradict our basic understanding of subtalar joint geometry (e.g., Inman, 1976), the subtalar joint axis of rotation is different in humans and chimpanzees (Lewis, 1980a; Rose, 1986; Prang, 2016), and so transverse and coronal plane motions may not be coupled to the same degree at this joint in both species. Indeed, although they exhibit similar peak eversion angles during bipedal and quadrupedal locomotion, chimpanzees exhibit considerably greater peak abduction angles during the former gait type. Therefore, one should not expect that chimpanzee-like subtalar joint mobility will necessarily result in increased tibial rotation during bipedal stance, as has been suggested for *Au. sediba* (DeSilva et al., 2013).

Interestingly, when considering motion after the first double-support phase, humans actually exhibit considerably more subtalar joint coronal plane motion than chimpanzees. Humans rapidly invert their subtalar joints in the second double-support phase as a result of external rotation of the lower limb and tightening of the plantar aponeurosis *via* the windlass mechanism (Sarrafian, 1987; Piazza, 2005). Chimpanzees exhibit little subtalar joint coronal plane motion after the first double-support phase, so it can be concluded that the human subtalar

joint is more dynamic during push-off. It must be acknowledged here that the total amount of subtalar motion measured for human subjects in this study is greater than that reported in most (but not all) multisegment foot kinematics studies. Most studies report total ranges between 5 and 15° (see Rankine et al., 2008 and references therein), compared to the 16° average measured here. This could be caused by soft tissue artifacts, which several studies have demonstrated to increase coronal plane range of motion measured between the tibia and calcaneus by up to 6° during human walking (Reinschmidt et al., 1997; Nester et al., 2007). However, the patterns of motion measured in this study are similar to those reported in other multisegment foot kinematics studies (e.g., Carson et al., 2001; Jenkyn and Nicol, 2007; Leardini et al., 2007a), and I assume that any soft tissue artifacts should affect ranges of motion in human and chimpanzee subjects to a similar degree. Therefore, the results of this study should still accurately represent differences between species.

The Midfoot Joints. My second hypothesis states that chimpanzees exhibit greater mobility between their rearfoot and forefoot segments than humans during a bipedal step. I predicted that this would include greater ranges of motion in the sagittal and coronal planes. I expect these motions to occur at the transverse tarsal joint complex and tarsometatarsal joints in both species. Surprisingly, this hypothesis, and its predictions, were largely refuted. In both the sagittal and transverse planes, humans use greater ranges of motion between the rearfoot and forefoot segments than chimpanzees. These differences are driven by high plantarflexion and adduction of the human midfoot joints in the second double support phase (Figs. 4.3a-4.4a). At the beginning of this phase, the heel is being lifted from the ground and the foot is dorsiflexing about the metatarsophalangeal joints. This motion tightens the plantar aponeurosis, which pulls the metatarsal heads posteriorly and inferiorly *via* the windlass mechanism (Hicks, 1954; Erdemir et al., 2004; Caravaggi et al., 2009), accounting for the dramatic plantarflexion of the human forefoot during this period. Meanwhile, the forefoot segments are adducted relative to the rearfoot to keep the center of pressure under the first ray during push-off (MacConaill and Basmajian, 1977; Sarrafian, 1987; Duerinck et al., 2014).

The rearfoot-forefoot kinematics measured for human subjects in this study are generally consistent with those described in other human multisegment foot kinematics studies (e.g., Carson et al., 2001; Leardini et al., 2007a; Levinger et al., 2010). The only notable disagreement pertains to coronal plane motion, where most studies have found slight inversion between the forefoot and rearfoot at the beginning of the second double-support phase, followed by eversion. In this study I measured dramatic inversion of the lateral forefoot and a highly variable motion pattern at the medial forefoot during this phase. However, these results make sense in light of the findings of Duerinck et al. (2014). They demonstrated that inversion of the lateral forefoot and eversion of medial forefoot occurs during push-off in human walking to raise the transverse arch and position the center of pressure under the first metatarsal. My results are consistent with their findings for the lateral forefoot. For the medial forefoot, they measured motion at a segment including metatarsals 1 and 2, as opposed to the metatarsals (2 and 3) used to represent this segment in my study. The medial forefoot segment I used was in between their medial and lateral forefoot segments, and therefore it makes sense that the coronal plane motion I measured was exactly between that which they found for their two segments.

The transverse and longitudinal arch mechanisms just described for the human foot are largely absent in the chimpanzee foot. After the first double-support phase, the most notable motion to occur between the chimpanzee rearfoot and forefoot segments is progressive dorsiflexion during heel lift (which begins around 25% of stance phase, see Chapter 5). This

motion represents the midtarsal break, and peaks at the end of single-support. Both the transverse tarsal and tarsometatarsal joints contribute to this motion (DeSilva, 2010; see Chapter 3), and it results in the significantly greater maximum midfoot dorsiflexion in chimpanzees compared to humans on the medial side of the foot. Otherwise, chimpanzees only exhibit markedly greater joint excursions than humans in the first double-support phase, when the chimpanzee forefoot segments are abducted at touchdown. The reason chimpanzees assume these abducted postures is unclear, but it may be related to their overall strategy of touching down with an inverted foot. During single support phase, relatively little rearfoot-forefoot motion occurs outside of the sagittal plane, except for gradual abduction of the lateral forefoot segment. In the second double support phase, chimpanzees rapidly supinate their lateral forefoot segment, although not to the same degree as in humans. Chimpanzees do, on average, use a significantly greater range of coronal plane motion between their rearfoot and medial forefoot segments than humans, providing partial support for the second prediction of my second hypothesis. However, inspection of Figure 4.4b reveals that this difference was entirely driven by Chimp L, who exhibited large inversion and eversion joint excursions during first and second double-support phases, respectively. Hence, the relatively high coronal plane mobility between the rearfoot and medial-forefoot segments measured for chimpanzees in this study are not representative of a consistent pattern between individuals.

Overall, the midfoot kinematics measured in this study contrast strikingly with the traditional dichotomy used to characterize human and chimpanzee foot function. The chimpanzee midfoot joints have long been characterized as highly mobile in order to enhance the prehensile capability of the foot. This mobility is thought to come at the expense the foot's overall rigidity, reducing its efficiency as a lever during push-off in terrestrial locomotion (Elftman and Manter, 1935a; b; Bojsen-Møller, 1979; Susman, 1983; Lovejoy et al., 2009; DeSilva, 2010). Humans, in contrast, are described as possessing joint and soft-tissue morphology that 'locks-up' the midfoot during push-off, enabling it to function as a stiff propulsive lever. Recently, this dichotomy has come under scrutiny from several directions. Multisegment foot kinematics studies have consistently demonstrated higher than previously appreciated midfoot mobility in humans, particularly in the second double-support phase (e.g., Carson et al., 2001; Leardini et al., 2007a; Lundgren et al., 2008). These findings have been somewhat affirmed in pedobarographic studies, which have demonstrated wide variation across humans in midfoot mobility on the basis of pressure distribution patterns (Crompton et al., 2010; Bates et al., 2013; DeSilva and Gill, 2013; DeSilva et al., 2015). In particular, Bates et al. (2013) demonstrated overlap between humans, bonobos, and orangutans in a pressure measurement related to midfoot dorsiflexion following heel lift. Most recently, in a quantitative analysis of passive mobility in cadaveric specimens, Greiner and Ball (2014) demonstrated similar ranges of motion in human and chimpanzee transverse tarsal and tarsometatarsal joints.

The results of the present study take these findings a step further by indicating that the chimpanzee midfoot is actually *less mobile* than the human midfoot during the second half of stance phase in bipedal walking. The human foot functions as a propulsive lever during push-off, but does so dynamically *via* intrinsic foot motion that accentuates the longitudinal and transverse arches. The chimpanzee foot, on the other hand, exhibits little of the rotatory motion that accompanies longitudinal arch function, but also does not deform as dramatically as previously assumed. This result is surprising based on the many descriptions of the midtarsal break, which is pronounced in chimpanzees, but uncommon in humans (DeSilva, 2010; Bates et al., 2013; DeSilva and Gill, 2013). This study indicates that chimpanzees do dorsiflex their midfoot joints

in a manner characteristic of a ‘break’ following heel lift. However, the actual magnitude of midfoot dorsiflexion was only significantly greater than that in humans between the rearfoot and the medial forefoot segment. With the exception of this motion, the human midfoot is more mobile than that of chimpanzees in ways that are less easily observable (i.e., coronal and transverse plane motion, forefoot plantarflexion). The results of this study are not surprising when considering the overall similarity in midfoot passive mobility between humans and chimpanzees (Greiner and Ball, 2014). When taking into account the fact that chimpanzees spend the majority of their travel time on the ground (Hunt, 1992; Doran, 1993), it should also not come as a surprise that the chimpanzee foot is evolved to provide a relatively stiff support during push-off on terrestrial substrates.

As discussed in Chapter 3 (Section 3.4.2), these subjects exhibited a less pronounced midtarsal break than some (but not all) of the other chimpanzees I have observed in video recordings. This is also not the first study to point out variability in midtarsal break magnitude among great apes. Griffin et al. (2010) commented that based on their plantar pressure distributions [as measured by Vereecke et al. (2003)], bonobos do not always exhibit midtarsal breaks when walking bipedally. It is important to emphasize that the results of this study represent *in vivo* foot kinematics from normal, healthy chimpanzees; that is to say, these results represent a possible outcome given basic chimpanzee foot anatomy. Therefore, the point previously argued, that chimpanzees can walk bipedally with less midfoot motion than humans, stands.

Based on this point, joint morphology should not be used to determine relative midfoot mobility in humans and chimpanzees during bipedalism (cf., Bates et al., 2013; Greiner and Ball, 2014). This extends to the interpretation of articular surface morphologies at the transverse tarsal and tarsometatarsal joints: For instance, the absence of a human-like calcaneal process on the proximal articular surface of the cuboid should not be interpreted as resulting in greater midfoot mobility during bipedal locomotion, because the 3-D kinematic data presented here show a greater lateral midfoot range of motion in humans than in chimpanzees. Curvature of the cuboid-metatarsal joint surfaces may also be an unreliable indicator of overall joint mobility during bipedalism; the dramatic range of motion measured at the cuboid-metatarsal joints in human subjects in this study is reflected in other studies of human intrinsic foot joint kinematics (e.g., Carson et al., 2001; Leardini et al., 2007b), including one that used markers mounted on bone pins (Lundgren et al., 2008). Differences between humans and chimpanzees at these joint surfaces may be related to other differences in overall foot function and substrate use, rather than just relative mobility. As demonstrated in Chapter 3, chimpanzees use different midfoot postures when climbing and walking on arboreal supports, compared to when walking on the ground. Their midfoot joint articular surface may be adapted to specifically facilitate these behaviors.

4.4.2 Chimpanzee Bipedal Versus Quadrupedal Foot Kinematics

My fourth hypothesis states that chimpanzees use similar foot kinematics during bipedal and quadrupedal gaits. My first prediction was that chimpanzees would use similar subtalar joint kinematics in both gaits. In terms of overall patterns of motion, this prediction was partially supported, but not in terms of range of motion (Fig. 4.2c). I found that chimpanzees use significantly greater inversion angles at touchdown during bipedalism compared to quadrupedalism. The reason for this difference is unclear, but following touchdown chimpanzees assume similarly everted joint postures in both gaits, although they exhibit more gradual inversion in the second half of stance during quadrupedalism. Chimpanzees also exhibit a

dramatic abduction of the subtalar joint following touchdown in bipedalism that is totally absent in quadrupedalism. Again, the reason for this motion is unclear, but may be related to the dramatic internal rotation of the hip immediately following touchdown displayed by chimpanzees during bipedal locomotion (O'Neill et al., 2015). However, no study has yet reported transverse plane motion for the chimpanzee lower limb during quadrupedal walking, and these data are necessary to validate this idea.

Chimpanzees also use greater overall ranges of motion and exhibit higher maximum dorsiflexion angles at the talocrural joint during bipedal walking as compared to quadrupedal walking. This result runs contrary to the findings of Pontzer et al. (2014), who measured similar ranges of motion between gaits at moderate walking speeds, and a greater range of motion during quadrupedalism at higher speeds. In the present study, subjects walked with higher estimated speeds during bipedalism than during quadrupedalism. However, this should not explain the discrepancy between my findings and those of Pontzer et al., because they measured *lower* ranges of motion at faster speeds. The difference between the findings of our respective studies may instead be due to individual variation among chimpanzees in ankle kinematics during bipedal walking.

My second prediction for the fourth hypothesis was that chimpanzees would exhibit similar midfoot kinematics during bipedal and quadrupedal locomotion. Both patterns *and* ranges of motion between the rearfoot and forefoot segments were similar in both gaits, upholding my prediction. The only significant differences between gait types were the presence of a slightly higher plantarflexion angle between the midfoot and lateral forefoot following touchdown, and a slightly higher peak dorsiflexion angle during quadrupedalism. The absolute difference in each of these cases, however, is $< 4^\circ$, and therefore unlikely to indicate a meaningful difference in foot mechanics. Given the difference in hind limb mediolateral forces between gaits reported by Pontzer et al. (2014), the near absence of midfoot kinematic differences between bipedalism and quadrupedalism is somewhat surprising. One might expect that the larger medially directed forces experienced by the foot during bipedal walking would cause larger angular excursions at the midfoot joints, but this does not appear to be the case. This result could be taken as further evidence that the chimpanzee foot is a relatively rigid structure that is capable of resisting the high forces incurred during terrestrial locomotion.

4.4.3 Metatarsophalangeal Joints

My third hypothesis states that humans dorsiflex their MTPJs more than chimpanzees during the push-off phase of a step, and I predicted that this would be the case at all five joints. This prediction was strongly supported (Fig. 4.4), extending Griffin et al.'s (2010) findings for the first two joints in bonobos. However, unlike the bonobos in Griffin et al.'s study, the chimpanzees in the present study did not show any overlap in peak MTPJ dorsiflexion angles for the first three MTPJs with humans. The difference between chimpanzees and humans is likely related to proximal lower limb kinematics, and the role these joints play in the human windlass mechanism (Bojsen-Møller, 1979; Griffin et al., 2010). Humans extend their hips and knees, and plantarflex their ankles to a much greater degree than chimpanzees during the second double-support phase of stance (O'Neill et al., 2015), resulting in feet that are positioned at a much greater angle to the ground during push-off. This drives the human MTPJs into higher passive dorsiflexion angles, which tightens the plantar aponeurosis and sets the windlass mechanism in motion. Chimpanzees possess a much less developed plantar aponeurosis than humans (Swindler

and Wood, 1973; Susman, 1983; pers. obs.), so greater dorsiflexion of the MTPJs would be unlikely to strongly influence midfoot mechanics.

Interspecies differences in MTPJ kinematics can be related back to differences in joint morphology. Compared to chimpanzees, humans possess metatarsal heads that are mediolaterally broad and dorsally domed (Stern and Susman, 1983; Latimer and Lovejoy, 1990; Fernández et al., 2015), with more anisotropic trabecular bone distributions (Griffin et al., 2010). Additionally, human proximal phalangeal bases are more dorsally ‘canted’ than those of chimpanzees (Stern and Susman, 1983; Latimer and Lovejoy, 1990; Duncan et al., 1994; Griffin and Richmond, 2010). These morphological differences are believed to allow humans to subject their MTPJs to higher loads while dorsiflexed than chimpanzees. The results of this study support these features as good predictors of MTPJ function during locomotion.

I also predicted that chimpanzees would use similar MTPJ kinematics during bipedal and quadrupedal locomotion. This prediction was supported for all joints except MTPJs 3 and 4, which dorsiflex more during quadrupedalism than bipedalism. MTPJs 2 and 5 also display slightly, but not significantly higher peak dorsiflexion angles during quadrupedalism. This difference between gaits may be related to the fact that the chimpanzees in my study used slightly greater ankle plantarflexion angles during the push-off of quadrupedal steps as compared to bipedal steps. This motion could passively force the MTPJs into slightly greater maximum dorsiflexion angles during quadrupedalism. In addition to characterizing between-species and bipedal *vs.* quadrupedal gait differences, this study demonstrates differences in peak dorsiflexion angles across the MTPJs within species. Humans exhibit similar peak dorsiflexion angles for their first three MTPJs, but diminishing peaks for their lateral two. Chimpanzees, on the other hand, exhibit significantly lower peak dorsiflexion angles at MTPJ 1 than at MTPJ 2, in contrast to the findings of Griffin et al. (2010) for bonobos. Additionally, the largest difference in peak dorsiflexion angles between humans and chimpanzees occurs at MTPJ 1. Like humans, the chimpanzee subjects in this study appeared to push-off with the medial sides of their feet, with digits 1-3 usually the last to leave the ground. This pattern is generally consistent with that previously described for chimpanzees (Elftman and Manter, 1935b; Wunderlich, 1999) and bonobos (Vereecke et al., 2003).

Given that humans and chimpanzees both push-off the medial forefoot, the large discrepancy between species in relative dorsiflexion angles at the first two digits is somewhat surprising. In passive mobility measurements, both chimpanzee subjects displayed a 25-30% greater range of dorsiflexion at MTPJ 2 compared to MTPJ 1. This result suggests some anatomical constraint in the relative mobility of the chimpanzee first MTPJ. Such a constraint could be necessary to provide joint stability during behaviors that require strong hallucal grasping, such as arboreal locomotion. Average peak dorsiflexion angles during locomotion were considerably lower (roughly 20° less) than the maximum passive angles at all MTPJs where these ranges were measured. This discrepancy suggests that passive range of motion may be an adequate indicator of relative mobility among joints, but not a good predictor of active joint kinematics during locomotion. Somewhat in contradiction to this notion, however, the passive mobility of MTPJ 5 did not clearly reflect its range of motion *in vivo*. This joint showed similar passive mobility to MTPJ 2 in one subject, but very low passive mobility in the other. Nevertheless, in both subjects this joint exhibited similar, very low peak dorsiflexion angles during push-off, indicating that passive mobility should not always be assumed to provide an accurate representation of joint motion *in vivo*.

The difference in relative dorsiflexion peaks between MTPJs 1 and 2 could be related to the axis about which chimpanzees push-off of their metatarsal heads prior to liftoff. Like humans, chimpanzees also exhibit diminishing peak dorsiflexion angles from MTPJ 2 to 5. However, the drop off in angle magnitude is much steeper in chimpanzees, suggesting that they push-off of a mediolateral axis that is centered on MTPJ 2, but does not run as close to the other metatarsal heads as in humans. This difference could be related to the more abducted lower limb posture of chimpanzees (O'Neill et al., 2015), which results in a foot positioned at a wide angle to the direction of travel. In this position, the hallux is directed medially, and digits 2-5 are directed lateral relative to the body's overall anteroposterior axis. Consequently, as the chimpanzee forefoot dorsiflexes about the head of the second metatarsal during push-off, MTPJ 2 will dorsiflex more than the lateral MTPJs. Additionally, because chimpanzees push-off the medial sides of their feet, their medial metatarsal heads and digits are exposed to relatively greater pressures at the end of stance (Wunderlich, 1999). This pattern of joint loading is also likely to contribute to the relatively greater dorsiflexion angles at these joints. Consequently, the more lateral MTPJs of chimpanzees likely require progressively less structural reinforcement against loading at high dorsiflexion angles. Whether this trend is reflected in bony morphology at these joints could prove a fruitful avenue of investigation.

4.4.4 Overall Foot Kinematics

The foot kinematics obtained from human subjects in this study are similar to those reported in previous multisegment foot model studies (e.g., Carson et al., 2001; Leardini et al., 2007a; Levinger et al., 2010). Following heel strike, the leg rotates internally with respect to the planted rearfoot. This rotation results in slight eversion of the rearfoot relative to the leg *via* pronation (eversion and abduction) at the subtalar joint (Close, 1972; Inman, 1976). These motions occur in the first double-support phase, as the foot is beginning to accommodate weight, and result in loose-packing of the midfoot joints (Donatelli, 1985). During this phase the arch lowers, which manifests as dorsiflexion between the forefoot and rearfoot segments, causing the plantar ligaments and muscles to stretch and absorb ground reaction forces (Ker et al., 1987; Kelly et al., 2015). During the first half of single-support phase, the lateral forefoot pronates relative to the rearfoot, further stretching the plantar soft tissues. As the heel lifts from the ground in the second half of single support phase, it drives the metatarsophalangeal joints into dorsiflexion, which tightens the plantar aponeurosis *via* the windlass mechanism (Hicks, 1954). This tightening, and action of extrinsic ankle plantarflexor musculature, inverts the rearfoot relative to the leg, returning the midfoot joints to a close-packed position to withstand high push-off forces (Bojsen-Møller, 1979; Sarrafian, 1987). The lifted rearfoot also abducts and dorsiflexes relative to the planted forefoot, raising the longitudinal arch and helping to position the center of pressure under the medial side of the distal forefoot (Leardini et al., 2007a). These motions are believed to enhance the foot's ability to perform as a propulsive lever during bipedal push-off (Levinger et al., 2010), as well as take advantage of the recoil of elastic soft tissues and intrinsic foot muscles that occurs with the rising of the longitudinal arch (Ker et al., 1987; Kelly et al., 2015).

During both bipedal and quadrupedal locomotion, chimpanzee foot kinematics lack many of the motion patterns that are related to arch function in humans. After contacting the substrate with highly inverted feet, chimpanzees rapidly evert and abduct the rearfoot in a manner similar to humans. However, unlike humans they do not exhibit midfoot dorsiflexion during this period; lacking an arch, the midfoot region is in full contact with the ground and therefore cannot deform

as a loading response. Beginning in single-support phase, chimpanzees begin to lift their heels, during which time their midfoot joints progressively dorsiflex, resulting in the commonly observed midtarsal break motion (e.g., Elftman and Manter, 1935b). Midfoot dorsiflexion peaks just after the second double-support phase, and is followed by slight, rapid dorsiflexion and eversion of the rearfoot relative to the planted forefoot. These motions occur while the metatarsophalangeal joints are near peak dorsiflexion, suggesting the possibility of an incipient windlass mechanism. Chimpanzees typically possess thin plantar aponeuroses (Susman, 1983; pers. obs.), so the presence of such a mechanism is certainly possible. However, the associated motions are small relative to those in humans, and are not accompanied by subtalar inversion. Therefore, these differences suggest that the chimpanzee midfoot joints maintain a degree of laxity during stance, and therefore are not designed to maximize propulsive force generation during push-off to the extent that they are in the human foot. However, the actual mechanical effect of the differences in human and chimpanzee foot kinematics requires further testing using inverse dynamic or forward modeling approaches.

These between-species differences in foot kinematics suggest that chimpanzees lack adaptations for maximizing energy absorption and push-off propulsion during terrestrial locomotion in favor of maintaining some postural versatility in the midfoot for arboreal behaviors. However, it bears reiteration that the chimpanzee midfoot exhibits relatively low overall mobility during terrestrial locomotion, meaning that it is still a relatively stiff structure that simply lacks the specialized adaptations for bipedal locomotion present in the human foot.

4.4.5 Conclusions

This study shows that reducing the differences in human and chimpanzee foot mechanics to relative amounts of mobility simplifies the complex kinematic patterns that actually distinguish intrinsic foot motion in these species. Contrary to my expectations, and most previous characterizations of chimpanzee foot mechanics (Elftman and Manter, 1935a; Bojsen-Møller, 1979; Susman, 1983; Langdon et al., 1991; Lovejoy et al., 2009; DeSilva, 2010), chimpanzees actually exhibit generally lower midfoot joint mobility than humans during stance phase while walking on terrestrial substrates. In humans, these joints, along with the subtalar joint, undergo a series of significant rotations in the second half of stance that are absent or reduced in chimpanzees. Specifically, following heel lift, as the MTPJs are passively dorsiflexed, the rearfoot inverts, and the forefoot plantarflexes and adducts, raising the longitudinal arch and positioning the center of pressure towards the distal end of the medial forefoot. This series of motions serves multiple purposes: First, it increases the moment arm ratio of the substrate reaction force to the ankle plantarflexors, enhancing push-off propulsion (Carrier et al., 1994). Second, it enables the foot to take advantage of the recoil of elastic soft tissues on the plantar surface of the foot during push-off (Ker et al., 1987). Third, it prevents a midtarsal break in the midfoot that occurs in chimpanzees during heel lift.

Although the midtarsal break is indeed more pronounced in chimpanzees than in humans, the magnitude of the difference in maximum midfoot dorsiflexion between species is actually quite small. In fact, the average peak dorsiflexion between the rearfoot and lateral forefoot in this study was the same in humans and chimpanzees. Therefore, the chimpanzee midfoot should not be characterized as more mobile than that of humans during terrestrial locomotion, but instead as lacking the anatomical specialization to produce the kinematic patterns associated with longitudinal arch function.

This finding bears on the results of recent investigations of humans with the condition known as *pes planus* or ‘flexible flatfoot.’ Flexible flatfoot is a common condition in humans, and is usually characterized by the following symptoms during weight-bearing: rearfoot eversion, medial arch drop, and forefoot abduction (Mosca, 2010). Although it was commonly thought that individuals with this condition would exhibit abnormally high midfoot mobility while walking (Elftman, 1969; Phillips and Phillips, 1983; Blackwood et al., 2005), multisegment foot kinematics studies have revealed that this is often not the case. Studies of adults (Hunt and Smith, 2004; Levinger et al., 2010) and adolescents (Twomey et al., 2010; Hösl et al., 2014) have found that although flatfooted individuals tend to exhibit absolutely lower arches and more abducted forefeet, their pedal joints exhibit similar ranges of motion to those of normal-arched individuals during walking. Flatfooted individuals have been found, however, to rely on alternative muscle activation patterns (Hunt and Smith, 2004; Murley et al., 2009), and to push-off with less ankle power (Hösl et al., 2014) than individuals with normal feet. Therefore, compromised arch function appears to influence certain aspects of foot mechanics during walking, but not overall foot mobility. This is consistent with my findings, which reveal that the absence of an arch in chimpanzees does not increase overall midfoot mobility, but does preclude human-like foot kinematics.

