October 2019

The Roles of Morphology and Posture on Gait Mechanics

Russell T. Johnson
University of Massachusetts Amherst

Recommended Citation

Johnson, Russell T., "The Roles of Morphology and Posture on Gait Mechanics" (2019). *Doctoral Dissertations*. 1683.
https://scholarworks.umass.edu/dissertations_2/1683

THE ROLES OF MORPHOLOGY AND POSTURE ON GAIT MECHANICS

A Dissertation Presented

by

RUSSELL T. JOHNSON

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

September 2019

Department of Kinesiology

THE ROLES OF MORPHOLOGY AND POSTURE ON GAIT MECHANICS

A Dissertation Presented

by

RUSSELL T. JOHNSON

Approved as to style and content by:

Brian R. Umberger, Chair

Katherine A. Boyer, Member

Frank Sup, Outside Member

Matthew C. O'Neill, Member

Jane A. Kent, Department Head
Kinesiology

DEDICATION

I dedicate this work to my parents for their love and support.

ACKNOWLEDGEMENTS

I have many people to thank who have guided, motivated, and supported me throughout my graduate school career.

I want to thank my dissertation committee. My advisor, Brian, your mentorship throughout my entire graduate school career has been so valuable to me and has made me the scientist I am today. You have consistently set an example of how to be a strong researcher and leader. Matt, I am thankful for our many conversations about chimpanzee gait. You have been a great resource as I learn more and more about evolutionary biomechanics. Kath, thank you for your mentorship throughout my graduate school career. I am thankful to have your perspective on many of the clinical applications of gait research. Frank, you have been a fantastic resource and have helped me become a better scientist through our many meetings and discussions.

Thank you to my fellow kinesiology graduate students, who have motivated and encouraged me throughout this journey. Ryan, Carl, and Jocelyn: you have been people I have consistently looked up to throughout graduate school and have been tremendous friends and running partners. Thank you to all the kinesiology faculty for always having a door open so that us graduate students can continuously learn from all of you. Thank you to the kinesiology staff for their support.

I want to thank my friends from my collegiate cross-country team at Springfield College for being entertaining, humorous, and helping me stay relaxed throughout the stress of life. I want to thank my family for always offering me support, in any way they could. Finally, I want to thank Alyssa for her support and for our many great adventures.

ABSTRACT

THE ROLES OF MORPHOLOGY AND POSTURE ON GAIT MECHANICS

SEPTEMBER 2019

RUSSELL T. JOHNSON, B.S., SPRINGFIELD COLLEGE
M.S., UNIVERSITY OF MASSACHUSETTS AMHERST
Ph.D. UNIVERSITY OF MASSACHUSETTS AMHERST
Directed by: Dr. Brian R. Umberger

Humans walk with an upright posture with extended limbs during stance and a double-peaked vertical ground reaction force. Our closest living relatives, chimpanzees, sometimes walk bipedally but do so with a flexed, abducted hind limb. Researchers have compared the bipedal gait of humans and chimpanzees in an effort to better understand the evolution of habitual bipedalism in humans. In addition, previous researchers have used the paradigm of humans walking with a crouched, chimpanzee-like gait pattern to try to infer how extinct human ancestors walked. However, it is not clear if the way humans perform this