These results join those of several recent studies that have undermined the traditional dichotomy between human and great ape midfoot mobility. These studies include plantar pressure investigations (Bates et al., 2013; DeSilva and Gill, 2013; DeSilva et al., 2015), and passive mobility quantifications (Greiner and Ball, 2014; Thompson et al., 2014) in humans and great apes. The findings of these studies agree with my results, and suggest that the chimpanzee midfoot is not highly mobile during terrestrial walking, as it has been previously characterized, but relatively rigid, at least in comparison to most other primates in which midtarsal mobility has been documented (Bennett et al., 1989; Meldrum, 1991; Gebo, 1992; Vereecke and Aerts, 2008; Berillon et al., 2010; DeSilva, 2010; Hirasaki et al., 2010; Greiner and Ball, 2014). As such, it is no longer appropriate to discuss human foot adaptation in terms of increasing overall *rigidity* if our sister species displays similar magnitudes of intrinsic foot motion during walking. Rather, human foot adaptation should be discussed more in terms of the evolution of the dynamic mechanism that raises the longitudinal arch during push-off.

Although chimpanzees displayed relatively small overall ranges of midfoot motion during terrestrial bipedal and quadrupedal locomotion in this study, they displayed much greater midfoot mobility in my previous investigation of locomotion on arboreal substrates (see Chapter 3). More specifically, compared to terrestrial quadrupedalism, chimpanzees tended to display greater ranges of subtalar and midfoot motion during pole walking, and greater maximum cuneiform-metatarsal joint excursion during climbing. Therefore, it should be acknowledged that the chimpanzee foot is capable of greater mobility than that displayed during terrestrial locomotion, and that this mobility is likely an adaptation for travel on arboreal substrates. It is likely, then, that the relatively more ‘rigid’ midfoot displayed by chimpanzees during ground walking is evidence that the chimpanzee foot capable of limiting motion during terrestrial travel. This limitation is likely facilitated by a combination of passive features, such as joint surface shape and soft tissue structures, as well active restraint by the lower limb muscles. As such, the chimpanzee foot should be viewed as adapted for both proficient arboreal and terrestrial locomotion, as one might expect given the highly varied locomotor repertoire of this species.

Contrary to my expectations, the chimpanzee foot was not more mobile during bipedalism than during quadrupedalism. In fact, the overall similarity in midfoot kinematics

between gaits suggests that the chimpanzee foot is well suited to handle the mechanical challenges of bipedal locomotion. Although chimpanzees displayed significantly greater talocrural and subtalar joint ranges of motion during bipedalism than during quadrupedalism, these proximal joint motions did not have a major effect on the mobility of the midfoot joints measured in this study. This result has important implications for hominin foot evolution: An early hominin with a chimpanzee-like foot would have been able to adopt bipedal locomotion without any major compromises to normal foot function. Therefore, the possession of a chimpanzee-like foot may not have posed a major obstacle to the adoption of facultative bipedalism in a human-chimpanzee last common ancestor.

Chapter 4: Tables

Table 4.1. Average stance durations and estimated dimensionless velocities for all subjects.

Species	Subject	Stance (s)	Estimated Dimensionless Velocity ^a
Human	Human A	0.59 ± 0.01	0.46 ± 0.01
	Human B	0.65 ± 0.01	0.43 ± 0.01
	Human C	0.69 ± 0.02	0.44 ± 0.02
	Human D	0.66 ± 0.01	0.47 ± 0.01
	Human E	0.68 ± 0.01	0.47 ± 0.01
	<i>Average</i>	<i>0.66 ± 0.04</i>	<i>0.45 ± 0.02</i>
Chimpanzee <i>Bipedal</i>	Chimp H	0.6 ± 0.06	0.42 ± 0.03
	Chimp L	0.58 ± 0.06	0.48 ± 0.02
	<i>Average</i>	<i>0.58 ± 0.05</i>	<i>0.46 ± 0.05</i>
	<i>Quadrupedal</i>	Chimp H	0.68 ± 0.02
Chimp L		0.73 ± 0.08	0.41 ± 0.05
<i>Average</i>		<i>0.71 ± 0.06</i>	<i>0.42 ± 0.04</i>

^a Calculated using linear regression equations developed in Chapter 2 (see Table 2.3).

Table 4.2. Average minimum and maximum angles, and ranges of motion between the leg and rearfoot segments for humans and chimpanzees.

Plane	Motion	Human	Chimpanzee (Bipedal)	Chimpanzee (Quadrupedal)
Sagittal	Plantarflexion	-11.8 ± 3.7°	-7.9 ± 3.6°	-11.4 ± 3.9°
	Dorsiflexion	6.5 ± 3.7°	21.3 ± 5°	13 ± 5.2°
	Range	18.3 ± 2.9°	29.2 ± 4.7°	24.4 ± 3.5°
Coronal	Eversion	-3.5 ± 2.7°	-8.7 ± 4.5°	-5.6 ± 5.9°
	Inversion	13.1 ± 3.3°	18.8 ± 6°	12.5 ± 8.2
	Range	16.6 ± 3.3°	27.5 ± 7.5°	18.1 ± 5.3
Transverse	Abduction	-6.7 ± 3°	-7.7 ± 3.7°	-3.3 ± 2.1°
	Adduction	1.2 ± 2°	3.4 ± 3.4°	4.8 ± 2.5°
	Range	7.9 ± 3.4°	11 ± 3.3°	8.1 ± 2.1°

Table 4.3. Average minimum and maximum angles, and ranges of motion between the rearfoot and lateral forefoot segments for humans and chimpanzees.

Plane	Motion	Human	Chimpanzee (Bipedal)	Chimpanzee (Quadrupedal)
Sagittal	Plantarflexion	$-14.1 \pm 2.5^\circ$	$-3.9 \pm 2.5^\circ$	$-0.4 \pm 1.7^\circ$
	Dorsiflexion	$6 \pm 2.8^\circ$	$6 \pm 3^\circ$	$8.2 \pm 1.9^\circ$
	Range	$20.1 \pm 2.3^\circ$	$9.9 \pm 2.5^\circ$	$8.6 \pm 1.7^\circ$
Coronal	Eversion	$-3.4 \pm 3.9^\circ$	$-5.2 \pm 3.4^\circ$	$-3.4 \pm 3.5^\circ$
	Inversion	$9.4 \pm 2.8^\circ$	$6.7 \pm 5.4^\circ$	$5.6 \pm 3.2^\circ$
	Range	$12.9 \pm 2.4^\circ$	$11.8 \pm 4.6^\circ$	$9 \pm 1.4^\circ$
Transverse	Abduction	$-3.1 \pm 1.9^\circ$	$-6.3 \pm 2^\circ$	$-7.7 \pm 2.2^\circ$
	Adduction	$7.9 \pm 2.2^\circ$	$0.6 \pm 2.9^\circ$	$0.7 \pm 0.8^\circ$
	Range	$10.9 \pm 2.2^\circ$	$6.9 \pm 2.5^\circ$	$8.4 \pm 2.2^\circ$

Table 4.4. Average minimum and maximum angles, and ranges of motion between the rearfoot and medial forefoot segments for humans and chimpanzees.

Plane	Motion	Human	Chimpanzee (Bipedal)	Chimpanzee (Quadrupedal)
Sagittal	Plantarflexion	$-12.8 \pm 3^\circ$	$-2.3 \pm 2.4^\circ$	$-0.9 \pm 3.1^\circ$
	Dorsiflexion	$5.7 \pm 2.1^\circ$	$7.8 \pm 3^\circ$	$10.3 \pm 3.4^\circ$
	Range	$18.5 \pm 3^\circ$	$10.2 \pm 2.2^\circ$	$11.2 \pm 1.4^\circ$
Coronal	Eversion	$-4.2 \pm 3.7^\circ$	$-5 \pm 4.2^\circ$	$-2.3 \pm 5.9^\circ$
	Inversion	$3.4 \pm 5.2^\circ$	$5.3 \pm 3.1^\circ$	$6 \pm 6.9^\circ$
	Range	$7.7 \pm 2.8^\circ$	$10.3 \pm 4^\circ$	$8.3 \pm 3.1^\circ$
Transverse	Abduction	$-1.4 \pm 2.3^\circ$	$-8.5 \pm 2.6^\circ$	$-7.7 \pm 2.4^\circ$
	Adduction	$8.3 \pm 1.6^\circ$	$0 \pm 2.4^\circ$	$1 \pm 1.8^\circ$
	Range	$9.8 \pm 2.7^\circ$	$8.5 \pm 2.6^\circ$	$8.7 \pm 3.3^\circ$

Table 4.5. Results of Wilcoxon rank-sum tests for differences between groups.

Joint	Plane	Human vs. Chimpanzee Bipedalism ^d			Chimpanzee Bipedalism vs. Quadrupedalism ^e		
		Min	Max	Range	Min	Max	Range
Leg-Rearfoot	Sagittal ^a	<i>H</i> (<i>P</i> = 2 E-3)	<i>C</i> (<i>P</i> = 3 E-8)	<i>C</i> (<i>P</i> = 2 E-6)	<i>QP</i> (<i>P</i> = 0.02)	<i>BP</i> (<i>P</i> = 1 E-3)	<i>BP</i> (<i>P</i> = 0.01)
	Coronal ^b	<i>C</i> (<i>P</i> = 1E-4)	<i>C</i> (<i>P</i> = 1 E-3)	<i>C</i> (<i>P</i> = 7 E-6)	<i>n.s.</i>	<i>BP</i> (<i>P</i> = 0.02)	<i>BP</i> (<i>P</i> = 4 E-3)
	Transverse ^c	<i>n.s.</i>	<i>C</i> (<i>P</i> = 0.03)	<i>C</i> (<i>P</i> = 4 E-3)	<i>BP</i> (<i>P</i> = 4 E-3)	<i>n.s.</i>	<i>BP</i> (<i>P</i> = 0.02)
Rearfoot-Lateral	Sagittal ^a	<i>H</i> (<i>P</i> = 1 E-8)	<i>n.s.</i>	<i>H</i> (<i>P</i> = 1 E-8)	<i>BP</i> (<i>P</i> = 0.03)	<i>n.s.</i>	<i>n.s.</i>
Forefoot	Coronal ^b	<i>n.s.</i>	<i>H</i> (<i>P</i> = 0.03)	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>
	Transverse ^c	<i>C</i> (<i>P</i> = 7 E-8)	<i>H</i> (<i>P</i> = 4 E-8)	<i>H</i> (<i>P</i> = 1 E-5)	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>
Rearfoot-Medial Forefoot	Sagittal ^a	<i>H</i> (<i>P</i> = 1 E-8)	<i>C</i> (<i>P</i> = 0.01)	<i>H</i> (<i>P</i> = 1 E-8)	<i>n.s.</i>	<i>QP</i> (<i>P</i> = 0.02)	<i>n.s.</i>
	Coronal ^b	<i>n.s.</i>	<i>n.s.</i>	<i>C</i> (<i>P</i> = 2 E-3)	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>
	Transverse ^c	<i>C</i> (<i>P</i> = 5 E-8)	<i>H</i> (<i>P</i> = 1 E-8)	<i>H</i> (<i>P</i> = 1 E-3)	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>

^a Minimum angles are plantarflexion angles, maximum angles are dorsiflexion angles.

^b Minimum angles are eversion angles, maximum angles are inversion angles.

^c Minimum angles are abduction angles, maximum angles are adduction angles.

^d *C* indicates that chimpanzee value is significantly greater, *H* indicates that human value is significantly greater, *n.s.* indicates that the difference between species is not significant ($P \geq 0.05$).

^e *BP* indicates that bipedal value is significantly greater, *QP* indicates that quadrupedal value is significantly greater, *n.s.* indicates that the difference between gaits is not significant ($P \geq 0.05$).

Table 4.6. Maximum passive dorsiflexion range of motion in chimpanzee subject metatarsophalangeal joints.

MTPJ	Chimp H	Chimp L	Average
1	36°	41°	39°
2	55°	55°	55°
5	54°	31°	43°

Table 4.7. Peak metatarsophalangeal joint dorsiflexion angles during push-off in humans and chimpanzees.

MTPJ	Humans	Chimpanzees (Bipedal)	Chimpanzees (Quadrupedal)
1	48±12°*	12 ± 7°	12 ± 4°
2	48±4°*	30 ± 6°	33 ± 5°
3	47±4°*	23 ± 5°	28 ± 3°*
4	41±7°*	14 ± 4°	17 ± 3°*
5	21±6°*	11 ± 3°	13 ± 6°

* Significantly greater than angle at corresponding joint in chimpanzee bipedalism.

Table 4.8. Results of Kruskal-Wallis post-hoc tests for differences in peak dorsiflexion angles among the MTPJs in humans and chimpanzees. Significant results are indicated where *P*-value is below alpha significance level determined by Bonferroni correction.

MTPJs in Comparison	Humans	Chimpanzees (Bipedal)	Chimpanzees (Quadrupedal)
1 vs. 2	n.s.	2 > 1 (<i>P</i> = 2 E-8)	2 > 1 (<i>P</i> = 8 E-6)
1 vs. 3	n.s.	3 > 1 (<i>P</i> = 2 E-4)	3 > 1 (<i>P</i> = 4 E-4)
1 vs. 4	n.s.	n.s.	n.s.
1 vs. 5	1 > 5 (<i>P</i> = 2 E-8)	n.s.	n.s.
2 vs. 3	n.s.	n.s.	n.s.
2 vs. 4	n.s.	2 > 4 (<i>P</i> = 3 E-7)	2 > 4 (<i>P</i> = 6 E-3)
2 vs. 5	2 > 5 (<i>P</i> = 1 E-8)	2 > 5 (<i>P</i> = 1 E-8)	2 > 5 (<i>P</i> = 7 E-5)
3 vs. 4	n.s.	3 > 4 (<i>P</i> = 2E-3)	n.s.
3 vs. 5	3 > 5 (<i>P</i> = 1E -8)	3 > 5 (<i>P</i> = 4 E-5)	3 > 5 (<i>P</i> = 5 E-8)
4 vs. 5	4 > 5 (<i>P</i> = 2E -4)	n.s.	n.s.

Chapter 4: Figures

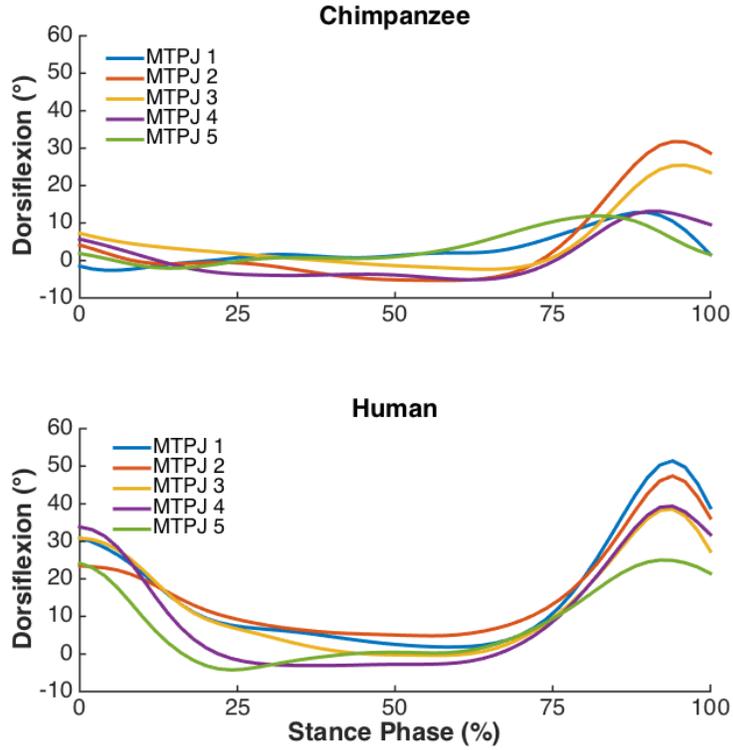


Figure 4.1. Examples of metatarsophalangeal joint motion during stance phase of steps from chimpanzee and human subjects. The peak dorsiflexion angles at the end of stance were used in statistical analyses.

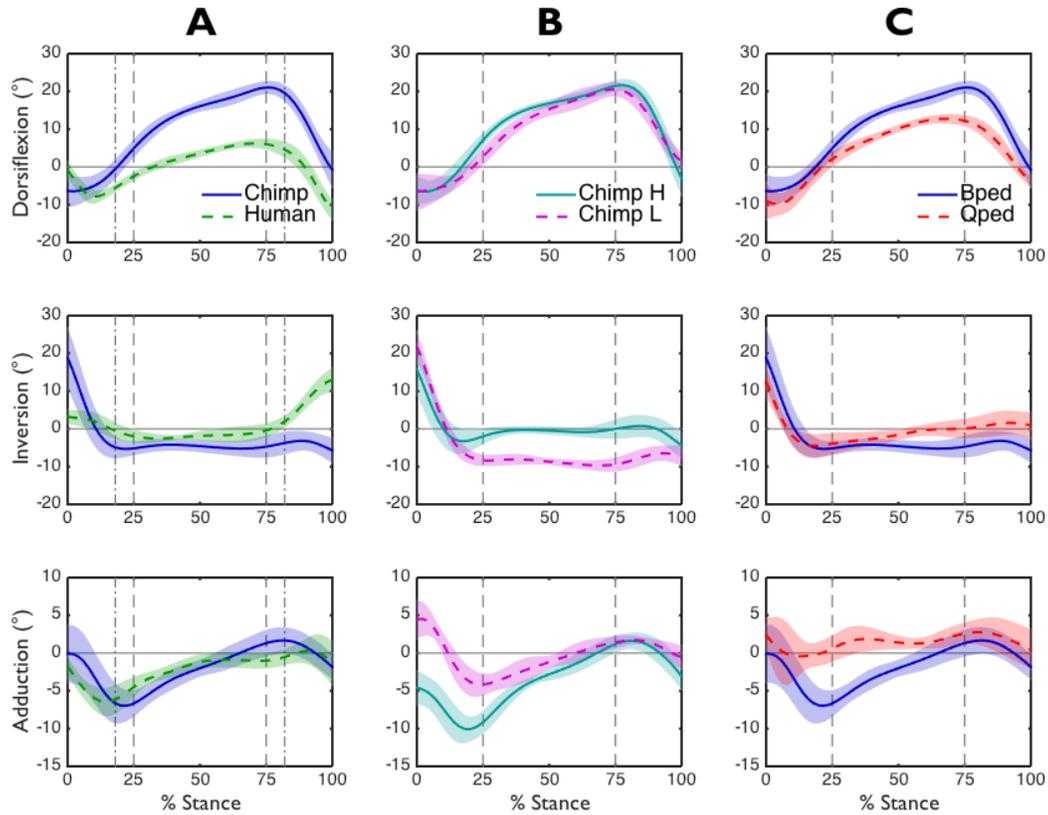


Figure 4.2. Average motion between the *leg* and *rearfoot* segments. Rows: top = sagittal plane motion, middle = coronal plane motion, bottom = transverse plane motion. Y-axis labels indicate positive motion. Columns: A) Human *versus* chimpanzee bipedal walking kinematics. B) Chimp H *versus* Chimp L bipedal walking kinematics. C) Chimpanzee bipedal *versus* quadrupedal walking kinematics. Touchdown is at 0% of stance, and liftoff is at 100% of stance. Vertical dashed lines indicate the beginning and end of single-support phase (dashed lines for chimpanzees, dash-dotted lines for humans).

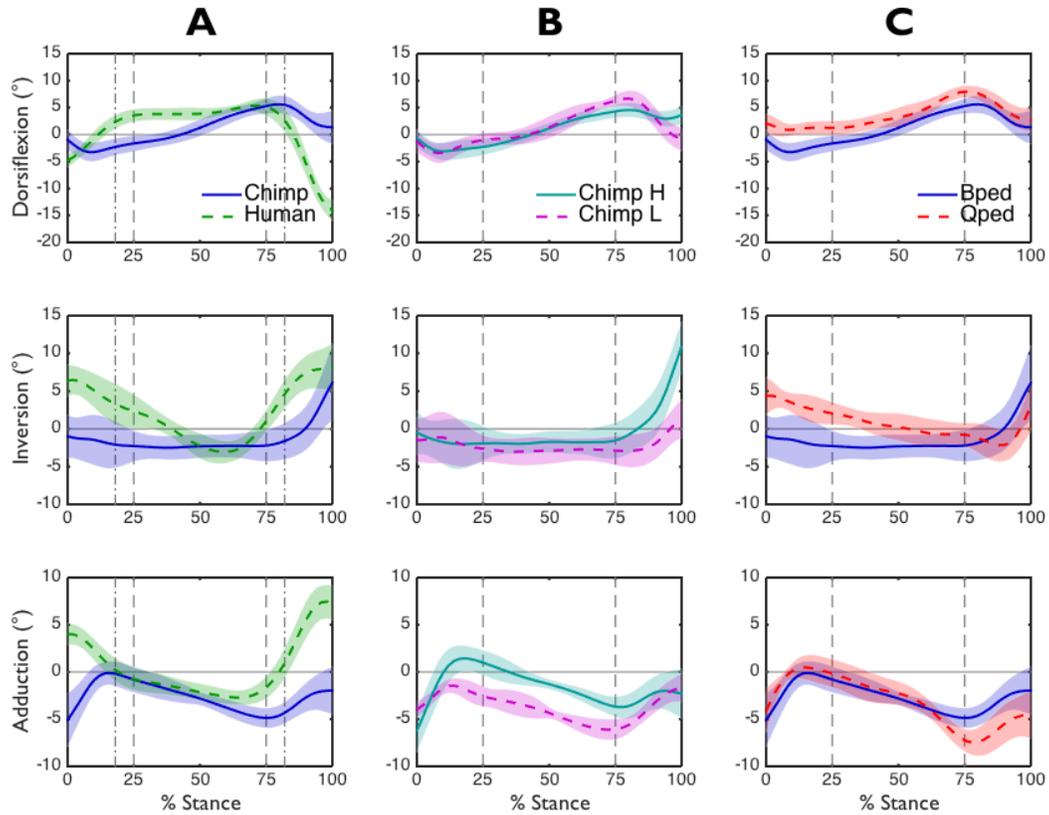


Figure 4.3. Average motion between the *rearfoot* and *lateral forefoot* segments. Rows: top = sagittal plane motion, middle = coronal plane motion, bottom = transverse plane motion. Y-axis labels indicate positive motion. Columns: A) Human *versus* chimpanzee bipedal walking kinematics. B) Chimp H *versus* Chimp L bipedal walking kinematics. C) Chimpanzee bipedal *versus* quadrupedal walking kinematics. Touchdown is at 0% of stance, and liftoff is at 100% of stance. Vertical dashed lines indicate the beginning and end of single-support phase (dashed lines for chimpanzees, dash-dotted lines for humans).

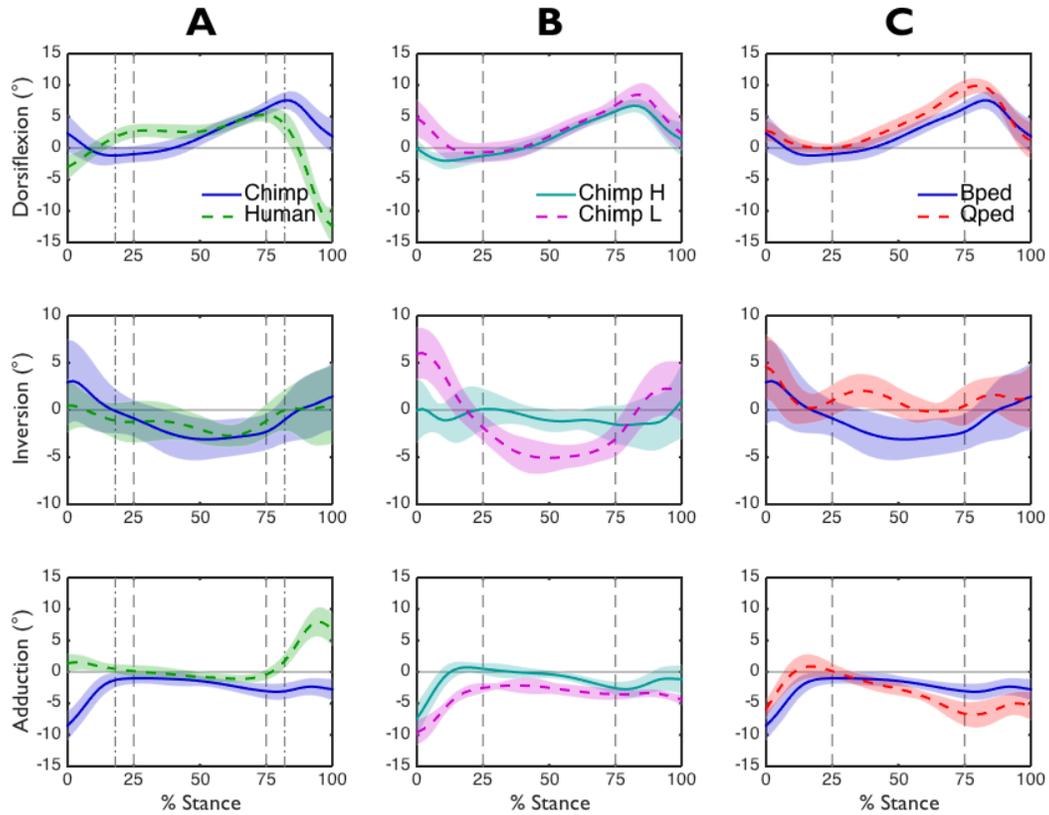


Figure 4.4. Average motion between the *rearfoot* and *medial forefoot* segments. Rows: top = sagittal plane motion, middle = coronal plane motion, bottom = transverse plane motion. Y-axis labels indicate positive motion. Columns: A) Human *versus* chimpanzee bipedal walking kinematics. B) Chimp H *versus* Chimp L bipedal walking kinematics. C) Chimpanzee bipedal *versus* quadrupedal walking kinematics. Touchdown is at 0% of stance, and liftoff is at 100% of stance. Vertical dashed lines indicate the beginning and end of single-support phase (dashed lines for chimpanzees, dash-dotted lines for humans).

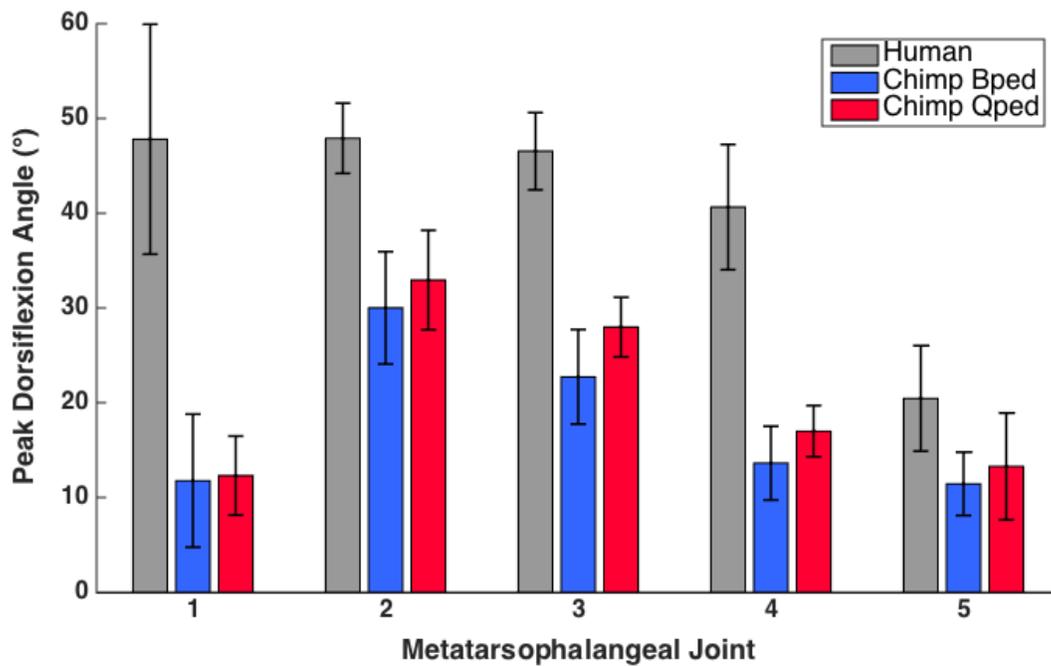


Figure 4.5. Average peak metatarsophalangeal joint dorsiflexion angles during push-off in humans and chimpanzees. Plus/minus one standard deviation is indicated by error bars.



Figure 4.6. Marker indicates position of the peroneal trochlea at touchdown (when the rearfoot is in its most inverted position relative to the leg), and midstance.

Chapter 5

Plantar Pressure Distributions and Foot Kinematics During Bipedal Walking

5.1 Introduction

5.1.1 Background

Numerous comparative studies have documented the multitude of anatomical differences between the feet of humans and African apes and have inferred differences in foot function during locomotion from their findings (e.g., Weidenreich, 1923; Morton, 1924; Bojsen-Møller, 1979; Lewis, 1980; Susman, 1983; Gomberg, 1985). These inferences have largely relied on gross observation of foot postures in non-human apes, leading to assumptions about the link between these postures and intrinsic joint motion. As previously elaborated, this approach is problematic due to the small size and complexity of the intrinsic foot joints, as well as their limited mobility during a given motion. Movement at these joints is very difficult to quantify in non-human apes *in vivo*, but a number of studies have attempted to deduce these movements on the basis of recordings of relative pressure distributions under the feet of these animals (Elftman and Manter, 1935b; Wunderlich, 1999; Vereecke et al., 2003, 2005; Crompton et al., 2012; Bates et al., 2013). This approach, which is sometimes referred to as pedobarography, has long been the primary means of experimentally investigating foot function in living non-human apes during locomotion.

Elftman and Manter (1935a; b) carried out the earliest such study, in which they recorded the changes in plantar pressure over the course of a step during bipedal locomotion in humans and one chimpanzee subject. From these recordings they were able to establish the relative amounts of pressure under different parts of the foot over the course of a step, and track the center of pressure by calculating the resultant of the pressure under all regions of the foot at each moment in the step. They found that the center of pressure under the chimpanzee foot swung medially early in stance, indicating weight bearing under the medial midfoot. This motion, they noted, was absent in human subjects due to the presence of the medial longitudinal arch, and indicated eversion of the subtalar joint in their chimpanzee subject during stance. They also found that the chimpanzee subject exhibited an increase in pressure under the fifth metatarsal base following heel lift, which they related to their observation that the midfoot briefly maintained contact with the ground during this period. They attributed this phenomenon to midfoot dorsiflexion about a highly mobile transverse tarsal joint complex in chimpanzees. This motion, which has come to be called the ‘midtarsal break’, has been a major subject of investigation in studies of hominoid foot functional morphology since this discovery (Bojsen-Møller, 1979; Susman, 1983; Langdon et al., 1991; Kidd, 1998; DeSilva, 2010; Greiner and Ball, 2014; Thompson et al., 2014).

Using a capacitor-based pressure sensing platform to measure pressure distributions in bonobos during bipedal and quadrupedal walking, Vereecke et al. (2003) observed sustained pressure in the lateral midfoot following heel lift that appeared to be related to the midtarsal

break. However, they argued from their data that this motion actually occurs at the cuboid-metatarsal joints, rather than the transverse tarsal joints, as suggested by Elftman and Manter (1935a; b). This notion was later taken up by researchers studying morphological correlates of midfoot mobility in non-human apes and fossil hominins (DeSilva, 2010; Ward et al., 2011; DeSilva et al., 2013; Proctor, 2013; Greiner and Ball, 2014). Vereecke et al. (2003) also measured relatively low medial midfoot pressures in their subjects, leading them to conclude that bonobos maintain relatively inverted foot postures during terrestrial locomotion (*contra* Elftman and Manter, 1935a; b). This finding has influenced several functional morphology studies of fossil hominin pedal remains (Lovejoy et al., 2009; DeSilva et al., 2013), which have assumed that all African apes use inverted foot postures when walking on the ground.

Griffin et al. (2010b) compared the metatarsophalangeal joint kinematic data that they collected from bonobos to the pressure data collected by Vereecke et al. (2003) to assess the relative correspondence between these datasets. Fitting their expectations, they found that bonobos exhibited both lower peak pressure under the hallux and lower peak first metatarsophalangeal joint dorsiflexion angles during push-off compared to humans. They also noted that based on the average pressure distribution patterns reported by Vereecke et al., some of the bipedal steps that they recorded must have lacked a midtarsal break.

Recently, several studies have attempted to directly investigate the link between pressure patterns and midfoot kinematics. DeSilva et al. (2015; DeSilva and Gill, 2013) and Bates et al. (2013) documented a correlation between high lateral midfoot peak pressures and a midtarsal break-like motion in human subjects. Bates et al. compared the human pressure data in their study to data collected from bonobos and a juvenile orangutan, and found that the human steps exhibiting a pressure signature indicative of a midtarsal break overlapped with those of the non-human apes in peak lateral midfoot pressure. From this result they concluded that high pressure in this region of the foot is a good indicator of midfoot joint motion in humans as well as non-human apes, and that these species share some previously unrecognized similarity in overall foot function during terrestrial locomotion.

Crompton et al. (2012) have also used hominoid plantar pressure data in reconstructions of foot mechanics and bipedal gait in the makers of the Laetoli footprints. These 3.66 My old footprints preserve the earliest non-morphological evidence of bipedal locomotion in an early hominin (Leakey and Hay, 1979). They have been interpreted as indicating either a fully modern bipedal gait with a human-like foot (Day and Wickens, 1980; White and Suwa, 1987; Tuttle et al., 1991; Harcourt-Smith and Aiello, 2004; Raichlen et al., 2010), or a more primitive gait with a slightly abducted hallux (Stern and Susman, 1983; Deloison, 1991; Bennett et al., 2009). Crompton et al. (2012) compared plantar pressure distributions from bonobos and an orangutan to the Laetoli footprints and topological depth profiles of footprints made by modern human subjects. By using these data to model lower limb kinematics, they concluded that the Laetoli print maker walked with human-like extended lower limbs, and with foot mechanics similar (but not identical) to those of modern humans.

Each of the studies discussed above has attempted to relate plantar pressure data obtained from non-human apes to intrinsic foot joint kinematics during locomotion. However, none of these studies have been capable of quantifying both joint kinematics and pressure distributions in these animals simultaneously. Several studies have found relationships between these types of data in humans (Bates et al., 2013; DeSilva and Gill, 2013; DeSilva et al., 2015), but we lack matching data from non-human apes, and can therefore only assume a relationship exists in these species as well. Because the plantar regions of human and non-human ape feet are characterized

by numerous soft and hard tissue differences (see Chapter 1, Section 1.2) this assumption may be invalid.

To test this assumption, I measured both plantar pressure distributions and 3-D intrinsic foot kinematics simultaneously in chimpanzees and humans during bipedal walking. Understanding the relationship between these variables is critical to studies of hominoid foot functional morphology, because it is easier to obtain plantar pressure measurements from non-human apes than it is to capture detailed 3-D joint kinematics. Plantar pressure recordings can be carried out with captive animals in zoo settings (Vereecke et al., 2003, 2005; Crompton et al., 2012; Matarazzo, 2013), because doing so only requires the placement of a pressure sensing platform within the animal's enclosure. Detailed 3-D kinematic data are much harder to obtain, because doing so requires precise camera calibration and the placement of advanced marker sets on subjects' bodies. Carrying out these steps, particularly the latter, is not possible in zoo or wild settings. Therefore, determining the relationship between plantar pressures and joint kinematics not only improves the understanding of chimpanzee foot function developed in this dissertation, but will also aid interpretations of pressure measurements in past and future non-human ape plantar pressure investigations.

5.1.2 Hypotheses

In this chapter I will test several hypotheses that are based on assumptions in previous studies about the relationship between plantar pressure variables and foot kinematics. To do so, I captured 3-D kinematic and pressure data simultaneously in two human and two chimpanzee subjects. I specifically analyzed bipedal steps in both species in order to increase the generality of my results with regard to fundamental relationships between foot kinematics and plantar pressure distributions. By holding gait constant, I was able to assess these relationships both within and between species. Bipedal pressure data also facilitate ready applicability to fossil biped gait reconstructions and footprint interpretation.

Hypothesis 1: The midtarsal break corresponds to relatively high plantar pressure values in the midfoot.

This hypothesis is based on the observations of Elftman and Manter (1935a; b) and Vereecke et al. (2003), who found that pressure under the lateral midfoot following heel lift coincides with a midtarsal break in *Pan* species during terrestrial locomotion. More recently, Bates et al. (2013) and DeSilva et al. (2015; DeSilva and Gill, 2013) found a positive relationship between peak lateral midfoot pressure and the amount of midfoot dorsiflexion following heel lift in human subjects. Therefore, I expected to find a similar relationship in the chimpanzees in this study. I also expected a relationship between midfoot dorsiflexion and a *medial* midfoot pressure peak in chimpanzees, as the chimpanzee medial midfoot fully contacts the ground and participates in the midtarsal break (Elftman and Manter, 1935a; Wunderlich, 1999; see Chapters 3 and 4), unlike in humans.

Different studies have related different types of midfoot pressure to the midtarsal break. Vereecke et al. (2003) simply described sustained lateral midfoot pressure following heel lift, whereas Elftman and Manter (1935b) described a pressure peak under the fifth metatarsal base during this period. Bates et al. (2013) and DeSilva et al. (2015; DeSilva and Gill, 2013) simply used peak lateral midfoot pressure at any time in stance, without specifying when this peak was measured with regard to heel lift. Therefore, I chose to investigate the relationships between midfoot dorsiflexion following heel lift and three different measurements of pressure: peak

midfoot pressure from any time during stance, peak midfoot pressure between the beginning of heel lift and the loss of midfoot contact, and the midfoot pressure impulse during this specific interval. The latter variable is calculated as the integral of the relationship between time and pressure, and should provide a means of measuring total midfoot pressure following heel lift, as opposed to a single instantaneous value. I made the following predictions for all three midfoot pressure variables measured in this study:

Prediction 1: Lateral midfoot pressure will be positively correlated with the amount of dorsiflexion between the rearfoot and lateral forefoot following heel lift in both humans and chimpanzees.

Prediction 2: Medial midfoot pressure will be positively correlated with the amount of dorsiflexion between the rearfoot and medial forefoot following heel lift in chimpanzees.

Hypothesis 2: Subtalar joint posture during stance is related to the relative amount of pressure under the medial midfoot in chimpanzees.

Studies of plantar pressure in chimpanzees and bonobos have yielded somewhat conflicting results with regard to pressure distribution under the medial midfoot. Elftman and Manter (1935b) reported relatively high medial midfoot pressure in their chimpanzee subject, which caused a medial swing in the anterior trajectory of the center of pressure during stance. They also reported that this subject used everted subtalar joint postures following touchdown. Conversely, Vereecke et al. (2003) reported relatively low medial midfoot pressures in their bonobo subjects during terrestrial walking, which they related to the use of relatively inverted subtalar joint postures, particularly during quadrupedal locomotion. Based on these studies, I expected the ratio of medial to lateral midfoot pressure during stance to be positively correlated with subtalar eversion angles during this time period. Furthermore, because I have found the chimpanzee subjects in this study to use everted subtalar joint postures throughout the majority of stance phase during bipedal locomotion (see Chapter 4), I expected these individuals to exhibit greater medial midfoot than lateral midfoot pressures.

In investigating this hypothesis, I examined the interval of stance from the beginning of single-support phase until the midfoot region is lifted from the substrate. This interval is the most relevant to the hypothesis, as it includes the period in which the chimpanzee subjects are likely to reach their maximum subtalar joint eversion angles (see Chapter 4), and also avoids the high lateral midfoot pressures associated with touchdown using a highly inverted and plantarflexed foot. The most relevant pressure variable for investigation here is impulse, which provides a measure of total pressure over a given interval of time. I made the following predictions:

Prediction 1: Peak eversion between the leg and rearfoot segments will be positively correlated with the ratio of medial midfoot pressure impulse to lateral midfoot pressure impulse in chimpanzees.

Prediction 2: Medial midfoot pressure impulse will be significantly greater than lateral midfoot pressure impulse in chimpanzees.

Hypothesis 3: Peak metatarsophalangeal joint dorsiflexion angles at push-off are correlated with pressure peaks at the metatarsal heads and the toes.

This hypothesis follows from the general assumption that dorsiflexion of the MTPJs at the end of a step is driven by loading of the forefoot during push-off. Consequently, humans, who push-off of the medial sides of their feet, exhibit the highest dorsiflexion angles at the medial MTPJs (Caravaggi et al., 2009; Griffin et al., 2010b; see Chapter 4). African apes, which

are thought to push-off with less power than humans during terrestrial locomotion (O'Neill et al., 2015), exhibit lower peak MTPJ dorsiflexion angles than humans (Griffin et al., 2010b; see Chapter 4). The differences in peak MTPJ dorsiflexion angles within and between species are also expected to reflect metatarsal head morphology, with joints exhibiting greater peaks exhibiting more robust heads and internal bony reinforcement (Susman et al., 1984; Latimer and Lovejoy, 1990; Griffin et al., 2010a; Fernández et al., 2015). These morphological features are believed to help resist the higher peak loads incurred at these joints, which we would expect to be related to peak pressures. This hypothesis was preliminarily supported by Griffin et al. (2010b), who compared their MTPJ kinematic data from bonobos and humans to the bonobo plantar pressure data collected by Vereecke et al. (2003). However, these data were from separate studies, so kinematic and pressure variables from the same steps could not be directly matched. Additionally, Griffin et al. only compared pressure and kinematic data for the first pedal ray. In this study, I tested the relationship between kinematic data and peak pressures at both the metatarsal heads and the digits across all five pedal rays. I also tested whether pressure variables exhibit patterns of difference across the five rays that are similar to the differences in peak MTPJ dorsiflexion angles that were revealed in Chapter 4. I made the following predictions:

Prediction 1: Peak metatarsophalangeal joint dorsiflexion angles at toe-off will be positively correlated with peak plantar pressure values at the metatarsal heads and the digits in humans and chimpanzees.

Prediction 2: Patterns of difference in peak metatarsophalangeal joint dorsiflexion angle between pedal rays will be similar to patterns of difference in metatarsal head and digit peak pressures in humans and chimpanzees.

5.2. Methods

5.2.1 Subjects

The subjects used in this investigation included both chimpanzee subjects, and two of the five human subjects used in the investigation carried out in Chapter 4, Human B and Human C. Table 5.1 includes information about the subjects' ages and weights during the time of data collection, as well as the average total plantar surface areas of their feet during a step. This latter measurement was obtained from the pressure platform used in this investigation (see below), and was calculated as the entire area of the foot detected by the platform over the entire duration of each step that I recorded during data collection. Body mass and foot area were used to standardize pressure measurements obtained from the platform for statistical analysis (see below).

5.2.2 Pressure Data Collection

To measure plantar pressure distributions, I used an emed-q100 platform (Novel Electronics Inc., St. Paul, MN), which was placed atop one of the force plates integrated into the runway in the Stony Brook Primate Locomotion Laboratory (see Fig. 2.7). This platform is 700 x 403 x 15.5 mm, with a pressure sensing area of 475 x 320 mm. The platform resolution is 4 sensors/cm², with a sensing range of 10-1,270 kPa, and a sampling frequency of 100 Hz. It was set up to begin recording instantly if a pressure above the detection threshold was registered. Pressure recordings were streamed instantly to a laptop computer equipped with emed/E (Novel Electronics Inc.) recording software.

Pressure and kinematic data were collected simultaneously during ground walking experiments. I used the same protocol for 3-D motion capture as described in previous chapters (see Chapter 2, Sections 2.3-4). I carried out the camera calibration by placing the calibration fixture in the location on the force plate where I placed the pressure platform during recording sessions. After the calibration procedure, the fixture was removed and the pressure platform was placed in the calibrated space. The pressure and video recordings could not be automatically synched, so corresponding trial numbers for steps recorded by emed/E and ProCapture software were logged during the experiments. The emed-q100 platform has a light that turns on when pressures beyond the detection threshold are registered. This enabled me to determine the precise initiation of stance phase in videos during the marker digitization phase of kinematic data processing. Following these steps, I was able to precisely synchronize video and pressure recordings.

I carried out locomotion experiments on the runway with human and chimpanzee subjects following the same procedures as described in Chapter 2, Section 2.3, using the same marker set. Chimp L expressed some trepidation walking over the pressure platform, and as a consequence used an awkward gait during bipedal locomotion. To address this problem, I placed a 1.5 cm thick vinyl pad across the force plates with a space cut out for the pressure pad. This made the area around the pad flush with the pad surface and also gave it similar haptic properties. Chimp L assumed a normal bipedal gait in experiments where this additional padding was laid down. Therefore, the data collected from Chimp L was from experiments where this padding was used, but the padding was not used in experiments with the other chimpanzee or the human subjects.

All subjects walked at self-selected speeds during locomotion experiments. Chimpanzee subjects walked using both bipedal and quadrupedal gaits; however only bipedal steps were included in the analyses.

5.2.3 Pressure Data Analysis

Pressure data were processed using Novel DatabaseLight software (Novel Electronics Inc.) in collaboration with Dr. Kevin Hatala (Max Planck Institute for the Study of Human Origins, Leipzig, Germany). For each step analyzed, he created masks to represent the following regions of the foot (with bones comprising these these regions indicated):

1. Rearfoot – Calcaneus.
2. Lateral midfoot – Cuboid, bases and shafts of metatarsals 4 and 5 (excluding head).
3. Medial midfoot – Navicular, cuneiforms, bases and shafts of metatarsals 1-3 (excluding head).
4. Metatarsal heads (1-5).
5. Digits (1-5) – Distal phalanx (pressure under other regions of the toes were very small or absent).

For the chimpanzee subjects, Hatala created these masks with the assistance of x-rays that I obtained of the subjects' feet. See Fig. 5.1 for an image of plantar pressure distribution with masks applied.

DatabaseLight calculates pressure at each time point as the average of all of the sensors within the specified mask region that register a pressure. From these regional pressures, I pooled steps within species and within subjects and calculated average pressure in each region across stance. I also extracted the pressure variables that I used in my analysis from these regional pressure values.

To address Hypotheses 1 and 2, I first determined the general timing of the interval between the initiation of heel lift and the loss of midfoot contact in all subjects by inspecting plots of average regional pressures across stance. From these plots, I determined that the initiation of heel lift occurred at roughly 25% of stance, when heel pressure began to decrease at a steady rate in all subjects (see Figs. 5.2-5.4). I also determined that loss of medial and lateral midfoot contact had occurred by roughly 85% of stance in all subjects (Figs. 5.2-5.4). I termed this interval the ‘heel-midfoot lift’ (HML) interval, and used it for the pressure variables that I extracted for Hypotheses 1 and 2. Specifically, I extracted peak pressures and the timing of peak pressures from the medial and lateral midfoot regions during the HML interval. I also calculated the pressure impulses in these regions during HML by integrating the regional pressure values over time. To address Prediction 1 of Hypothesis 2, I calculated the ratio of medial midfoot HML pressure impulse to lateral midfoot HML pressure impulse, and I will subsequently refer to this ratio as the med/lat midfoot impulse. Finally, I also extracted medial and lateral midfoot peak pressures and timing of peak pressures from the entire duration of stance without regard to HML.

To address Hypothesis 3, I extracted peak pressures and timing of peak pressures for all of the metatarsal heads and digits in the second half of stance. This cut-off was used because in some trials the peak pressures in the MT5 region of the chimpanzee subjects (Fig. 5.3) would occur around touchdown. However, I was only interested in peak pressures that occurred near the timing of peak MTPJ dorsiflexion, and thus I disregarded peaks prior to 50% of stance.

5.2.4 Kinematic Data Analysis

Kinematic data analysis was similar to that described in Chapter 4; I did not include the midfoot segment in analyses due to relatively high marker triad deformation in this region. I calculated 3-D joint angles across stance between the following segment pairs: leg-rearfoot, rearfoot-medial forefoot, and rearfoot-lateral forefoot. To address Hypothesis 1, I calculated dorsiflexion excursion between the rearfoot and medial and lateral forefoot segments during the HML interval. Dorsiflexion excursion was defined as the maximum sagittal plane angle minus the minimum sagittal plane angle *that preceded the maximum* during this interval. To address Hypothesis 2, I calculated the maximum eversion angle between the leg and rearfoot segments that occurred during the HML interval. Finally, to address Hypothesis 3, I calculated the maximum MTPJ angles that occurred in the second half of stance. I also calculated the relative timing of these maximum values with regard to stance duration.

5.2.5 Statistics

To test the hypotheses in this study, I used non-parametric statistical tests (Sokal and Rohlf, 2005). I chose to use non-parametric statistics because pooling steps between subjects sometimes results in non-normally distributed data, violating the assumption of parametric statistics. For all statistical tests, I standardized pressure variables by body mass and foot plantar surface area prior to pooling steps between subjects. Greater body mass and smaller foot area will increase pressure values when all other variables are held equal. To account for variation between subjects in either of these features during statistical analyses, I divided all pressure variables from each step by the ratio of body mass to the foot area registered by the platform during that step. Foot area was calculated as the total area from the time-averaged pressure distribution registered by all sensors over the duration of the step. This resulted in pressure

values in units of gravitational acceleration (g), and pressure impulses in units of $g*ms$ (milliseconds).

Below, I describe the specific tests conducted for each hypothesis investigated in this chapter. For all tests, I pooled steps between subjects in each species, and I conducted tests on each species separately.

Hypothesis 1. For Prediction 1, I calculated rank correlation coefficients between rearfoot-lateral forefoot dorsiflexion excursion and the three lateral midfoot pressure variables previously described for both chimpanzees and humans. For Prediction 2, I calculated rank correlation coefficients between rearfoot-medial forefoot dorsiflexion excursion and the three medial midfoot pressure variables previously described for chimpanzees only.

Hypothesis 2. For Prediction 1, I calculated the rank correlation coefficient between maximum leg-rearfoot eversion and the med/lat impulse during HML. For Prediction 2, I used a Wilcoxon Rank-Sum test to test for difference between medial and lateral midfoot pressure impulses during HML.

Hypothesis 3. For Prediction 1, I pooled data from all five pedal rays within species and calculated rank correlation coefficients between peak MTPJ dorsiflexion angles and peak metatarsal head and digit pressures in the second half of stance. For Prediction 2, I calculated non-parametric Kruskal-Wallis statistics to test for significant differences between pedal rays in MTPJ dorsiflexion angles, metatarsal head pressures, and digit pressures. I carried out post-hoc Kruskal-Wallis tests for pairwise comparisons between joint pairs (using MATLAB's 'multcompare' function). A sequential Bonferroni correction was used to adjust the alpha significance levels (0.05) for these tests (Abdi, 2010).

5.3 Results

I selected five bipedal steps for analysis from each human and chimpanzee subject. Using the linear regression equations described in Chapter 2, I estimated dimensionless velocity for each step that I selected (Table 5.2). I estimated similar average dimensionless walking velocities for both Humans B and C (0.43 ± 0.01 and 0.44 ± 0.02 , respectively), and Chimps H and L (0.43 ± 0.04 and 0.46 ± 0.03 , respectively).

5.3.1 Pressure Distributions Across Stance

Average pressure distributions by region over stance for both species, and both human and chimpanzee subjects individually are depicted in Figs. 5.2-5.4. Representative examples of the path of the center of pressure (COP) over the course of stance for each subject are depicted in Fig. 5.5. Patterns of motion for each joint in both species overall, as well as chimpanzee and human subjects individually, are presented in Figures 5.6-8. Maximum dorsiflexion angles at push-off for each subject are presented in Fig. 5.9. Kinematic and pressure variables used in analyses are presented in Tables 5.3 and 5.4. What follows is a qualitative description of the human and chimpanzee plantar pressure distribution patterns measured across stance in this study.

As expected, both humans and chimpanzees began stance with high heel pressures (Fig. 5.3), which is consistent with their designation as 'heel-strikers' (Gebo, 1992; Schmitt and Larson, 1995). However, chimpanzees also displayed high lateral midfoot pressure at the beginning of stance, which is likely related to their use of highly inverted and plantarflexed ankles joint postures at touchdown. Both species exhibited a steady drop in heel pressure beginning at roughly 25% of stance phase, coinciding with the initiation of heel lift. The heel had

completely left the substrate by ~65% of stance in humans, and ~75% of stance in chimpanzees. Both species displayed peak metatarsal head pressures between roughly 65-85% of stance, with metatarsal heads 1-3 peaking later, and metatarsal heads 4 and 5 peaking earlier (Table 5.4). Digit pressures peaked slightly later in both species, usually between 80 and 90% of stance.

Paths of the COP were different between species, but relatively similar within species (Fig. 5.5). In chimpanzees, the COP typically began at the lateral midfoot or fifth metatarsal head at touchdown, then immediately moved to the heel. COP gradually moved forward through the center of the midfoot, and then traveled between the first and second digits during liftoff, with the first or second distal phalanx region the last part of the foot to leave the substrate. Human COPs were similar to those previously described in other studies (e.g., Elftman and Manter, 1935b); pressure began at the heel, traveled forward through the center of the midfoot, curved medially in the forefoot, and ended at the first digit at toe-off.

Humans displayed higher peak pressures in most regions of the foot than chimpanzees, which is not surprising considering the greater body size of humans, but somewhat smaller foot areas in humans (Table 5.1). This difference was particularly marked for the heel region, metatarsal heads 1-3, and digit 1. Chimpanzees, on the other hand, displayed higher peak pressures in the medial and lateral midfoot regions (Table 5.3). Additionally, pressures were detected under these regions roughly 10% longer in stance in chimpanzees compared to humans.

Both chimpanzee subjects displayed relatively greater medial midfoot pressures than lateral midfoot pressures throughout most of stance, except in the first 10%, when the lateral midfoot contacts the substrate before the medial midfoot touches down. The chimpanzee subjects exhibited several notable differences in metatarsal head pressures (Fig. 5.4). In Chimp H, the highest peak pressures were located under the second metatarsal head and the lowest under the first metatarsal head, whereas in Chimp L the highest peak pressures were under the third metatarsal head, and metatarsal heads 1, 2 and 4 displayed similar peaks (Table 5.4). Chimp L also displayed higher peak pressures under the first digit than Chimp H.

Between the human subjects, Human B displayed higher peak pressures in the heel, medial midfoot, and second metatarsal head than Human C (Fig. 5.5; Tables 5.3-5.4). This difference is surprising, considering that Human B has slightly lower body mass than Human C, but a slightly larger foot area. Human C, however, displayed much higher peak pressures under digit 1 during push-off.

5.3.2 Midtarsal Break

Scatterplots depicting the relationships between pressure variables and midfoot dorsiflexion are presented in Fig. 5.10. Rank correlation coefficients and *P*-values calculated for these relationships are listed in Table 5.5. For the lateral midfoot, none of the pressure variables investigated were significantly correlated with rearfoot-lateral forefoot dorsiflexion in humans. However, two of the three pressure variables were significantly correlated with dorsiflexion among chimpanzee subjects ($P < 0.01$). Among these, the relationship between HML pressure impulse and dorsiflexion angle had the highest ($r = 0.69$) (Fig. 5.10c). The correlation coefficient was slightly lower ($r = 0.60$) for the relationship between HML pressure peak and dorsiflexion (Fig. 5.10b), and the relationship between overall pressure peak and dorsiflexion angle was non-significant (Fig. 5.10a). I did not statistically assess the relationship between pressure and midfoot dorsiflexion angle with all steps of both species pooled, but inspection of Fig. 5.10a-c suggests that the relationship would have been positive for all pressure variables; as pressure values increase, midfoot dorsiflexion angles goes up regardless of species.

None of the medial midfoot pressure variables were significantly correlated with rearfoot-medial forefoot dorsiflexion excursion in chimpanzees (Fig. 5.10d-f).

With regard to timing of midfoot pressure peaks, peak pressures overall showed similar timing to peak pressures during the HML interval, except in the chimpanzee lateral midfoot region. Overall peak pressure in this region occurred at 12% of stance on average, versus 39% of stance for the HML peak. Otherwise, peak pressures coincided closely with HML peak pressures in the chimpanzee medial midfoot (32% of stance, both), and the human lateral midfoot (48% and 50% respectively).

5.3.3 Foot Eversion

A scatterplot depicting the relationship between peak leg-rearfoot eversion and the med/lat midfoot impulse following heel lift for chimpanzees is presented in Fig. 5.11. The average peak eversion angle during HML across steps was $10 \pm 5^\circ$, and the average med/lat midfoot impulse during HML was 1.3 ± 0.5 . The relationship between these variables was not significant ($P = 0.43$). However, the medial midfoot HML pressure impulse was significantly greater than the lateral midfoot HML pressure impulse in chimpanzee subjects based on the Wilcoxon Rank-Sum test ($P = 0.04$) (see Table 5.3 for HML impulse values).

5.3.4 Metatarsophalangeal Joints

Scatterplots depicting the relationships between MTPJ peak dorsiflexion angles and metatarsal head and digit pressures are presented in Fig. 5.12. Rank correlation coefficients and p-values calculated for these relationships are listed in Table 5.6. Peak dorsiflexion angles were significantly correlated with both metatarsal head and digit pressures in both humans and chimpanzees ($P < 0.001$ in all comparisons). For chimpanzee subjects, the relationship between dorsiflexion angle and metatarsal head pressure had a higher correlation coefficient ($r = 0.45$) than that between dorsiflexion angle and digit pressure ($r = 0.39$). The converse was true in humans; dorsiflexion angle had a higher correlation coefficient with digit pressure ($r = 0.5$) than metatarsal head pressure ($r = 0.32$). I did not statistically assess the relationship between pressure and MTPJ dorsiflexion angle with all steps of both species pooled, but inspection of Fig. 5.12, suggests that the relationships found within species are not upheld between species; chimpanzee peak MTPJ dorsiflexion angles are generally lower than those of humans at the same pressure values.

Kruskal-Wallis tests indicated significant differences between the pedal rays in MTPJ dorsiflexion angle, metatarsal head pressure, and digit pressure for both humans and chimpanzees ($P < 1 \text{ E-}4$). Results of post-hoc tests are presented in Tables 5.7 and 5.8. For chimpanzees, significant differences between pedal rays in MTPJ dorsiflexion angles were most closely reflected by differences in metatarsal head pressures (Table 5.7). In both cases, significant differences were found between rays 1 and 2, 2 and 5, and 3 and 5, and the directionality of these differences was always the same. MTPJ dorsiflexion and digit pressure only showed similar significant patterns at two joint pairs: 2 vs. 5, and 3 vs. 5. For humans, difference patterns across pedal rays in MTPJ dorsiflexion angle were not closely reflected by differences in metatarsal head or digit pressure (Table 5.8). For MTPJ dorsiflexion angle, significant differences were only found between ray 5 and rays 1-3. For metatarsal head pressures, however, significant differences were found between rays 2-3 and ray 4. For digit pressures, a significant difference was found between ray 1 and ray 4.

Lastly, relative timing of peak MTPJ dorsiflexion angles and pedal ray pressure peaks showed similar patterns in humans and chimpanzees: Metatarsal head pressure peaks occurred first (roughly 65-80% of stance), followed by digit pressure peaks (roughly 80-90% of stance), then MTPJ dorsiflexion peaks (roughly 90-95% of stance). There was also a temporal trend in peak pressures under the metatarsal heads in both humans and chimpanzees. Peak pressures occurred earlier at the lateral heads and later at the medial heads, suggesting a mediolateral roll-off pattern of the forefoot in both species.

5.4 Discussion

5.4.1 The Midtarsal Break

The first hypothesis of this chapter states that midfoot dorsiflexion following heel lift is correlated with sustained, high pressure under the midfoot regions. I predicted that this would be the case for the lateral forefoot region in both humans and chimpanzees, and used three different measurements of midfoot pressure to test this prediction: peak pressure, HML peak pressure, and HML pressure impulse. These variables were based on indicators of themidtarsal break used by previous plantar pressure studies (Elftman and Manter, 1935b; Vereecke et al., 2003; Crompton et al., 2010; Bates et al., 2013; DeSilva and Gill, 2013). Of these variables, both peak pressure and pressure impulse during HML are significantly correlated with lateral midfoot dorsiflexion in chimpanzees, partially supporting my first prediction. The other variable, overall peak pressure, is not correlated with lateral midfoot dorsiflexion, likely due to the fact that the timing of this peak in the lateral midfoot usually occurs early in stance (12% stance, on average), well before the initiation of heel lift. This early peak is related to the inverted foot posture of the chimpanzee foot at touchdown, which results in high forces experienced by the lateral midfoot at the beginning of stance.

The lack of a significant relationship between overall peak pressure and lateral midfoot dorsiflexion in chimpanzees suggests that this pressure variable is not a good indicator of the presence of amidtarsal break. Nevertheless, overall peak pressure is the variable used by DeSilva et al. (2015; DeSilva and Gill, 2013) and Bates et al. (2013) to signifymidtarsal break-like motion in humans and non-human apes. My results suggest that their approach could have resulted in misclassification ofmidtarsal breaks in cases where high pressure was detected prior to the period during which a break could actually occur. Interestingly, their approach was actually derived from a study that used pressure peaks as an indicator of general foot dysfunction in diabetic patients, but which made no mention of midfoot dorsiflexion during walking (Bus et al., 2011). Based on my findings, I suggest that this approach is not ideal for classification of amidtarsal break.

My results do suggest, however, two variables that appear to classifymidtarsal break magnitude more reliably than overall peak pressure. The best variable is pressure impulse during HML, which provides a measure of the total pressure sustained by the midfoot after heel lift. This variable has a relatively strong relationship withmidtarsal break magnitude in chimpanzees, and is intuitively related to the concept of the break as maintained midfoot contact with the substrate following heel lift (Elftman and Manter, 1935b; Susman, 1983; Vereecke et al., 2003). This variable has a correlation coefficient of 0.69 with lateral midfoot dorsiflexion, meaning it explains 48% of the variance in lateral midfoot dorsiflexion. The other variable that performs nearly as well is peak pressure during HML ($r = 0.6$). Both of these variables are specific to the

interval of stance during which the midtarsal break occurs, and therefore are logically related to midfoot dorsiflexion. However, a significant amount of variance in midfoot motion is not explained by either variable, meaning that one should not assume high midfoot pressure always indicates a midtarsal break. Therefore, one should not diagnose the presence of a midtarsal break with total certainty based on pressure data alone.

It must be acknowledged here that I did not find a significant relationship between lateral midfoot dorsiflexion and any of the pressure variables for the human steps that I analyzed in this study. I cannot, therefore, assume that any of the pressure variables investigated here will be good indicators of a midtarsal break-like motion in humans. However, my inability to detect a significant pressure-dorsiflexion relationship among human steps is likely due to the very small range of lateral midfoot dorsiflexion excursions displayed by the human subjects in this study. It is quite possible that a larger sample of subjects with a broader range of midfoot dorsiflexion angles would show a stronger relationship to pressure variables, as was the case in the investigations carried out by Bates et al. (2013) and DeSilva et al. (2015). The fact that humans and chimpanzees showed a similar trend in the relationship between pressure and midfoot motion when looking across all steps in this study lends some support to this notion. Therefore, a good prospective future study with a larger sample of human subjects would be to compare the HML pressure variables measured in this study to the pressure variables used in previous studies to determine if they are better indicators of midfoot motion in humans as well as chimpanzees.

My second prediction concerning the midtarsal break was that high medial midfoot pressure would be positively correlated with dorsiflexion between the rearfoot and medial forefoot segments. The results of my study clearly show that none of the pressure variables that I measured are good indicators of medial midfoot dorsiflexion in chimpanzees. This finding is surprising, as the subjects in this study exhibited similar medial and lateral midfoot dorsiflexion excursions following heel lift (Table 5.3). The lack of a clear relationship between medial midfoot pressure and kinematics could be related to the plantar soft tissue anatomy of chimpanzees. Given that the chimpanzee medial midfoot is clearly weight-bearing during bipedal locomotion, one might expect a greater midtarsal break to correspond with greater pressure under the large navicular tuberosity in chimpanzees (Harcourt-Smith and Aiello, 2004). However, the intrinsic foot musculature related to hallux function, including the large adductor hallucis muscle present in chimpanzees (Aiello and Dean, 1990) could mask such a pressure signal. There may simply be less intervening soft tissue on the lateral side of the foot to mask the relationship between midtarsal break magnitude and pressure under the fifth metatarsal head.

The absence of a pressure signal for midfoot dorsiflexion under the medial side of the foot helps to explain why this region has received so little attention in discussions of the midtarsal break (Vereecke et al., 2003; DeSilva, 2010; Bates et al., 2013). This provides a clear example of a case in which plantar pressure data fail to reflect an aspect of intrinsic foot function. This finding, therefore, points to limitation in the extent to which plantar pressure data can be used to reconstruct foot kinematics.

5.4.2 Foot Eversion

The second hypothesis of this chapter states that subtalar joint motion is correlated with the relative amount of pressure under the medial midfoot in chimpanzees. I predicted that the ratio of medial midfoot to lateral midfoot pressure impulse during HML would be positively correlated with eversion between the leg and rearfoot segments. This prediction was not supported, as there was clearly no relationship between these variables among the steps that I

analyzed in this study. I expected this relationship to exist based on my measurement of high subtalar eversion angles in chimpanzees following the end of the first double-support phase (Fig. 5.6; also see Chapter 4). Similarly, Elftman and Manter (1935b) had reported high medial midfoot pressure in their chimpanzee subject, which they related to an everted foot position during bipedal walking. However, eversion does not appear to be strongly correlated with higher relative medial midfoot pressures. Nevertheless, I did find that the subjects in this study exhibited significantly greater pressure impulses under their medial midfoot regions compared to their lateral midfoot regions. This finding suggests the potential for a relationship between subtalar joint posture and midfoot pressure distributions. The range of subtalar joint postures captured in this study among the chimpanzee steps was relatively low (7-17°); it is possible that a stronger pressure signal would have been revealed in a sample of steps representing a wider range of joint postures.

The results of this study provide an interesting point of disagreement with the findings of Vereecke et al. (2003). The bonobos in their study exhibited relatively higher pressures on their lateral midfeet, which led Vereecke et al. to conclude that bonobos walk with relatively inverted foot postures. It is entirely possible that the bonobos in their study used different subtalar postures than the chimpanzees in my study or the chimpanzee subject in Elftman and Manter's (1935b) study. However, due to the lack of a clear correlation between subtalar joint posture and medial midfoot pressure, this notion requires further investigation. Interestingly, Vereecke et al. (2003) found that their subjects exhibited relatively higher medial midfoot pressure during bipedal locomotion than during quadrupedal locomotion. Wunderlich (1999) measured chimpanzee plantar pressures during quadrupedal locomotion and found a midfoot pressure distribution pattern intermediate between that measured here and that reported by Vereecke et al. (2003). The subjects in her study displayed slightly higher lateral midfoot versus medial midfoot pressures, but they still displayed relatively higher medial midfoot pressures than did the bonobos in Vereecke et al.'s study. However, considering the similarity in the results obtained by Wunderlich and Vereecke et al. for subjects that walked quadrupedally, the cause of difference in medial versus lateral midfoot support may be more strongly determined by gait than by species. Future investigation of plantar pressure distributions in the subjects from the present study during quadrupedal walking will help to shed light on this question.

5.4.3 Metatarsophalangeal Joint Motion

The third hypothesis of this chapter states that peak MTPJ dorsiflexion angles at push-off are correlated with peak pressures under the metatarsal heads and digits. I predicted that this would be the case for both humans and chimpanzees, and my results support this prediction. In chimpanzees, metatarsal head pressures are more strongly correlated with MTPJ angles, whereas digit pressures are more strongly correlated in humans. In neither case, however, is this relationship particularly strong; pressure values explain only 20-25% of the variance in joint angles. However, these results provide some support for the notion that higher MTPJ dorsiflexion angles are related to greater relative loading of different regions of the forefoot.

This notion received only mixed support in tests of my second prediction, which stated that patterns of difference in MTPJ angles between the pedal rays would be similar to patterns of difference in pressure variables. In chimpanzees, MTPJ dorsiflexion and metatarsal head pressure show similar patterns of difference among the pedal rays. In particular, rays 2 and 3 tend to exhibit both higher dorsiflexion angles and metatarsal head pressures than the other rays. However, the differences are not as consistent between joint angle and digit pressure, and in

humans there are relatively few points of similarity among the pressure and kinematic differences across the rays. This means that the rays that experience the highest pressures in humans during walking do not always display significantly higher MTPJ dorsiflexion angles than the other rays.

Overall, these findings suggest that the relative loading of different regions of the forefoot is at least partly related to dorsiflexion of the MTPJs in these regions, particularly in chimpanzees. Therefore, we can expect that bony morphology of the pedal rays exhibiting the highest dorsiflexion angles should show evidence of structural reinforcement against relatively higher stresses, as has been previously suggested (Susman et al., 1984; Latimer and Lovejoy, 1990; Griffin et al., 2010b; Fernández et al., 2015). However, dorsiflexion angles should not be taken as an absolute indicator of relative forefoot loading; chimpanzees and humans show broad overlap in pressure peaks under their metatarsal heads and digits, yet very little overlap in MTPJ dorsiflexion angles. MTPJ dorsiflexion is likely to be driven largely by proximal lower limb joint kinematics, such as ankle plantarflexion angle during push-off. More plantarflexed ankle postures during this period will result in higher peak MTPJ dorsiflexion angles when all else is held equal. Therefore, MTPJ dorsiflexion and forefoot loading are not inherently related to one another.

One other important finding concerning forefoot pressure distribution bears mentioning here. All subjects in this study show similar timings of peak pressures under their metatarsal heads and digits. In both species, the timing of peak pressures under the heads of metatarsals 2-5 exhibits a similar lateral-to-medial temporal sequence, with the fifth metatarsal head peaking first, and the second metatarsal head peaking last. These results demonstrate that chimpanzees and humans use a very similar forefoot roll-off pattern during bipedal walking. That is, peak pressure under the metatarsal heads travels from the lateral to the medial side of the forefoot, and both species exhibit a medial forefoot push-off. This finding deviates from notions about non-human ape forefoot function expressed in some previous studies (Vereecke et al., 2003; Crompton et al., 2012), and supports the findings of Elftman and Manter (1935b) in suggesting general similarity between humans and chimpanzees during push-off. This forefoot loading pattern could be related to similar activity in the peroneal muscles in both species; Larson et al. (2014) report that humans and chimpanzees⁸ activate these muscles over a similar period of time in the second half of stance. The peroneal muscles are evertors that are known to redirect weight support to the medial side of the foot prior to push-off in humans (Reeser et al., 1983; Stern, 1997), so they could be performing a similar function in chimpanzees. Interestingly, both humans and chimpanzees show significantly greater peak pressures under their second metatarsal heads compared to their first. Additionally, both species exhibit relatively high pressures under their first digit during push-off. Taken altogether, these results suggest broad similarity between humans and chimpanzees in the relative patterns of forefoot pressure distribution during bipedal walking.

⁸ The results reported by Larson et al. (2014) disagree with those reported by Stern and Susman (1983) and Jungers et al. (1993) for chimpanzee peroneal muscle activity during bipedal locomotion; in the latter studies, variable or no activity were reported for these muscles in chimpanzee subjects. However, the data from Larson et al. (2014) were collected from the chimpanzee subjects used in this study, and therefore are assumed to represent the muscle activity of these individuals during bipedal walking.

5.4.4 Conclusions

The plantar pressure distributions measured in this chapter provide a picture of chimpanzee foot function that is complementary to the joint kinematics described in this and previous chapters. The high lateral midfoot plantar pressures that occur at touchdown are related to high inversion angles at the subtalar joint, as previously suggested (Vereecke et al., 2003). Over the first 25% of stance, as the subtalar joint goes from a highly inverted position to an everted position, pressure under the medial midfoot increases until it is greater than that under the lateral midfoot. Additionally, the COP travels through the center and medial side of the midfoot, but *never* through the lateral midfoot. These findings lend further credence to the notion that African apes do not necessarily use inverted subtalar joint postures throughout stance (*contra* Weidenreich, 1923; Tuttle, 1970; Lewis, 1983; Latimer et al., 1987; Gebo, 1992; Vereecke et al., 2003; DeSilva et al., 2013). As the heel lifts from the substrate, heel pressure decreases, but relatively high midfoot pressure is maintained. This coincides with dorsiflexion between the rearfoot and forefoot segments, confirming the presence of a midtarsal break in chimpanzees. In the forefoot, peak pressures occur at the lateral metatarsal heads earlier, indicating a lateral to medial pressure shift and push-off from the medial side of the foot. The location of this push-off is reflected in the relative peak MTPJ dorsiflexion angles, with joints 2-5 exhibiting a lateral-to-medial gradient of increasing angular excursions.

Several notable similarities and differences in human and chimpanzee pressure distributions bear further discussion. Humans show relatively low midfoot pressures that are not closely related to midfoot dorsiflexion, as in chimpanzees. However, forefoot pressure patterns are surprisingly similar between species. Both species show a medial pressure shift across the metatarsal heads, with highest peak pressures occurring on the medial side of the foot. Surprisingly, both species display relatively high pressures under their halluces during push-off. This finding provides one of the major inconsistencies between joint kinematics and pressure distributions uncovered in this chapter; namely, although chimpanzees exhibit very low hallucal dorsiflexion angles during push-off, they still display high pressures under the first digit. This result runs contrary to the suggestion that the hallux plays only a minor role in propulsion during push-off in *Pan* species (Wunderlich, 1999; Vereecke et al., 2003; Crompton et al., 2012). Why the first MTPJ does not dorsiflex to a similar degree as the other medial MTPJs remains to be determined, but could be due to some anatomical constraints, as suggested by the relatively low passive dorsiflexion range of motion measured at this joint (see Chapter 4). Nevertheless, this chapter supports a previously underappreciated link between human and chimpanzee forefoot mechanics.

Given this similarity, it is interesting to note discrepancies between my findings and those of Vereecke et al. (2003). The bonobos in their study tended to exhibit much higher pressures on the lateral sides of their feet, and also displayed high lateral metatarsal head pressures, suggesting a lateral foot push-off. This result is quite different from my findings, and suggests either a species level difference in foot mechanics, or perhaps a difference related to the use of bipedal versus quadrupedal gaits. The role of gait in foot plantar pressure distributions will be explored in future studies using additional plantar pressure data collected from the subjects in this study during quadrupedal locomotion. However, one more explanation for the discrepancy between study findings could be related to digit posture. Vereecke et al. (2003) reported that the subjects in their study maintained their lateral digits in curled postures on the ground, effectively forcing plantar pressures to the lateral sides of the feet. This contrasts with the subjects in my study, who always walked with extended pedal digits. This difference in digit posture could

account for differences in plantar pressure distributions, although it should be noted that Elftman and Manter (1935b) reported that their subject used curled digits while walking, yet their pressure findings are generally similar to mine.

The differences in plantar pressures and foot kinematics measured in my study and those measured by Vereecke et al. (2003) have important implications for the study of human evolution. Several recent fossil hominin functional morphology studies have taken the results of Vereecke et al. (2003), as well as descriptions of African ape foot postures by earlier researchers (Weidenreich, 1923; Tuttle, 1970; Lewis, 1983; Gebo, 1992), to be representative of non-human ape foot function (Lovejoy et al., 2009; DeSilva et al., 2013). However, the results of this chapter provide a contrasting view to that of Vereecke et al. (2003), and suggest that non-human apes such as chimpanzees are fully capable of walking with everted foot postures, and pushing-off of the forefoot in a manner somewhat similar to humans (albeit, with an abducted hallux). This makes the chimpanzee foot a good model for reconstructing bipedal gait in fossil hominins with foot morphology intermediate between that of humans and African apes.

On a final, related note, the results of this study have some bearing on interpretation of the Laetoli footprints. Although plantar pressure distributions should not be assumed to relate directly to footprints made in soft sediment (Crompton et al., 2012; Hatala et al., 2013), several aspects of the depth profiles that have been described for the G-1 footprints⁹ from the Laetoli trackway recall the chimpanzee pressure distributions measured in this study. The G-1 footprints are the best preserved out of the three footprint trails at this site, and have been the primary target of quantitative and descriptive analyses of the Laetoli trackway (Day and Wickens, 1980; Stern and Susman, 1983; White and Suwa, 1987; Deloison, 1991; Raichlen et al., 2010; Crompton et al., 2012). These prints tend to show medial midfoot impressions that are relatively deep, but more shallow than the lateral midfoot impressions (Day and Wickens, 1980; Crompton et al., 2012). This pattern may be indicative of a hominin with some medial midfoot weight support, but less than that exhibited by the chimpanzees in this study. Alternatively, depending on the influence of peak *vs.* average pressure on footprint shape, the deeper lateral side of the footprint could actually be caused by a chimpanzee-like touchdown with an inverted foot. The forefoot impressions of the G-1 prints have been described as getting deeper from lateral to medial until the location corresponding to the first metatarsal head, which is relatively shallow (Leakey and Hay, 1979; Bennett et al., 2009). This condition is reminiscent of the plantar pressure distribution uncovered here for chimpanzees, wherein metatarsal head pressures are higher from rays 5 to 2, and then lower again for the head of the first metatarsal. Finally, the G-1 footprints possess relatively deep hallux impressions (Day and Wickens, 1980), which corresponds to the high digit 1 peak pressure measured for both human and chimpanzee subjects in this study. The G-1 prints clearly indicate the use of a hallux in a position that is more adducted than that used by the chimpanzees in this study. However, several metrical analyses of these prints have provided evidence that the Laetoli print-makers walked with halluces abducted to a position beyond that of which modern humans are capable (Deloison, 1991; Bennett et al., 2009). Overall, the topography of these footprints suggests a fossil hominin that walked bipedally with a plantar pressure distribution somewhat intermediate between those exhibited by chimpanzees and

⁹ Here I use the pressure depth profile of the G-1 Laetoli footprints as described by Crompton et al. (2012), who laser-scanned casts of these prints to create 3-D models. From these models, they calculated an ‘average’ footprint which they used in analysis, and which I use to inform my discussion here.

modern humans. The Laetoli print-makers, therefore, may have possessed foot morphology and joint mechanics that were intermediate between those of chimpanzees and humans as well.

Chapter 5: Tables

Table 5.1. Human and chimpanzee subject information.

Subject	Age (years)	Body Mass (kg)	Average Foot Area (cm ²)
Chimp H	8	47.7	135 ± 2
Chimp L	8.8	49.5	139 ± 3
Human B	26	62.6	125 ± 2
Human C	28	64.1	123 ± 3

Table 5.2. Average stance durations and estimated dimensionless velocities for all subjects.

Species	Subject	Stance (s)	Estimated Dimensionless Velocity ^a
Human	Human B	0.65 ± 0.01	0.43 ± 0.01
	Human C	0.69 ± 0.02	0.44 ± 0.02
	<i>Average</i>	<i>0.67 ± 0.03</i>	<i>0.43 ± 0.02</i>
Chimpanzee	Chimp H	0.59 ± 0.08	0.43 ± 0.04
	Chimp L	0.61 ± 0.05	0.46 ± 0.03
	<i>Average</i>	<i>0.6 ± 0.06</i>	<i>0.46 ± 0.05</i>

^a Calculated using linear regression equations developed in Chapter 2 (see Table 2.3).

Table 5.3. Pressure and kinematic variables quantified for analysis of midtarsal break in medial and lateral midfoot regions.

Species	Midfoot Region	Dorsiflexion ^a (°)	Impulse (HML) ^b (kPa*ms)	Peak Pressure		Peak Pressure (HML) ^c	
				Pressure (kPa)	Timing (% stance)	Pressure (kPa)	Timing (% stance)
Chimpanzee	Lateral	9.1 ± 2.2	1601 ± 346	64.7 ± 8.6	12 ± 15	55.3 ± 8.5	39 ± 10
	Medial	9.2 ± 2.3	2049 ± 382	72.5 ± 13.8	32 ± 9	71.8 ± 13.4	32 ± 8
Human	Lateral	2.4 ± 2	954 ± 193	39.9 ± 5.2	48 ± 16	39.3 ± 5.6	50 ± 11

^a Calculated as dorsiflexion excursion between 25 and 85% of stance between the rearfoot and lateral forefoot segments for the lateral midfoot region, and between the rearfoot and medial forefoot segments for the medial midfoot region.

^b Refers to pressure impulse calculated during ‘heel-midfoot lift’ (HML), which occurs from 25 to 85% of stance.

^c Refers to pressure peak during ‘heel-midfoot lift’ (HML), which occurs from 25 to 85% of stance.

Table 5.4. Pressure and kinematic variables quantified for analysis of the metatarsophalangeal joints.

Species	Joint	Peak Dorsiflexion		Metatarsal Head Peak Pressure		Digit Peak Pressure	
		Angle (°)	Timing (% stance)	Pressure (kPa)	Timing (% stance)	Pressure (kPa)	Timing (% stance)
Chimpanzee	1	13 ± 9	89 ± 3	61 ± 41	74 ± 6	117 ± 26	86 ± 5
	2	31 ± 5	95 ± 1	147 ± 39	81 ± 8	88 ± 24	90 ± 4
	3	23 ± 4	96 ± 2	148 ± 31	77 ± 6	88 ± 34	88 ± 10
	4	15 ± 3	94 ± 4	93 ± 32	72 ± 7	47 ± 9	88 ± 2
	5	10 ± 3	86 ± 3	64 ± 22	68 ± 7	18 ± 6	75 ± 11
Human	1	48 ± 7	93 ± 1	141 ± 24	79 ± 2	174 ± 35	86 ± 3
	2	50 ± 4	93 ± 2	201 ± 24	81 ± 5	98 ± 19	82 ± 3
	3	47 ± 4	93 ± 2	169 ± 6	74 ± 4	82 ± 17	85 ± 2
	4	40 ± 9	92 ± 2	116 ± 17	68 ± 6	66 ± 15	87 ± 3
	5	26 ± 4	92 ± 4	116 ± 26	64 ± 9	45 ± 20	82 ± 11

Table 5.5. Rank correlation coefficients and *P*-values calculated for relationships between midfoot dorsiflexion and pressure variables.

Species	Pressure Variable	Lateral Midfoot		Medial Midfoot	
		<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Chimpanzee	Peak	-	0.05	-	0.92
	Peak (25-85%)	0.6	8 E-3	-	0.92
	Impulse (25-85%)	0.69	2 E -3	-	0.96
Human	Peak	-	0.33	-	-
	Peak (25-85%)	-	0.39	-	-
	Impulse (25-85%)	-	0.21	-	-

Table 5.6. Rank correlation coefficients and *P*-values calculated for relationships between metatarsophalangeal joint dorsiflexion and pressure variables.

Species	Metatarsal Head Peak Pressure		Digit Peak Pressure	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Chimpanzee	0.45	2 E-6	0.39	4 E-6
Human	0.32	5 E-4	0.5	2 E-7

Table 5.7. Results of Kruskal-Wallis post-hoc tests comparing peak dorsiflexion angles among the MTPJs and pressure variables among the pedal rays in chimpanzees. Significant results are indicated where *P*-value is below alpha significance level determined by Bonferroni correction.

Pedal Rays Compared	MTPJ Dorsiflexion	MT Head Peak Pressure	Digit Peak Pressure
1 vs. 2	2 > 1 (<i>P</i> = 2 E-3)	2 > 1 (<i>P</i> = 1 E-3)	n.s.
1 vs. 3	n.s.	3 > 1 (<i>P</i> = 6 E-4)	n.s.
1 vs. 4	n.s.	n.s.	1 > 4 (<i>P</i> = 8 E-4)
1 vs. 5	n.s.	n.s.	1 > 5 (<i>P</i> = 2 E-6)
2 vs. 3	n.s.	n.s.	n.s.
2 vs. 4	2 > 4 (<i>P</i> = 3 E-3)	n.s.	n.s.
2 vs. 5	2 > 5 (<i>P</i> = 2 E-6)	2 > 5 (<i>P</i> = 9 E-4)	2 > 5 (<i>P</i> = 7 E-4)
3 vs. 4	n.s.	n.s.	n.s.
3 vs. 5	3 > 5 (<i>P</i> = 8 E-4)	3 > 5 (<i>P</i> = 6 E-4)	3 > 5 (<i>P</i> = 1 E-3)
4 vs. 5	n.s.	n.s.	n.s.

Table 5.8. Results of Kruskal-Wallis post-hoc tests comparing peak dorsiflexion angles among the MTPJs and pressure variables among the pedal rays in humans. Significant results are indicated where *P*-value is below alpha significance level determined by Bonferroni correction.

Pedal Rays Compared	MTPJ Dorsiflexion	MT Head Peak Pressure	Digit Peak Pressure
1 vs. 2	n.s.	n.s.	n.s.
1 vs. 3	n.s.	n.s.	n.s.
1 vs. 4	n.s.	n.s.	1 > 4 (<i>P</i> = 8 E-5)
1 vs. 5	1 > 5 (<i>P</i> = 4 E-4)	n.s.	1 > 5 (<i>P</i> = 2 E-7)
2 vs. 3	n.s.	n.s.	n.s.
2 vs. 4	n.s.	2 > 4 (<i>P</i> = 2 E-5)	n.s.
2 vs. 5	2 > 5 (<i>P</i> = 4 E-5)	2 > 5 (<i>P</i> = 4 E-5)	2 > 5 (<i>P</i> = 4 E-3)
3 vs. 4	n.s.	3 > 4 (<i>P</i> = 3 E-3)	n.s.
3 vs. 5	3 > 5 (<i>P</i> = 1 E-3)	3 > 5 (<i>P</i> = 6 E-3)	n.s.
4 vs. 5	n.s.	n.s.	n.s.

Chapter 5: Figures

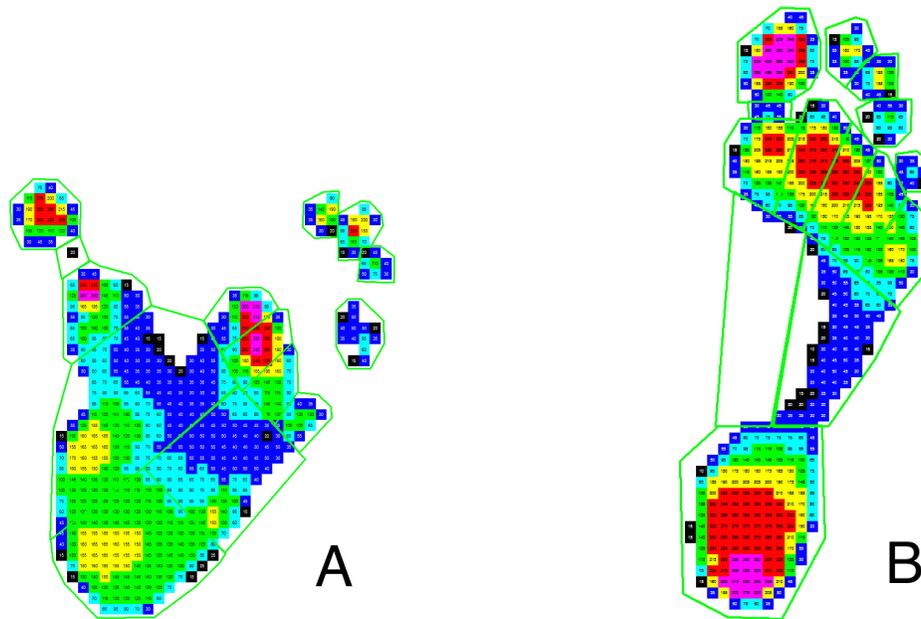


Fig. 5.1. Plantar pressure distributions time-averaged across stance with masks applied to the regions of the foot that were analyzed in this study. A) Chimp L; B) Human C

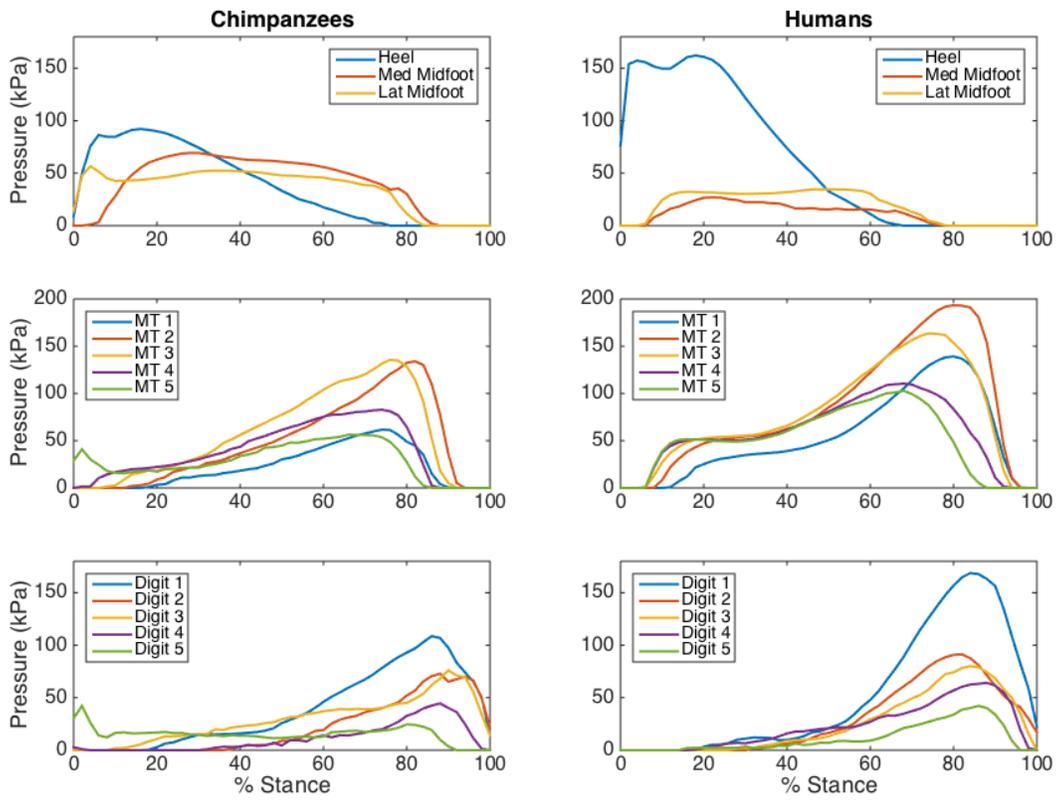


Fig. 5.2. Average pressure by region in human and chimpanzee subjects over stance phase. Pressure data pooled between subjects within species. Touchdown is at 0% of stance, and liftoff is at 100% of stance.

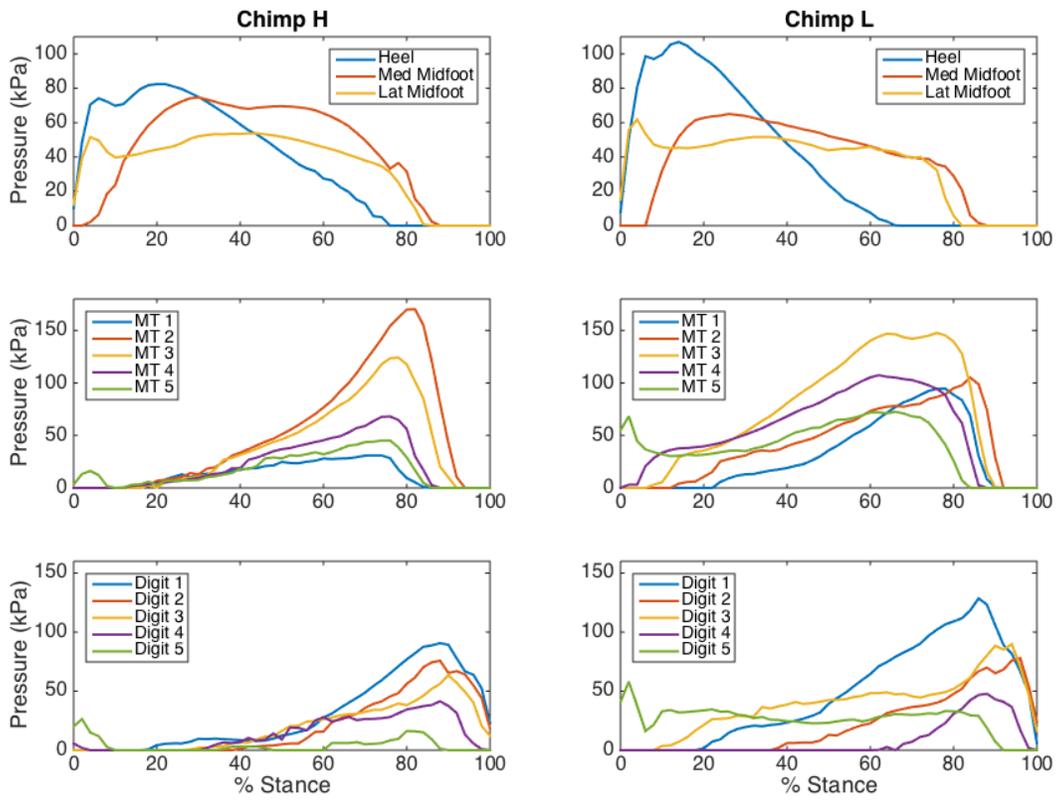


Fig. 5.3. Average pressure by region in chimpanzee subjects over stance phase. Touchdown is at 0% of stance, and liftoff is at 100% of stance.

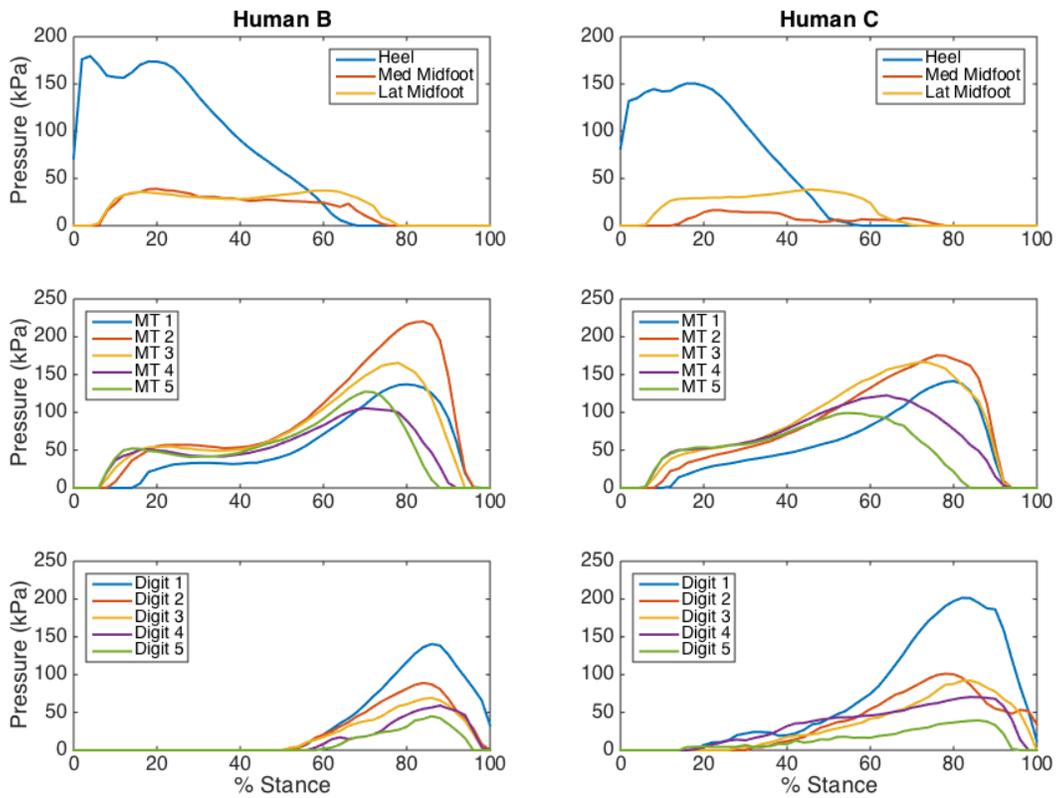


Fig. 5.4. Average pressure by region in human subjects over stance phase. Touchdown is at 0% of stance, and liftoff is at 100% of stance.

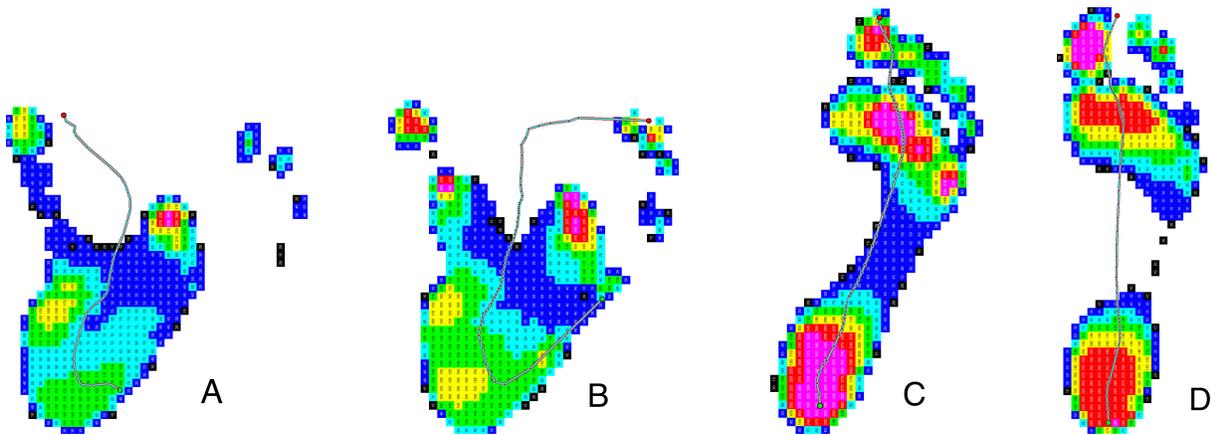


Fig. 5.5. Examples of paths of center of pressure in steps where pressure has been time-averaged across stance. A) Chimp H; B) Chimp L; C) Human B; D) Human C.

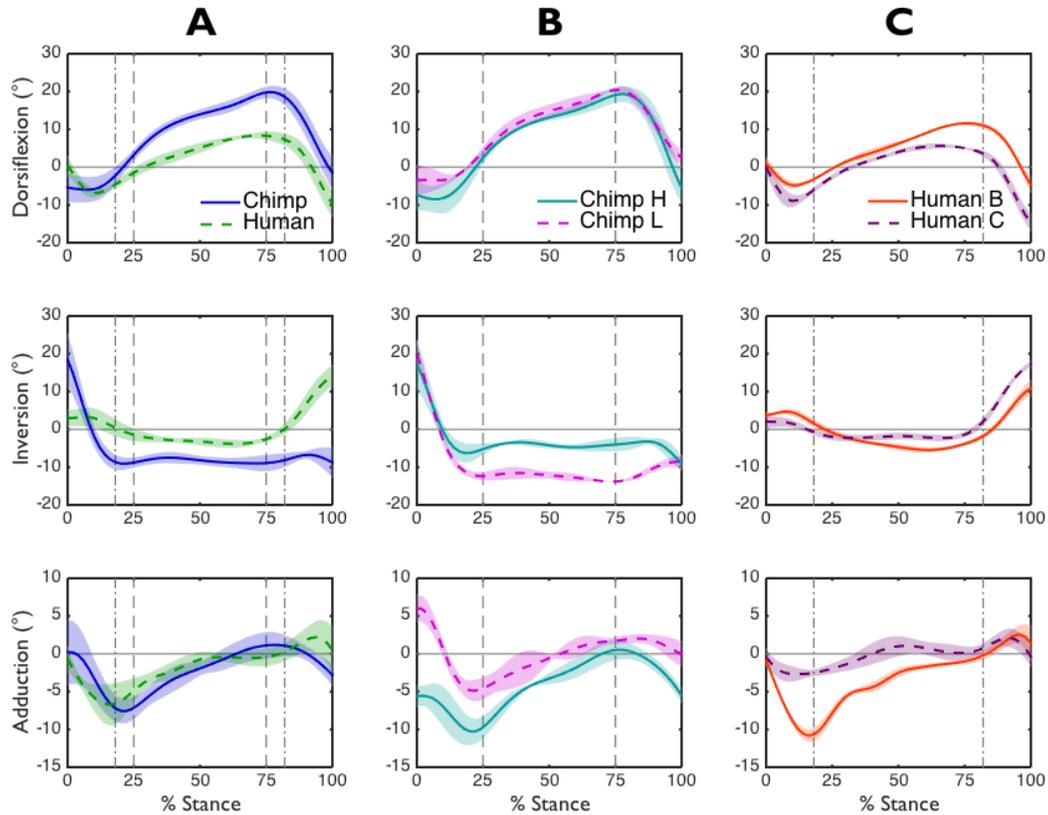


Fig. 5.6. Average motion between the *leg* and *rearfoot* segments. Rows: Top = sagittal plane motion, middle = coronal plane motion, bottom = transverse plane motion. Y-axis labels indicate positive motion. Columns: A) Human *versus* chimpanzee bipedal walking kinematics. B) Chimp H *versus* Chimp L bipedal walking kinematics. C) Human B *versus* Human C walking kinematics. Touchdown is at 0% of stance, and liftoff is at 100% of stance. Vertical dashed lines indicate the beginning and end of single-support phase (dashed lines for chimpanzees, dash-dotted lines for humans).

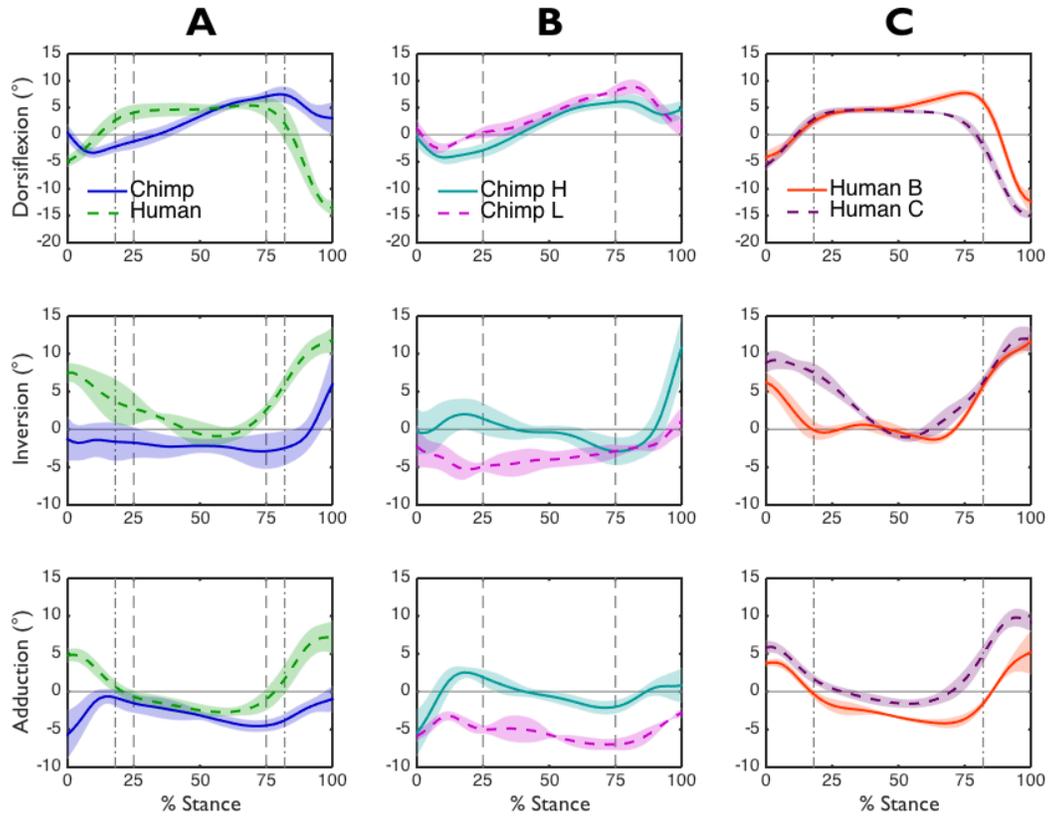


Fig. 5.7. Average motion between the *rearfoot* and *lateral forefoot* segments. Rows: Top = sagittal plane motion, middle = coronal plane motion, bottom = transverse plane motion. Y-axis labels indicate positive motion. Columns: A) Human *versus* chimpanzee bipedal walking kinematics. B) Chimp H *versus* Chimp L bipedal walking kinematics. C) Human B *versus* Human C walking kinematics. Touchdown is at 0% of stance, and liftoff is at 100% of stance. Vertical dashed lines indicate the beginning and end of single-support phase (dashed lines for chimpanzees, dash-dotted lines for humans).

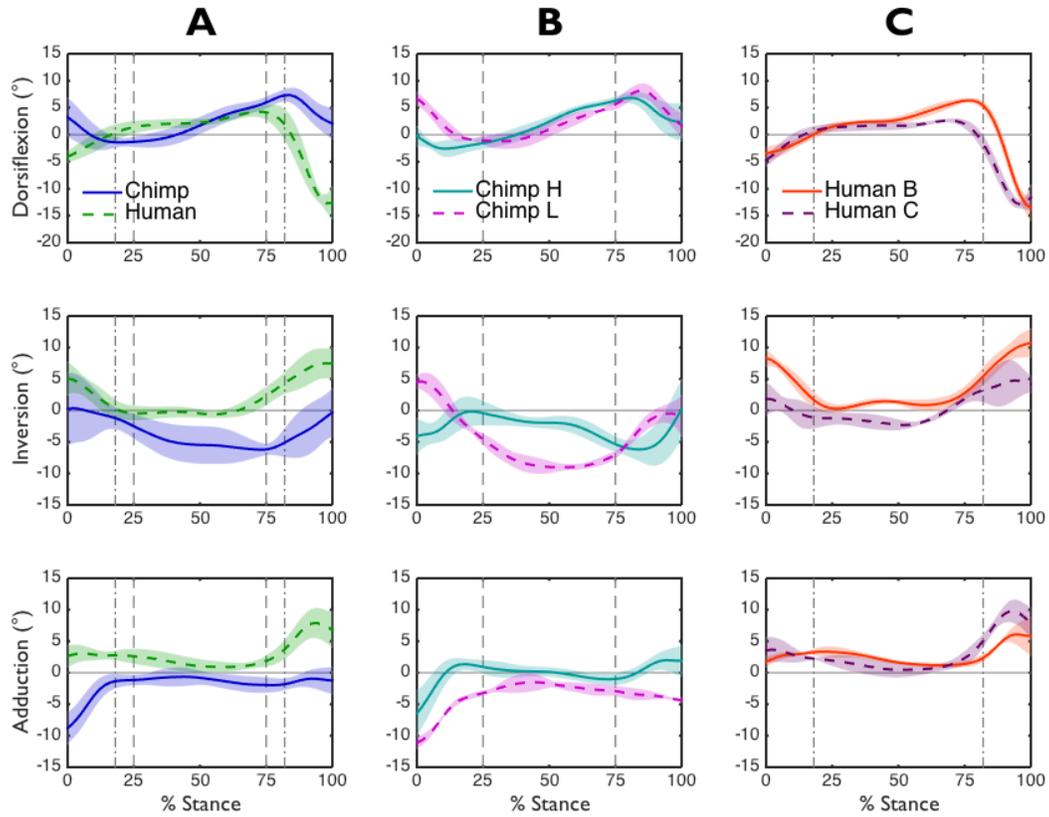


Fig. 5.8. Average motion between the *rearfoot* and *medial forefoot* segments. Rows: Top = sagittal plane motion, middle = coronal plane motion, bottom = transverse plane motion. Y-axis labels indicate positive motion. Columns: A) Human *versus* chimpanzee bipedal walking kinematics. B) Chimp H *versus* Chimp L bipedal walking kinematics. C) Human B *versus* Human C walking kinematics. Touchdown is at 0% of stance, and liftoff is at 100% of stance. Vertical dashed lines indicate the beginning and end of single-support phase (dashed lines for chimpanzees, dash-dotted lines for humans).

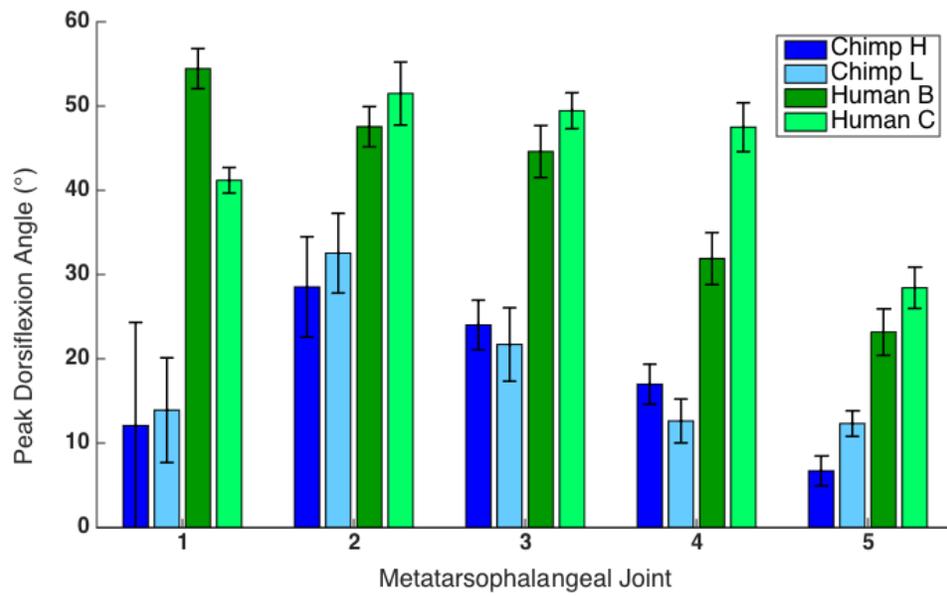


Fig. 5.9. Average peak metatarsophalangeal joint dorsiflexion angles during push-off in humans and chimpanzees. Plus-minus one standard deviation is indicated by error bars.

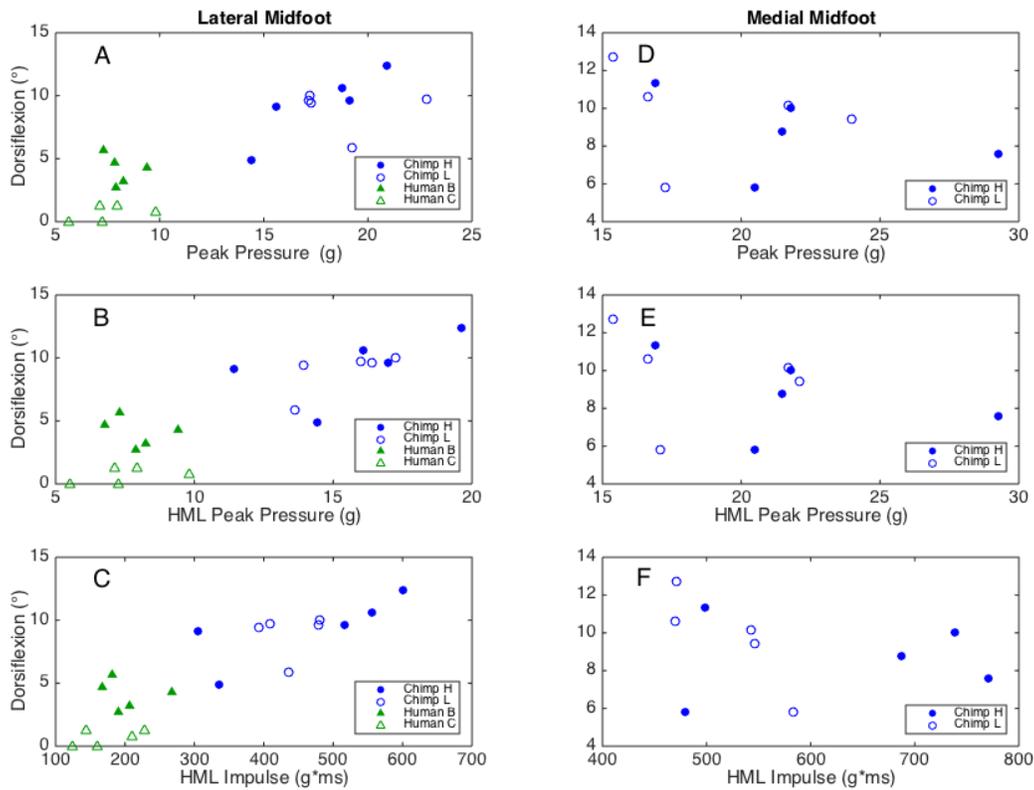


Fig. 5.10. Midfoot pressure variables plotted against dorsiflexion excursion during heel-midfoot lift ('HML'; between 25 and 85% of stance). Lateral midfoot dorsiflexion calculated as sagittal plane motion between rearfoot and lateral forefoot segments. Medial midfoot dorsiflexion calculated as sagittal plane motion between rearfoot and medial forefoot segments. Pressure variables in plots are peak pressure (A, D), peak pressure during HML (B, E), and pressure impulse during HML (C, F). All pressure variables were standardized by dividing by body mass/plantar foot surface area. Resulting values are in units of g (gravitational acceleration constant) for peak pressures, and $g*ms$ (milliseconds) for pressure impulse.

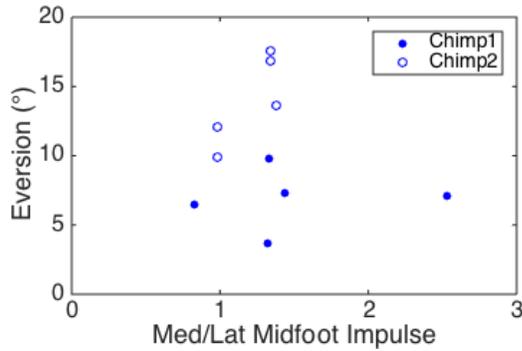


Fig. 5.11. Relationship between peak eversion angle between the leg and rearfoot segments during heel-midfoot lift ('HML'; between 25 and 85% of stance), and the ratio of medial midfoot pressure impulse to lateral midfoot pressure impulse during HML ('Med/Lat Midfoot Impulse'). Pressure variables standardized by dividing by body mass/plantar foot surface area.

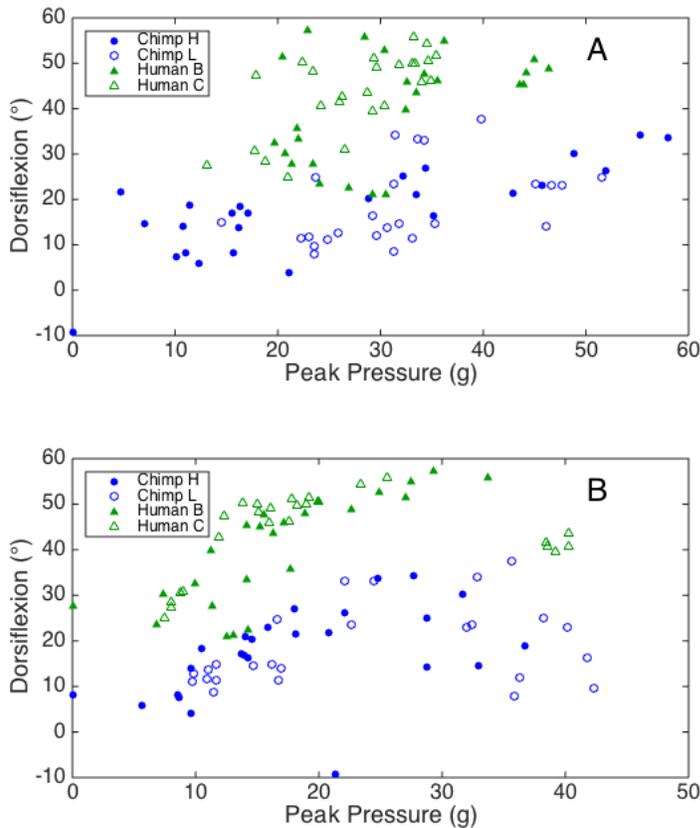


Fig. 5.12. Relationship between maximum dorsiflexion angles at the metatarsophalangeal joints during push-off and the following pressure variables: A) Peak pressure under the metatarsal heads, and B) peak pressures under the digits. All pressure variables standardized by dividing by (body mass/plantar foot surface area). Resulting values are in units of g (gravitational acceleration constant).

Chapter 6

Conclusions and Future Directions

6.1 Summary

I will begin this chapter by summarizing the results of Chapters 3-5. In an effort to synthesize the findings of these chapters into a unified picture of chimpanzee foot kinematics, I will order this discussion by region of the foot, beginning with the ankle joint complex. I will follow this with sections on the midfoot joints and the metatarsophalangeal joints, and conclude with an overall synthesis of results across joints.

6.1.1 Ankle Joint Complex

Talocrural Joint. The ankle joint complex can be thought of as consisting of the talocrural and subtalar joints, or ‘upper’ and ‘lower’ ankle joints (Elftman and Manter, 1935a). The chimpanzee talocrural joint possesses a suite of features that are thought to represent adaptations for arboreal locomotion, and in particular vertical climbing. These include joint articular surface geometry that is used to place the foot in advantageous postures when climbing with high talocrural dorsiflexion angles (Lewis, 1980a; Latimer et al., 1987), and a relatively wide anterior margin of the talar trochlea for close-packing the joint in these positions (DeSilva, 2009). As expected, and previously documented in wild chimpanzees (DeSilva, 2009), the chimpanzees in this study use highly dorsiflexed talocrural joint postures during vertical climbing. These postures are believed to bring the chimpanzee center of mass closer to the climbing substrate, thereby reducing the overturning moment of gravity (Cartmill, 1985). However, chimpanzees use similar talocrural joint dorsiflexion angles during above branch walking on horizontally oriented arboreal supports. These postures increase balance and stability on such supports by lowering the center of mass to reduce lateral toppling moments (Cartmill, 1985; Chadwell and Young, 2015), and diminish the high limb stresses incurred by walking with flexed limb postures *via* joint compliance (Schmitt, 1999; Larney and Larson, 2004). Thus, the use of high talocrural joint dorsiflexion postures appears to be a general characteristic of chimpanzee arboreal locomotion, rather than specific to vertical climbing. Furthermore, Ventkataraman et al. (2013) have ably demonstrated that proficient human tree climbers use chimpanzee-like ankle joint postures while climbing, indicating that chimpanzee-like ankle morphology is not necessary to achieve high dorsiflexion angles. Rather, a high dorsiflexion range of motion in the chimpanzee ankle appears to be advantageous for arboreal locomotion in general.

A second major point that previous studies have argued with regard to talocrural joint function in chimpanzees is the axis about which this joint rotates, and the foot postures that result. Inman (1976) demonstrated that the human talocrural joint axis is not exactly mediolaterally oriented relative to the cardinal planes of the leg, and therefore motion at this joint is not pure plantarflexion-dorsiflexion, but includes small transverse and coronal plane components as well. Lewis (1980a) and Latimer et al. (1987) found the chimpanzee talocrural joint to be even further

from the leg's mediolateral axis than in humans, and argued that this joint is designed to guide the foot into increasingly abducted and inverted postures at higher dorsiflexion angles. This would place the foot in an ideal position to optimize the pedal grasp on arboreal supports during behaviors such as climbing.

It was difficult for me to directly address this notion, as my methodology prevented me from distinguishing motion between the talocrural and subtalar joints in the coronal and transverse planes due to my inability to specifically track the position of the talus. Nevertheless, if the chimpanzee talocrural joint *is* functionally adapted to place the foot in the specific positions suggested by Lewis (1980a) and Latimer et al. (1987) during arboreal locomotion, then I expect that motion between the leg and rearfoot segments should reflect these positions on arboreal supports, regardless of what additional motion is occurring at the subtalar joint. To the contrary, increasing dorsiflexion angles are not consistently coupled with both increasing abduction and inversion angles in the subjects in this study during arboreal locomotion. High dorsiflexion angles, which occur throughout most of stance during both arboreal modes, are associated with highly abducted but *everted* postures during pole-walking, and inverted but mostly neutral transverse plane postures during climbing. During both bipedal and quadrupedal locomotion on the ground, dorsiflexion, abduction, and inversion are poorly coupled as well. This does not mean that these motions do not coincide during the natural arc of the chimpanzee leg over the talus, but rather that motion of the subtalar joint may mitigate the expected position of the foot based solely on talocrural joint motion.

Latimer et al. (1987) and DeSilva (2009) also argued that the disparity in heights of the medial and lateral margins of the talar trochlea results in a relatively 'inverted set' of the chimpanzee foot relative to the leg, meaning that the talocrural joint is most ideally situated to resist loads when the foot is inverted, as in climbing. This notion is supported with regard to climbing behavior, where chimpanzees maintain both an inverted and dorsiflexed foot throughout the majority of stance. Thus, the chimpanzee talocrural joint may be ideally suited for weight-bearing during climbing. This notion agrees with recent discoveries concerning talocrural joint morphology in different species of gorilla with different locomotor repertoires (Dunn et al., 2014; Knigge et al., 2015). The more arboreal lowland gorillas (*Gorilla gorilla*) possess more inverted talocrural joint sets than the more terrestrial mountain gorillas (*Gorilla beringei*), suggesting this aspect of joint morphology is indeed reflective of overall arboreality. However, it should be kept in mind that climbing still makes up a relatively small percentage of overall daily travel time in chimpanzees and lowland gorillas (Doran and Hunt, 1994; Doran, 1996), and mountain gorillas are still fully capable of proficient arboreal locomotion (Doran, 1997). Therefore, talocrural joint morphology should not be used to diagnose the *existence* of arboreal behavior in an animal's locomotor repertoire (*contra* Latimer et al., 1987; DeSilva, 2009), but instead perhaps the relative *amount* of arboreality.

Another important finding is that the chimpanzee foot maintains a relatively everted position through most of stance in all locomotor modes investigated in this study other than vertical climbing. Therefore, the inverted set of the talocrural joint does not result in an inverted foot position in chimpanzees during most locomotor behaviors. This, once again, is likely due to positioning of the subtalar joint, which may counter the neutral set of the talocrural joint. As such, I conclude that one cannot directly infer foot posture during locomotion from talocrural joint morphology alone.

Subtalar Joint. Elftman and Manter (1935a) called the subtalar joint the 'lower ankle joint', and its function during locomotion is believed to be intimately linked to that of the

talocrural joint in both humans and non-human apes (Close et al., 1967; Inman, 1976; Lewis, 1980b). Due to the difficulty of quantifying subtalar joint motion *in vivo* or *in vitro*, most previous investigations of the chimpanzee subtalar joint have focused on features of the articular surface morphology that are believed to be related to axis of rotation and range of motion (Elftman and Manter, 1935a; Lewis, 1980b; Deloison, 1985; Rose, 1986; Latimer and Lovejoy, 1989; Prang, 2016). These studies have suggested a higher range of motion in chimpanzees compared to humans, with an axis of rotation that enables chimpanzees to adopt highly inverted foot postures during arboreal locomotion. I found that chimpanzees do possess a greater passive range of motion at the subtalar joint than humans. Surprisingly, however, chimpanzees possess a similar inversion range to humans, but a much greater eversion range. Furthermore, chimpanzees utilize highly everted subtalar joint postures throughout the majority of stance in both terrestrial locomotion and above branch arboreal support walking. Therefore, I conclude that the chimpanzee subtalar joint is actually adapted to enable everted joint postures during most locomotor behaviors. This may allow chimpanzees to offset the position of the foot from that caused by the naturally inverted position of the talocrural joint during behaviors where a more everted foot posture is advantageous.

There is, however, a period in stance where the subtalar joint is highly inverted in the non-climbing locomotor modes investigated here: touchdown. Consistent with previous observations of footstrike in *Pan* species (Elftman and Manter, 1935b; Susman, 1983; Vereecke et al., 2003), the chimpanzees in this study contact the substrate with a highly inverted foot, then subsequently bring the medial side of the foot down. The purpose of this touchdown strategy remains a mystery, but it may simply reflect the neutral position of the chimpanzee foot when it is not weight-bearing, as one might predict from the talocrural joint set. It must be emphasized here, however, that following touchdown, chimpanzees rapidly evert their feet to place the medial midfoot in contact with the underlying substrate. Pressure results verify the relatively high proportion of weight-support by the chimpanzee medial midfoot relative to the lateral midfoot, although a direct relationship between medial midfoot pressure and subtalar eversion was not uncovered in this study. Nevertheless, these results contradict a notion about non-human ape locomotion that has recently become popular in the literature, namely that these species walk with inverted feet and maintain weight-support along the foot's lateral border (Vereecke et al., 2003; Lovejoy et al., 2009a; Crompton et al., 2012; DeSilva et al., 2013). This may be true for bonobos (Vereecke et al., 2003), but is clearly not the case for chimpanzees in this study, or previous studies of chimpanzee locomotion (Elftman and Manter, 1935b; Wunderlich, 1999).

In addition to inversion-eversion, a considerable amount of transverse plane abduction-adduction should occur at the chimpanzee subtalar joint, based on its reconstructed axis of rotation (Rose, 1986). Although this did appear to be the case during the locomotor modes investigated in this study, transverse and coronal plane rotations of the subtalar joint were not closely coupled; that is to say, inversion was not accompanied by a consistent amount of adduction, and eversion was not accompanied by a consistent amount of abduction. This result is surprising, as motion in these planes should be coupled when considering the subtalar joint axis of rotation (Close et al., 1967; Inman, 1976). This inconsistency in planar motions in chimpanzees is most strikingly apparent when considering subtalar motion during bipedal and quadrupedal locomotion on the ground. In the former mode, a large amount of subtalar abduction follows touchdown, whereas very little transverse plane motion occurs during the same period in the latter mode. However, the amount of subtalar eversion that occurs during this period is similar in both modes. This result once again suggests that foot motion relative to the leg is more

complicated than that reconstructed solely on the basis of joint axes of rotation. Again, the complexity of the interacting joints of the chimpanzee ankle means that articular surface morphology cannot provide a direct means of determining of foot posture in these species during locomotion.

6.1.2 The Midfoot Joints

Transverse tarsal joint complex. Elftman and Manter (1935a,b) were the first researchers to hone in on the transverse tarsal joint complex as a site of major arthrological divergence in the feet of humans and chimpanzees. They argued that morphological features of the joints participating in this complex, the talonavicular and calcaneocuboid joints, result in the midtarsal break characteristic of chimpanzee walking, but absent in humans. Later studies highlighted other aspects of joint anatomy that could be related to the midtarsal break (Bojsen-Møller, 1979; Lewis, 1980b; Gomberg, 1985), and quantified sagittal plane mobility at the transverse tarsal joints (DeSilva, 2010; Greiner and Ball, 2014; Thompson et al., 2014). One chimpanzee in the present study, Chimp L, does show a midtarsal break-like motion at these joints during terrestrial quadrupedalism, but the other does not. Therefore, the role of these joints in the midtarsal break appears to be variable, which is consistent with recent studies that have found variability in the joints' passive mobilities between chimpanzee individuals (Greiner and Ball, 2014; Thompson et al., 2014).

On arboreal substrates, function of the transverse tarsal joint complex is again somewhat variable between subjects. Chimp L uses the complex to pronate the midfoot during horizontal support walking, and supinate the foot during climbing. Chimp H, on the other hand, uses lower joint ranges of motion during arboreal locomotion, consistent with his lack of a midtarsal break at these joints (but see tarsometatarsal joints). However, both subjects show similar patterns of motion at this joint during arboreal locomotion, and in both subjects the coronal plane ranges of motion at this joint are higher during pole walking than during other locomotor modes. This result suggests that the chimpanzee transverse tarsal joint may be designed to facilitate longitudinal rotation of the foot in order to enhance arboreal support grasping, although this notion requires further investigation.

Tarsometatarsal joints. The cuboid-metatarsal joints have received recent attention as another site of midtarsal break motion in chimpanzees and other primates (Vereecke et al., 2003; DeSilva, 2010; Greiner and Ball, 2014), and investigations of articular surface morphology have revealed features predictive of high mobility at these joints (DeSilva, 2010; Proctor, 2013; DeSilva et al., 2015). As with the transverse tarsal joint complex, the chimpanzees in this study are variable with regard to the presence of a midtarsal break at the cuboid-metatarsal joints; Chimp H exhibits a cuboid-metatarsal break, but Chimp L does not. In essence, both chimpanzees dorsiflex in the midfoot region, but this movement occurs predominantly at the transverse tarsal joints in one subject and at the tarsometatarsal joints in the other. Both subjects do, however, show similar cuboid-metatarsal joint kinematics during climbing: they dorsiflex the joints during midstance, and supinate them towards push-off. I was unable to capture cuboid-metatarsal joint motion during pole walking in Chimp L, but Chimp H shows high joint mobility during this behavior. Therefore, chimpanzees utilize the mobility at the cuboid-metatarsal joints during arboreal locomotion, although this mobility does not always manifest itself as a midtarsal break during terrestrial locomotion. Recently, Greiner and Ball (2014) measured similar passive ranges of motion in the cuboid-metatarsal joints of cadaveric humans and chimpanzees, which indicated the absence of a joint mobility difference between species. Based on the results of this

study, humans and chimpanzees may simply utilize similar ranges of cuboid-metatarsal joint mobility for different purposes: in humans, this mobility facilitates longitudinal arch raising during the dynamic windlass mechanism, and in chimpanzees, this mobility is used to enhance arboreal support grasping.

Although no previous study has suggested the potential for high mobility at the intermediate and lateral cuneiform-metatarsal joints, the chimpanzees in this study exhibit relatively high ranges of motion at these joints during all locomotor behaviors. This finding is surprising considering the absence of obvious morphological signifiers of mobility at these joints, but makes sense in the light of pressure data collected in this study. During terrestrial bipedalism, chimpanzees experience greater pressures under the midfoot and forefoot regions on the medial side of the foot than on the lateral side. We can infer that the forces indicated by these pressures exert a torque on the cuneiform-metatarsal joints, causing them to dorsiflex in a midtarsal-break like motion during terrestrial locomotion. Although I was unable to measure chimpanzee plantar pressures on arboreal supports, Wunderlich (1999) reported that the subjects in her study experienced exceptionally high medial midfoot and forefoot pressure during horizontal pole-walking. Thus, it is likely that chimpanzees utilize cuneiform-metatarsal joint mobility for arboreal locomotion in a manner similar to their use of the cuboid-metatarsal joints during these behaviors. Whether the kinematics of the cuneiform-metatarsal joints are somehow reflected in their articular surface morphology remains to be investigated.

Overall midfoot motion. I was unable to capture accurate midfoot segment motion in chimpanzees during bipedal locomotion due to midfoot triad deformation. This prevented me from comparing the kinematics of specific midfoot joints between humans and chimpanzees, but I was able to compare midfoot motion patterns between species more generally. Surprisingly, chimpanzees display relatively less mobile midfeet overall than humans during bipedal walking. Chimpanzees do exhibit a greater midtarsal break motion, measured as midfoot dorsiflexion following heel lift, which manifests as high lateral midfoot pressure. However, the average magnitude of this motion in chimpanzees is only $\sim 7^\circ$ greater than that in humans, and the biomechanical consequences of such a minor difference are unclear. Otherwise, the chimpanzee foot is relatively rigid during much of stance phase, in contrast to the human foot, which exhibits dramatic forefoot supination prior to push-off. This finding goes against the prevailing dichotomy of hominoid foot function, which views the human foot as rigid and the chimpanzee foot as highly mobile (Elftman and Manter, 1935a; Susman, 1983; Langdon, 1986; Lovejoy et al., 2009a; DeSilva, 2010; Ward et al., 2011; Harcourt-Smith et al., 2015), but which has recently come under some scrutiny (Crompton et al., 2010; Bates et al., 2013; Greiner and Ball, 2014). The results of this study suggest that chimpanzees possess a midfoot capable of maintaining considerable rigidity during terrestrial locomotion, whereas humans possess a foot adapted for highly dynamic midfoot mobility as part of longitudinal arch function.

6.1.3 Metatarsophalangeal Joints

MTPJ morphology has long been cited as a key feature distinguishing the feet of bipedal hominins from those of non-human apes. Bipedal locomotion is thought to require a suite of adaptations to enable high loading of the MTPJs when they are in highly dorsiflexed postures (Stern and Susman, 1983; Latimer and Lovejoy, 1990a; Duncan et al., 1994; Griffin and Richmond, 2010; Fernández et al., 2015). Lacking these adaptations, chimpanzees and other non-human primates are thought to be incapable of pushing off with high MTPJ dorsiflexion angles during terrestrial locomotion. The results of this study fit this expectation, with

chimpanzees exhibiting significantly lower peak dorsiflexion angles than humans at all five MTPJs. However, these angles were lower than the maximum passive dorsiflexion angles that I measured for the chimpanzee MTPJs, suggesting that chimpanzees did not utilize the full range of dorsiflexion available to them during terrestrial locomotion. This is likely due to the fact that chimpanzees do not plantarflex their ankles as much as humans during push-off (O'Neill et al., 2015; see Chapter 4), resulting in lower dorsiflexion torques at the MTPJs. Unlike humans, chimpanzees lack a well-developed plantar aponeurosis, and therefore do not incur the mechanical benefits of a windlass mechanism at higher MTPJ dorsiflexion angles.

Relative dorsiflexion angles of the chimpanzee MTPJs are reflected in relative plantar pressures under the metatarsal heads: the highest peak pressures and dorsiflexion angles occur at rays 2 and 3, whereas the lowest pressures and angles occur at rays 1, 4 and 5. Interestingly, chimpanzees display a temporal sequence for peak metatarsal head plantar pressures similar to that of humans, in which forefoot pressure travels from lateral to medial across the metatarsal heads prior to push-off. This pattern suggests a shift in weight support to the second metatarsal head for push-off from the medial side of the foot. Unlike in humans, chimpanzee feet are abducted relative to the direction of travel, such that the hallux points medially, and the other digits are directed somewhat laterally. As push-off is centered near the head of the second metatarsal, the pedal rays exhibit progressively lower MTPJ dorsiflexion angles during liftoff the further they are from the second ray.

The role of the hallux during terrestrial locomotion in chimpanzee is somewhat different from that of the other digits. The chimpanzees in this study use widely abducted hallux postures, but bear relatively little weight under this ray during the first half of stance. In the second half, the amount of pressure under the hallux increases as the heel is lifted from the substrate and more weight is born under the forefoot. During push-off, chimpanzees experience relatively low pressure under the first metatarsal head, but relatively high pressure at the tip of the hallux, indicating the use of this digit in propulsion. Nevertheless, the first MTPJ exhibits a low peak dorsiflexion angle, potentially due in part to its distance from the second and third metatarsal heads where the axis of push-off is located.

6.1.4 Synthesis of Findings

The traditional understanding of chimpanzee foot function has been developed in comparison to that of human feet. Due to the closely shared ancestry of humans and chimpanzees, but radically different locomotor repertoires, researchers have tended to view the feet of these species in a dichotomy: the human foot as optimally adapted for terrestrial bipedalism, and the chimpanzee foot as adapted for locomotion on arboreal substrates. The natural extension of this dichotomy is that the chimpanzee foot is somewhat maladapted for terrestrial locomotion, as epitomized by the midtarsal break that occurs during heel lift when chimpanzees travel on the ground. However, when considering evidence that the vast majority of chimpanzee locomotion in the wild occurs on terrestrial substrates (Doran and Hunt, 1994), the notion of the chimpanzee foot as primarily adapted for arboreal locomotion becomes paradoxical. The inherent challenges associated with quantifying non-human primate foot mechanics *in vivo* have prevented us from developing a more nuanced understanding of chimpanzee foot function. In this dissertation, I was able to meet these challenges by measuring detailed 3-D kinematics of the intrinsic foot joints and plantar pressure distributions in chimpanzees during a variety of locomotor modes.

A direct comparison of chimpanzee foot kinematics during terrestrial locomotion to those of humans, as well as to chimpanzee foot kinematics during arboreal locomotion, reveals that the

chimpanzee foot is adapted for proficient travel on both the ground and in the trees. Critical to this conclusion is the function of the chimpanzee midfoot joints during terrestrial locomotion. Contrary to my expectations, these joints are not highly mobile in chimpanzees when they walk on the ground. Although chimpanzees do exhibit a midtarsal break, this motion is not as dramatic as it has sometimes been described in the literature (Vereecke et al., 2003; Lovejoy et al., 2009a; DeSilva, 2010), at least not among the chimpanzees in this study¹⁰. Rather, it manifests as 5-10° of midfoot dorsiflexion following heel lift, which is slightly greater than that measured in humans. Other than the small midtarsal break motion, the chimpanzee midfoot is relatively rigid throughout most of stance, at least in comparison to that of humans. The longitudinally arched human midfoot deforms slightly under weight-bearing, and then springs into supination at the end of stance, making it a much more dynamically mobile structure than the chimpanzee foot over the course of a step. Nevertheless, the relative rigidity of the chimpanzee foot likely improves its role as a stable lever during terrestrial locomotion. Chimpanzees touchdown with inverted feet, but then evert their feet to distribute plantar pressure under the medial and lateral halves of the foot during midstance, increasing the foot's base of support. Like humans, chimpanzees position weight over the medial side of the foot prior to push-off, creating a stable line of leverage with the ankle joint that may allow them to more effectively use ankle power for forward propulsion. MTPJ dorsiflexion is limited in chimpanzees relative to humans, although chimpanzees do use their digits, and in particular their halluces, to generate some power during propulsion.

Despite its relative rigidity on the ground, the chimpanzee foot becomes a more pliable grasping structure during arboreal locomotion, particularly during above branch travel. The transverse tarsal and tarsometatarsal joints demonstrate high mobility during horizontal support walking, which helps to facilitate the foot's conformation to the substrate, thereby improving pedal grasp and overall stability. However, the chimpanzee midfoot demonstrates less overall mobility during arboreal locomotion than that which has been described for cercopithecines. During both climbing (Hirasaki et al., 1993; Drapeau and Harmon, 2013) and above branch walking (Meldrum, 1991; Gebo, 1993), cercopithecines display substantial midfoot dorsiflexion and supination, which may improve stability during arboreal locomotion by enhancing the pedal grasp and bringing the body's center of mass closer to the support (Cartmill, 1985; Meldrum, 1991). The high mobility of the cercopithecine foot is also evidenced by substantial midfoot dorsiflexion that occurs during terrestrial locomotion (Meldrum, 1991; DeSilva, 2010; Hirasaki et al., 2010), even in large species such as baboons (Berillon et al., 2010). Lacking the dramatic midfoot mobility of cercopithecines (Greiner and Ball, 2014), chimpanzees require alternative mechanisms for maintaining stability during arboreal locomotion. The powerful grasping hallux

¹⁰ I have already commented on the extent to which the subjects in this study may or may not represent the "average" condition for all chimpanzees (see Chapter 3, section 3.4.2; Chapter 4, section 4.4.1). Whether or not their condition is "average" is something of a moot point, as these individuals are inside of the normal range of variation based on my inspection of foot postures in videos of seven other chimpanzees from previous experiments carried out at the Stony Brook Primate Locomotion Laboratory. The subjects in this study were healthy and highly active during the period of data collection, and based on my inspection of x-rays taken of the subjects' feet, had no obvious foot abnormality. Thus, these subjects exhibit foot mechanics that can be considered to be within the normal range of variation for chimpanzees.

and long pedal digits provide one obvious means, and adaptations of the talocrural and subtalar joints provide another.

Chimpanzees possess high talocrural joint ranges of motion, which they utilize during both climbing and above branch walking by adopting highly dorsiflexed ankle postures. This contrasts with the more extended ankle postures used by cercopithecines during arboreal locomotion (Meldrum, 1991; Gebo, 1993; Hirasaki et al., 1993; DeSilva, 2009; Drapeau and Harmon, 2013). High talocrural dorsiflexion enables chimpanzees to bring their bodies closer to the substrate in the absence of high midfoot mobility. This is particularly important during vertical climbing, when chimpanzees must minimize the overturning moments of their bodies to reduce the risk of fatal falls (DeSilva, 2009). During climbing, chimpanzees load their hind limbs in compression, resulting in highly flexed joints. Only the forefoot contacts the substrate, and the high reaction force at this point of contact results in tarsometatarsal joint dorsiflexion. Nevertheless, the peak magnitude of this dorsiflexion is only $\sim 10\text{-}15^\circ$, which is probably less than that used by cercopithecines during climbing (Hirasaki et al., 1993; DeSilva, 2009; Drapeau and Harmon, 2013).

Chimpanzees also utilize highly mobile subtalar joints to improve stability on arboreal supports. Subtalar inversion enables them to place a greater percentage of their forefoot against the support during climbing, thereby increasing friction between their foot and the substrate and preventing slippage. During above branch locomotion, chimpanzees utilize their exceptionally high subtalar eversion ranges of motion to position their feet atop the support, near the body's midline. This position contrasts with that described by Meldrum (1991) for cercopithecines, which place their feet in relatively supinated positions which contact the sides of arboreal supports. Although no study to my knowledge has quantified subtalar joint range of motion in cercopithecines, Rose (1986) made qualitative observations of relative joint mobility in a range of anthropoid species based on osteoligamentous manipulations. He reported that African apes possess a considerably greater potential range of subtalar joint motion than cercopithecines. This finding supports the notion that chimpanzees have evolved especially large subtalar joint ranges to make up for limited midfoot mobility during arboreal locomotion.

Overall, the chimpanzee foot is a structure that is specially adapted for both proficient terrestrial and arboreal substrate locomotion. The relatively stiff midfoot provides a stable base of support and effective lever for push-off on the ground, and the highly mobile talocrural and subtalar joints enable optimal positioning of the foot to achieve a strong pedal grasp in the trees. Certain aspects of chimpanzee pedal anatomy, such as long lateral digits and an abducent hallux, represent clear compromises in favor of arboreality, and are likely to limit the absolute propulsive power that can be imparted by the foot during terrestrial locomotion. However, the chimpanzee midfoot is also clearly compromised in ways to improve terrestrial locomotor performance at the expense of optimal arboreal support grasping. Therefore, the chimpanzee foot is not optimized for performance on the ground or on branches, but is adapted to perform adeptly in both settings.

This picture of chimpanzee foot function sheds new light on the human foot, and its unique adaptations to obligate terrestrial bipedality. First, the human foot is not an exceptionally rigid structure, but relatively mobile in a manner that sets it apart from the feet of chimpanzees and other primates. Adduction of the hallux and shortening of the toes have robbed the human foot of its prehensility, but it retains substantial midfoot mobility that enables the foot to conform to uneven terrain, and to store elastic energy in plantar soft tissue structures during weight-bearing (Ker et al., 1987; Kelly et al., 2014b). Elastic recoil of the soft tissues and tightening of

the plantar aponeurosis during push-off result in dramatic midfoot supination at the end of a step that contributes to foot propulsion and enables a powerful push-off at the ankle. It is therefore inaccurate to characterize the human foot as rigid, at least relative to the foot of a chimpanzee. If humans evolved from an ancestor with a chimpanzee-like foot, they would not have needed to lose midfoot mobility, but instead repurpose it in a manner to aid in forward propulsion. The development of a truss-like longitudinal arch would have served exactly this purpose, but likely would have required adduction of the hallux and resulting loss of prehensility. Adduction of the hallux would have served the additional function, however, of providing a larger and more robust base of support during push-off than that afforded by the heads of metatarsal 2 and 3 in chimpanzees. After these changes, reduction in digit length would have reduced bending stress on the phalanges during push-off (Preuschoft, 1970), resulting in further loss of grasping capabilities, but the capability of withstanding greater propulsive forces.

Humans additionally would have lost some of the high subtalar and talocrural mobility present in a chimpanzee-like ankle. Although humans retain a chimpanzee-like range of subtalar inversion, which they utilize during foot supination at the end of stance, the loss of eversion range of motion was likely necessary for optimal longitudinal arch function. Living humans with hypereverting subtalar joints tend to exhibit reduced arch height and forefoot abduction, which are believed to compromise the function of the foot during push-off (Murley et al., 2009; Levinger et al., 2010; Hösl et al., 2014). Humans may have also lost some talocrural joint mobility in order to enhance joint stability in the range of postures that occur during a typical bipedal step (DeSilva, 2009). However, one must be cautious when discussing typical human talocrural joint mobility, as researchers have demonstrated the ability of modern human foragers to exhibit chimpanzee-like ranges of dorsiflexion during tree climbing (Venkataraman et al., 2013; Kraft et al., 2014). Their findings suggest that reduced ankle mobility in most humans may actually be related to the evolution of triceps surae musculature that is capable of high power generation at the expense of lengthening capability. It is unknown whether the ankle hypermobility of tree-climbing humans adversely affects their bipedal walking performance in any way, but the findings of these studies suggest the retention of at least the capacity for chimpanzee-like talocrural dorsiflexion in humans.

In establishing an evolutionary trajectory of the human foot, the chimpanzee foot makes a suitable starting point. Although chimpanzees rarely walk bipedally in the wild, they exhibit nearly identical foot kinematics when using bipedal and quadrupedal walking gaits. This is surprising in light of the higher forces experienced by the hind limb during the former gait (Pontzer et al., 2014), but suggests that chimpanzee feet can maintain their basic mechanics in face of these higher forces. This means that chimpanzee-like foot anatomy would have been sufficient for facultative bipedalism in a hypothetical last common ancestor of humans and chimpanzees. Further modification of the foot during human evolution would have then served to improve specific aspects of performance during bipedal locomotion. Therefore, the functional morphology of the chimpanzee foot has important implications for the fossil hominin record.

6.2 Fossil Hominins

In this section I will examine the implications of the dissertation research for human evolution by discussing the fossil hominin record, focusing on instances where significant pedal morphology has been preserved. I will restrict detailed discussion mainly to fossils from the Pliocene and early Pleistocene; few associated fossil hominin foot specimens have been found prior to this time window, and most of those following it preserve essentially modern human-like

morphology (Day and Napier, 1964; Trinkaus, 1983; Pontzer et al., 2010; Jungers et al., 2015; Pablos et al., 2015).

6.2.1 *Ardipithecus ramidus*

At 4.4 My old, *Ar. ramidus* is the earliest fossil hominin for which significant foot remains have been preserved (Lovejoy et al., 2009a). The ARA-VP-6/500 specimen includes a remarkably well-preserved foot retaining complete or partial remains of most foot bones, although it lacks a calcaneus. The most striking feature of this specimen is its widely abducted, fully opposable hallux, which is similar to that of chimpanzees. The head of the first metatarsal lacks doming, indicating a limited dorsiflexion capacity during terrestrial push-off. The specimen also possesses long, dramatically curved pedal phalanges, suggesting a foot that was well-adapted for arboreal support grasping. Based on these features, Lovejoy et al. (2009a) have argued that the *Ar. ramidus* foot was well-adapted to above branch arboreal locomotion, but poorly adapted to vertical climbing and quadrumanous suspension. In defense of the second assertion, they refer to several features that they argue would have served to stiffen the midfoot, in contrast to the feet of chimpanzees and other African apes, which they view as highly mobile. First, they describe the presence of an os peroneum facet, indicating greater peroneus longus leverage; second, they argue that the peroneus longus groove on the inferior surface of the cuboid would have redirected the tendon of this muscle in an orientation that would have enhanced its ability to stiffen the midfoot in a manner distinct from that of chimpanzees. I reject these arguments on the following counts:

First, large ossa peronea are present in both gibbons and macaques (Manners-Smith, 1908; Le Minor, 1987), and yet both these species have been observed to exhibit substantial midfoot dorsiflexion both passively and while walking, well beyond that typically reported for chimpanzees (Vereecke and Aerts, 2008; DeSilva, 2010; Hirasaki et al., 2010; Greiner and Ball, 2014). Therefore, presence or absence of an os peroneum should have no relationship to absolute midfoot mobility. Second, they argue that orientation of the chimpanzee peroneus longus tendon promotes its ability to adduct the hallux, as opposed to stiffen the midfoot, which they argue to be its function in humans and *Ar. ramidus*. However, peroneus longus activation has been studied in multiple non-human primate species, including chimpanzees, and all of these studies found its role in hallucal adduction to be minimal (Stern and Susman, 1983; Boyer et al., 2007; Kingston et al., 2010; Patel et al., 2015); in all primates, peroneus longus consistently serves primarily as a foot evertor. Third, the role of peroneus longus in midfoot stiffening is unsupported by EMG studies of human subjects with *pes planus* (pathological flatfoot); in these studies afflicted individuals exhibit *reduced* peroneus longus activity relative to individuals with normal-height arches (Hunt and Smith, 2004; Murley et al., 2009). If peroneus longus aided midfoot stiffening, we would expect it to exhibit higher activation in flatfooted individuals to make up for midfoot laxity, yet the opposite appears to be the case. Therefore, os peroneum and cuboid groove morphology provide no evidence for greater midfoot stiffness in *Ar. ramidus* relative to that in chimpanzees.

Lovejoy et al. (2009a) do describe, however, several features of the *Ar. ramidus* pedal remains that are more convincing indicators of a foot that is better-suited to terrestrial locomotion than that of chimpanzees. First, *Ar. ramidus* possessed a midfoot region that was elongate relative to that of chimpanzees, which would have increased the outlever of the foot, thereby increasing power generation during push-off. Second, the *Ar. ramidus* third metatarsal head is dorsally domed to suggest a greater dorsiflexion angle at push-off than that in

chimpanzees. This would occur if *Ar. ramidus* used more extended lower limb joints and a more plantarflexed ankle at push-off, which could enable greater propulsive force. However, based on its abducent hallux, *Ar. ramidus* likely lacked a longitudinal arch, and therefore would have been unlikely to accrue the mechanical benefits of a windlass mechanism at higher dorsiflexion angles.

One more important aspect of *Ar. ramidus* foot function that was downplayed by Lovejoy et al. (2009a) is a talar axis angle that is similar to that of quadrupedal primates, which is indicative of a wider stance width in neutral position than that in humans (White et al., 2015). This detail suggests that *Ar. ramidus* may have walked with a stance width approximating that used by chimpanzees during bipedal locomotion. This possibility, when considered with the other features of *Ar. ramidus* foot morphology, suggests that the chimpanzee foot makes an excellent model for *Ar. ramidus* foot function during bipedal locomotion. Like chimpanzees, *Ar. ramidus* likely walked with a relatively stiff midfoot, but without being able to reap the benefits of a windlass mechanism or plantar ligament recoil facilitated by a longitudinal arch. Nevertheless, chimpanzee morphology was likely to have been fully sufficient for facultative bipedalism in this species, particularly if *Ar. ramidus* possessed a slightly longer foot for greater propulsion during push-off.

The relative talocrural and subtalar mobility in *Ar. ramidus* cannot be deduced from current descriptions of the pedal material, and thus it is difficult to determine if this species would have been as adept on arboreal substrates as chimpanzees. However, considering the digital morphology so far described, along with its chimpanzee-like calcaneocuboid joint morphology, it is probably safe to say that the *Ar. ramidus* foot was well suited for arboreal locomotion. The overall picture of pedal morphology in this species then suggests a foot similar to that of chimpanzees that was suited to both proficient arboreal and terrestrial locomotion, although likely somewhat better at generating propulsive force during a bipedal push-off.

Considering the terrestrial adaptations in the feet of humans, chimpanzees, and *Ar. ramidus*, it is tempting to argue for a semi-terrestrial last common ancestor of *Homo* and *Pan*. The most parsimonious explanation for shared foot morphology would be a quadrupedal common ancestor, given the knuckle-walking behavior of the extant African apes (Richmond et al., 2001; but see Kivell and Schmitt, 2009). This is essentially the argument put forward by Gebo (1992) based on the similarity of foot strike posture in humans and African apes, and the *Ar. ramidus* fossils fit this scenario nicely. However, one should not base an argument about human origins on a single region of the body, and Lovejoy et al. (2009b) have made the convincing argument that the *Ar. ramidus* hand and wrist lack any features suggestive of a knuckle-walking ancestor. This suggests either parallel evolution of a rigid midfoot for terrestrial locomotion, or the rapid loss of any trace of knuckle-walking ancestry in the *Ardipithecus* upper limb. Exploring these two scenarios in depth is outside the scope of this dissertation, so I will assume both to be possibilities for now.

6.2.2 *Australopithecus afarensis*, the Burtele foot, and the Laetoli footprints

The first *Australopithecus* remains appear in the fossil record of East Africa roughly at 4.2 Ma, shortly after *Ar. ramidus* (White et al., 2006). However, very little diagnostic pedal material shows up until 3.4-3.2 Ma, with a large array of mostly unassociated foot bones recovered from sites in the Hadar formation (Johanson et al., 1982; Latimer et al., 1982). Much ink has been spilled over the terrestrial *versus* arboreal affinities of this material, so I will attempt to restrict the following discussion to the most salient points. First, the hallucal abductability of this species is hotly debated, largely due to the limited, fragmentary specimens preserving

interpretable first tarsometatarsal joint morphology. Different researchers have interpreted this morphology as indicating minor amounts of abductability (Stern and Susman, 1983; Berillon, 1999), or a fully adducted human-like first digit (Latimer and Lovejoy, 1990b). Recently, Proctor et al. (2008; Proctor, 2010) conducted a 3-D geometric morphometric analysis of the proximal articular surface of the hallux and found *Au. afarensis* specimens to fall intermediate between humans and African apes. This result strongly suggests a first tarsometatarsal joint that was at least somewhat mobile in *Au. afarensis*, and therefore not fully human-like. If this is the case, then this species likely lacked a pronounced longitudinal arch, because hallucal mobility would reduce arch functionality. However, Ward et al. (2011) argue that the torsion of a fourth metatarsal specimen (AL 333-160) attributed to *Au. afarensis* is indicative of human-like transverse and longitudinal arches, although reanalyses of this specimen in several other studies find torsion to be an ambiguous indicator of foot arching (Mitchell et al., 2012; Drapeau and Harmon, 2013). Therefore, until more diagnostic first tarsometatarsal joint morphology is recovered, I will assume that *Au. afarensis* had a slightly abductable hallux, and therefore likely lacked a human-like arching system.

DeSilva (2010) and Ward et al. (2011) have argued that preserved cuboid-metatarsal joint articular surface morphology attributed to *Au. afarensis* is human-like, and therefore consistent with midfoot rigidity. However, as this dissertation has demonstrated, the human lateral midfoot is far from rigid, at least in comparison to that of chimpanzees. Although I did not quantify cuboid-metatarsal joint motion in humans specifically, Lundgren et al. (2008) measured an average of 13° of sagittal plane motion between the fifth metatarsal and the cuboid in humans during normal walking using bone pin-mounted markers. This is greater than the sagittal plane range of motion that I measured for the whole lateral midfoot in chimpanzees during bipedal walking (~10°), suggesting that humans actually have more mobile cuboid-metatarsal joints than chimpanzees *in vivo*. Therefore, cuboid-metatarsal joint morphology should not necessarily be assumed to provide a good measure of lateral midfoot stiffness between species. Therefore, this feature is not necessarily diagnostic of the evolution of greater midfoot rigidity in *Au. afarensis*.

With regard to its pedal digits, *Au. afarensis* possesses relatively long, curved phalanges, that are suggestive of some use in arboreal support grasping (Stern and Susman, 1983; Richmond, 2007). However, the heads of its metatarsals are domed in a manner to suggest propulsive push-off with highly dorsiflexed MTPJs during bipedal locomotion (Stern and Susman, 1983; Latimer and Lovejoy, 1990a). This is solid evidence that *Au. afarensis* was able to generate greater propulsive force at push-off than chimpanzees (although, perhaps still without the benefit of a windlass mechanism, depending on the presence of a longitudinal arch). However, proximal phalangeal base canting in *Au. afarensis* is intermediate between that of humans and chimpanzees (Duncan et al., 1994; Griffin et al., 2010a), and the dorsal surfaces of its metatarsal heads are relatively narrow (Susman et al., 1984), both of which indicate this species still lacked fully modern forefoot mechanics.

With regard to evidence of arboreal proficiency, *Au. afarensis* ankle morphology is somewhat ambiguous. Although the overall talar trochlea geometry is human-like (Latimer et al., 1987; DeSilva, 2009), joint articular length and curvature suggests a greater range of motion than that present in humans (Stern and Susman, 1983; Latimer et al., 1987). Additionally, Venkataraman et al. (2013) have demonstrated that chimpanzee-like talocrural joint morphology is not necessary to climb with ankle dorsiflexion postures like those of chimpanzees. Subtalar joint morphology is again ambiguous, with different authors finding its posterior facet curvature to be similar (Deloison, 1985; Stern, 2000) or different (Latimer and Lovejoy, 1989; Prang,

2016) to that of humans. A chimpanzee-like subtalar joint mobility should not be necessary, however, to adopt the subtalar postures used by chimpanzees during climbing. Chimpanzees invert their feet when climbing, but only to a moderate degree ($\sim 10^\circ$) that is well within the range of motion that has been measured for modern humans (Grimston et al., 1993; Menadue et al., 2006). Therefore, a human-like subtalar joint range of motion in *Au. afarensis* would still enable chimpanzee-like climbing postures.

The full sum of evidence from *Au. afarensis* pedal remains suggests a foot fully capable of reasonably proficient climbing, as well as a moderately powerful push-off during terrestrial bipedalism. Although *Au. afarensis* was probably still capable of arboreal and terrestrial locomotion, adaptations of the foot suggest that this species relied more on terrestrial substrates for travel than chimpanzees. This continues a trajectory in hominin evolution from a more chimpanzee-like foot in *Ar. ramidus*, to a more human-like foot in *Au. afarensis*, albeit one that retained some specialization for arboreal locomotion. However, two other discoveries from the middle Pliocene that temporally overlap with *Au. afarensis* complicate this trajectory: the Burtele foot specimen, and the Laetoli footprints.

Although contemporaneous with *Au. afarensis* at 3.4 My old, the Burtele foot (BRT-VP-2/73) has been described as belonging to a hominin with dramatically different bipedal gait mechanics (Haile-Selassie et al., 2012). This argument is based on its first metatarsal, which displays torsion and proximal articular surface curvature indicative of an opposable and widely abducent hallux. Proportions of other metatarsals preserved for this specimen tend to indicate a closer resemblance to gorillas than modern humans. Nevertheless, Haile-Selassie et al. (2012) insist that this foot belonged to a biped largely on the basis of dorsal doming of its lateral metatarsal heads, and dorsal canting of the proximal phalanges. They suggest that this hominin walked with a bipedal gait similar to that of *Ar. ramidus*, indicating diversity in bipedal gait types among hominins in the mid-Pliocene. If their assessment of dorsal doming is true, the Burtele foot likely did belong to a biped that retained significant arboreal proficiency. However, they provide no metric proof of doming in these specimens, and the presence of this feature is ambiguous in the images that they provide. Additionally, humans have been found to display substantial overlap with African apes in proximal phalangeal base canting, so this feature is not truly diagnostic of bipedalism (Duncan et al., 1994; Griffin and Richmond, 2010). Therefore, until a more rigorous quantification of doming is provided, the bipedality of the species represented by this specimen should be considered uncertain.

The Laetoli footprints, although most commonly argued to have been made by *Au. afarensis* (Stern and Susman, 1983; White and Suwa, 1987; Crompton et al., 2012), are also argued to have been produced by an as yet unidentified bipedal hominin with more human-like foot morphology and mechanics (Tuttle, 1981; Harcourt-Smith and Aiello, 2004). The latter arguments revolve around features such as the long pedal phalanges and robust navicular tuberosity of *Au. afarensis*, which these authors believe are inconsistent with what they view as the modern human-like prints. In Chapter 5 I discuss the G-1 Laetoli footprint trail in the context of human and chimpanzee plantar pressure distributions, and suggest several aspects of these prints that are qualitatively consistent with a print-maker using foot mechanics intermediate between these species: A moderate medial midfoot impression, greater depth across the forefoot lateral to medial from metatarsal heads 5 to 2, a shallow impression for the first metatarsal head, and a deep impression for the first toe (based off average G-1 print description in Crompton et al., 2012). Given that *Au. afarensis* likely possessed a slightly abducent hallux, and the first toe impression in the G1 footprints is slightly divergent from the others (Deloison, 1991; Bennett et

al., 2009), I interpret these footprints and their relative depth distributions to be consistent with *Au. afarensis* foot mechanics.

6.2.3 *Australopithecus sediba* and the South African hominins

As discussed in Chapter 1, most of the fossil hominin foot specimens from the Pliocene of South Africa are undated and unassociated, and therefore difficult to discuss in the broader context of human foot evolution. An exception, however, are the pedal remains attributed to StW 573, the so-called ‘Little Foot’ specimen, which could be as old as 3.8 My (Granger et al., 2015; but see Pickering and Kramers, 2010). Although a relatively complete foot has been described for this specimen (Clarke and Tobias, 1995), metrical analyses have only been conducted on the first tarsometatarsal joint, and these have yielded conflicting results. Whereas several multivariate studies of the medial cuneiform have suggested it to be human-like (Harcourt-Smith and Aiello, 2004; Kidd and Oxnard, 2005), one study of the proximal first metatarsal base found its morphology to be intermediate between that of humans and chimpanzees (Proctor, 2010). Therefore, more of the pedal remains of this specimen must be analyzed before a reliable overall assessment of foot morphology can be made.

Au. sediba is the only other securely dated fossil hominin for which associated pedal remains representing a significant amount of the foot skeleton have been found. At 1.98 My old, the MH2 specimen preserves a surprisingly slender, chimpanzee-like calcaneus (Zipfel et al., 2011; Prang, 2015), which is distinct from the more robust calcaneus of *Au. afarensis* (Latimer and Lovejoy, 1989). It also lacks a lateral plantar process, and its posterior subtalar facet exhibits a large radius of curvature, which led DeSilva et al. (2013) to conclude that *Au. sediba* would have walked with a bipedal gait similar to that exhibited by modern humans who have been diagnosed as ‘hyper-pronators’. This condition is described as being characterized by high rearfoot eversion, resulting in midfoot laxity and exaggerated tibial rotation. Interestingly, DeSilva et al. (2013) disregard extant African apes as a useful model for reconstructing *Au. sediba* foot mechanics, due to their contention that these species maintain inverted foot postures during stance. As indicated by both the pressure and kinematic data collected in this dissertation, this is a faulty assumption. I argue that chimpanzees make a good model for understanding *Au. sediba* rearfoot mechanics due to the remarkably similar calcaneal morphology shared by these species (Zipfel et al., 2011; DeSilva et al., 2013; Prang, 2015).

If one can take shared morphology as an indicator of similar function, then we can reconstruct *Au. sediba* as contacting the ground with a highly inverted rearfoot, which was then rapidly everted beyond subtalar neutral position. However, this would not necessarily cause the exaggerated tibial rotation suggested by DeSilva et al. (2013), because the chimpanzee and human subjects in my study exhibited nearly identical patterns and magnitudes of leg-rearfoot transverse plane rotation. Therefore, we need not assume the cascade of kinematic events in the lower limb suggested by DeSilva et al.’s model. The degree to which high calcaneal eversion may have influenced more distal foot kinematics is difficult to determine, however. Although originally thought to be a strong determinant of midfoot hypermobility and arch collapse (Elftman, 1960; Close et al., 1967; Phillips and Phillips, 1983; Blackwood et al., 2005), more recent research indicates that rearfoot eversion is not always a strong predictor of forefoot kinematics (Lundberg and Svensson, 1993; Stacoff et al., 2000; Nigg, 2001; Hunt and Smith, 2004; Twomey et al., 2010). Therefore, it should not be assumed that the rearfoot kinematics of *Au. sediba* would have compromised the function of the rest of the foot.

Therefore, in spite of its chimpanzee-like rearfoot, *Au. sediba* may have still been capable of walking with a human-like gait. It is difficult to interpret the biomechanical consequences of the absence of a lateral plantar process in *Au. sediba*. African apes lack this morphology, and yet do not suffer any apparent ill consequences during terrestrial locomotion. They do not require any additional osteological buttressing on the lateral side of the foot, as some have suggested (Lewis, 1983; Gebo, 1992), but maintain a slightly everted joint with the peroneal trochlea well clear of the ground (see Chapter 4, Figure 4.6). Without a lateral plantar process, chimpanzees and other African apes likely maintain weight support on the slender calcaneus medially, and soft tissue laterally. In dissection of a chimpanzee foot, I found a thick sub-calcaneal fat pad on the lateral side of the heel, and beneath this extensive intrinsic foot musculature. The same condition may have been true in *Au. sediba*, which would have allowed it to maintain balance and resist calcaneal strain during foot strike. If so, the possession of extensive intrinsic foot musculature could be related to an adaptation for enhanced pedal grasping during arboreal locomotion. The evidence for high subtalar mobility in *Au. sediba* supports this scenario, suggesting that this hominin might have engaged in considerable arboreal locomotion, but without necessarily suffering any major detriment to its bipedal locomotor capabilities.

6.2.4 Fossil Record Summary

This brief tour of early fossil hominin foot evolution supports a scenario in which the earliest hominins possessed feet similar to those of living chimpanzees. These feet would have been well-suited for both proficient arboreal locomotion and facultative bipedalism. By the middle Pliocene the hominin foot would have become further specialized to deliver greater propulsive force during push-off in bipedal locomotion. This adaptation would have come at the expense of pedal grasping capabilities during arboreal locomotion, although the foot would have retained a number of adaptations to enable climbing proficiency. It is possible that there was considerable variation in foot morphology, and therefore variation in bipedal gait mechanics among the hominin species living during this time period, although this notion requires more fossil evidence to be substantiated. By the early Pleistocene, hominin specimens attributed to *Homo* had achieved nearly human-like foot morphology¹¹ (Day and Napier, 1964; Bennett et al., 2009; Pontzer et al., 2010; Jungers et al., 2015), indicating greatly reduced reliance on arboreal locomotion. However, the nearly contemporary *Au. sediba* possessed a foot indicative of considerably arboreality, providing support for the notion of variation in bipedal gait mechanics among hominin species during at this particular point in time. This species also suggests the possibility of evolutionary reversal among early hominins, from a trajectory away from arboreal locomotion, back to arboreal specialization. However, by the middle Pleistocene, any trace of chimpanzee-like pedal morphology had disappeared, and hominins had achieved an essentially modern human foot (Trinkaus, 1983; Harcourt-Smith and Aiello, 2004; Pablos et al., 2015).

¹¹ A notable counterpoint to this generalization is the nonhuman ape-like talus of the OH 8 foot specimen that is usually attributed to *Homo habilis* (Day and Napier, 1964). Multivariate analyses of this talus have consistently placed it outside the range of variation of modern humans and even earlier hominins such as australopithecines (e.g., Kidd et al., 1996; Harcourt-Smith and Aiello, 2004). However, no study to my knowledge has suggested a convincing functional consequence of this primitive talar shape morphology. Lacking an adequate framework to interpret variation in talar shape, I will refrain from discussing the functional implications of this primitive aspect of the OH 8 specimen.

Two fossil hominin species that do not fit snugly into this picture are the Indonesian hominin *H. floresiensis*, and the recently described South African hominin *H. naledi* (Berger et al., 2015). *H. floresiensis* is a chronologically recent species whose phylogenetic position is uncertain due to dramatic morphological divergence from other hominin species, most likely as a consequence of its isolation on the island of Flores (Brown et al., 2004; Morwood et al., 2005). The forefoot of this species is remarkably long, with primitive midfoot morphology, but a fully adducted hallux (Jungers et al., 2009). Lacking obvious affinity to chimpanzee pedal morphology, I will refrain from commenting on this species except to say that it almost certainly used foot mechanics distinct from those of both modern humans *and* chimpanzees. The morphological affinities of the *H. naledi* foot are much more straightforward; it preserves a completely associated foot that resembles that of a modern humans in nearly every manner that has been described, indicating human-like biomechanics (Harcourt-Smith et al., 2015). However, the phylogenetic position and age of this species are still unknown, and thus its overall implications for hominin foot evolution are unclear.

6.3 Future Directions

6.3.1 Joint Morphology

Having collected detailed 3-D kinematic data from the intrinsic foot joint of humans and chimpanzees, I can investigate the degree to which the differences in joint function between species reflect morphological differences. In my investigation of human and chimpanzee kinematics, I maintained as many factors constant as possible, including substrate type, speed of locomotion, and gait type. By doing so, I can hypothesize that differences in joint kinematics between species are due to anatomical differences that are the product of adaptive evolution. I can test these hypotheses in interspecies morphological investigations. Significant interspecies differences in joint kinematics that mirror significant differences in joint morphology will indicate true form-function relationships. These relationships provide insight into the historical circumstances surrounding the evolution of a given trait. They can also be used to inform the investigation of other organisms, including extinct organisms in which relevant morphology has been preserved in fossils.

Although this sequence of steps for investigating form-function relationships is simple and intuitive, it has rarely been executed carefully in investigations of hominoid foot morphology. Among the handful of studies to have used experimentally collected biomechanical data to develop and test hypotheses related to pedal morphology (Elftman and Manter, 1935a; b; Wunderlich, 1999; DeSilva, 2010; Griffin et al., 2010a), none has been able to capture marker-based 3-D kinematic data for the intrinsic foot joints. These data lend themselves directly to morphological hypotheses, because aspects of joint shape and curvature should reflect motion and loading patterns *in vivo* (MacConaill, 1946, 1966; Inman, 1976; Hamrick, 1996). Among the joints investigated in this dissertation, several make excellent candidates to test hypotheses about form-function relationships. I have already begun analysis on one group of candidates, the MTPJs, in collaboration with Peter Fernández (PhD candidate, IDPAS, Stony Brook University).

In this dissertation I uncovered significant differences in peak MTPJ dorsiflexion angles across all five rays in humans and chimpanzees during bipedal locomotion (see Chapter 4). I also uncovered significant differences between the pedal rays within species. Finally, among chimpanzee subjects, differences in peak dorsiflexion angles between rays were generally reflected in differences in peak pressures under their respective metatarsal heads (see Chapter 5).

These results allow me to hypothesize that humans and chimpanzees will exhibit significant differences in the shapes of the articulating surfaces at their metatarsophalangeal joints, and in particular, in features that have been proposed to be related to peak dorsiflexion angles at push-off (e.g., metatarsal head dorsal doming, dorsal canting of phalangeal bases). Additionally, I hypothesize that MTPJ articular surface morphology will reflect between ray MTPJ dorsiflexion angles within species.

Preliminary analyses of 3-D geometric morphometric quantification of metatarsal head shape support both hypotheses. In a PCA (principal component analysis) of shape variation, the metatarsal heads of humans and chimpanzees show no overlap across the first PC (principal component), which captures changes in shape related to dorsal versus plantar doming of the articular surface. Along the second PC, metatarsal heads are separated from one another within both species from rays 2-5, with metatarsal heads exhibiting diminishing relative widths moving laterally across the forefoot. These patterns mirror exactly the patterns of peak MTPJ dorsiflexion across digits 2-5 measured in humans and chimpanzees during terrestrial locomotion (see Fig. 4.5). Due to the use of several landmarks specific to the shape of the first metatarsal head, we have not been able to compare it to the other metatarsal heads yet. However, we are still working on this aspect of the analysis, as well as a statistical approach to integrating our morphological, kinematic, and pedobarographic datasets.

This research is still ongoing, but I can begin to form hypotheses about articular surface morphology in other joints investigated in this dissertation. One example is the subtalar joint, for which I quantified differences in both active and passive ranges of motion in humans and chimpanzees. From my results, I hypothesize that chimpanzee subtalar joint morphology will reflect an ability to assume more everted joint postures than that of humans while being loaded in locomotion. This functional difference may reflect differences in congruity of talar and calcaneal joints surfaces, which may allow greater lateral excursion of the talus on the stationary calcaneus (as proposed by Rose, 1986).

6.3.2 Plantar Pressure Distributions

There are several additional directions to take the investigation of plantar pressure and pedal joint kinematics that was carried out in Chapter 5 of this dissertation. In this chapter, I only investigated chimpanzee pressure distributions during bipedal locomotion; however pressure patterns may be different when subjects walk using quadrupedal gaits. The data collected by Wunderlich (1999) and Vereecke et al. (2003) suggest that *Pan* species may distribute a greater proportion of pressure under their lateral midfoot and forefoot regions during quadrupedal locomotion than during bipedal locomotion. Significant differences between gaits in pressure distributions for the chimpanzee subjects in this study would be an interesting result, considering that these subjects exhibit nearly identical midfoot kinematics during both terrestrial gaits. I have collected kinematic and plantar pressure data from chimpanzee subjects during quadrupedal walking, so this question is ready to be investigated.

Another possibility for the kinematic and pressure data collected in this dissertation would be to carry out more advanced statistical modeling such that the latter variable can be used to predict the former. Plantar pressure data are easier to obtain from non-human primates than detailed 3-D kinematic data, as they do not necessitate a controlled laboratory setting to acquire. Therefore, future investigations collecting pressure data from captive settings such as zoos may wish to use these data to reconstruct intrinsic foot kinematics in a more rigorous manner than has been previously carried out. With the data collected in this dissertation, I may be able to

construct linear mixed effects models that enable the prediction of kinematic variables, such as midfoot dorsiflexion or forefoot eversion, from pressure distribution patterns. Although I have not yet begun to explore this modeling approach, it is an intriguing possibility that would vastly increase the applicability of this dataset to other investigations of non-human primate plantar pressure distributions.

Finally, by reaching out to other investigators that have collected African ape plantar pressure data, I may be able to combine the datasets from these studies to investigate questions about interspecies differences in pressure distributions, as well as differences across substrates. I have previously discussed differences in the pressure data collected in this study with those collected by Vereecke et al (2003) from bonobos. However, actually combining datasets could allow for direct quantitative comparison of interspecies differences. Wunderlich (1999) collected plantar pressure data from chimpanzees during locomotion on both terrestrial *and* arboreal substrates. She used a flexible pressure-sensing pad, which allowed her to measure plantar pressure distribution in her subjects while they were walking on horizontal pole supports and climbing vertical pole supports. Combining her pressure data with my kinematic data from these locomotor modes would provide further insight into the function of the chimpanzee foot during arboreal locomotion.

6.3.3 Musculoskeletal Modeling

Musculoskeletal modeling enables the integration of different types of experimental data to investigate various aspects of locomotor performance in dynamic simulations. Recent studies have used musculoskeletal models of human feet to test questions related to intrinsic foot muscle activity (Kelly et al., 2014a; b), plantar aponeurosis function (Caravaggi et al., 2009, 2010), and the detrimental consequences of flatfoot deformity (Spratley et al., 2013). O'Neill et al. (2013) recently developed a 3-D musculoskeletal model of the chimpanzee hind limb that has thus far been used to quantify bipedal joint kinematics (O'Neill et al., 2015) and to investigate elastic properties of the fascia lata (Eng et al., 2015). However, this model currently treats the rearfoot and midfoot as rigid segments, and models the ankle joint complex as a hinge. The data collected in this dissertation can be used to create a more accurate representation of foot joint motion for this model, which can then be used to investigate a number of different questions concerning extrinsic foot muscle function and joint mechanics during locomotion.

One interesting question that I can address with a model-based approach is the function of the peroneus longus muscle during chimpanzee locomotion. Stern and Susman (1983) found this muscle's activity to be highly variable when chimpanzees walked on the ground, and consequently suggested it was used primarily when the foot is inverted on arboreal substrates. Lovejoy et al. (2009a) argued that this muscle serves primarily as a hallucal adductor in chimpanzees, and thus is not significantly involved in terrestrial locomotion. However, Larson et al. (2014) measured human-like peroneus longus activity during bipedal locomotion in the chimpanzees that were used as subjects in this study, suggesting that it may contribute to forward propulsion during a step. Pressure data from this dissertation indicate a human-like forefoot roll-off pattern, further supporting the notion of a human-like role for the peroneus longus in chimpanzees. By integrating kinematic data from the intrinsic foot joints collected in this dissertation with muscle activation data collected by Larson et al. (2014), I can use the musculoskeletal model developed by O'Neill et al. (2013) to determine the extent to which the chimpanzee peroneus longus can contribute to forward propulsion during bipedal locomotion. Investigating this question will allow me to test previous notions about the chimpanzee peroneus

longus (Stern and Susman, 1983; Lovejoy et al., 2009a), as well as inform interpretations of the chimpanzee-like peroneal trochlea morphology in *Au. afarensis* (Stern and Susman, 1983; Latimer and Lovejoy, 1989) and *Au. sediba* (Zipfel et al., 2011).

I can also use the O'Neill et al.'s (2013) model to explore the relationship between MTPJ kinematics and articular surface morphology in humans and chimpanzees. Most comparative studies of MTPJ morphology assume that in chimpanzees and other non-human apes, peak dorsiflexion angles during push-off are limited by joint anatomy that is improperly suited to withstand high forces at high dorsiflexion angles (e.g., Stern and Susman, 1983; Susman and Brain, 1988; Latimer and Lovejoy, 1990a; Griffin et al., 2010a; Fernández et al., 2015). However, no study has actually quantified joint moments in the chimpanzee MTPJs during this phase of stance, and hence, the extent to which they are actually exposed to dangerously high forces is unknown. Human and chimpanzee MTPJ dorsiflexion may simply be the result of proximal hind limb joint kinematics (e.g., ankle plantarflexion), in which case differences between species may reflect passive processes rather than mechanical constraints. To test this possibility, I can use an inverse dynamics approach to determine MTPJ moments in humans and chimpanzees during bipedal locomotion. By taking a model-based approach, I can non-dimensionalize the moments, and thereby determine whether they are similar in both species. In the eventuality that these moments are lower in chimpanzees, I would conclude that joint morphology does not necessarily reflect a morphological constraint.

One final question that could be explored through a model-based approach is the effect of midfoot mobility on ankle plantarflexor power generation during push-off. It is generally assumed that the chimpanzee midtarsal break diminishes the foot's ability to function as a torque converting lever during push-off in terrestrial locomotion (Elftman and Manter, 1935a; Bojsen-Møller, 1979; Susman, 1983; Lovejoy et al., 2009a). The mechanical basis of this diminished function, however, is rarely specified. One consequence of greater midfoot mobility could be reduced efficiency of the plantarflexors, at least relative to that in humans, by reducing the gearing ratio of these muscles during push-off. If midfoot dorsiflexion results in a more proximally located center of contact of the foot, the ankle plantarflexors will be less effective at converting ankle power into propulsive force (Carrier et al., 1994). I can use the kinematic data collected in this dissertation to determine the extent to which chimpanzee plantarflexor performance during push-off is affected by midfoot joint mobility. This investigation will provide important insight into not just chimpanzee foot function, but the adaptive advantages of modern human foot anatomy on locomotor performance. In doing so, it will illuminate the processes that have favored the evolution of a longitudinally arched foot in hominins over a foot with prehensile capabilities.

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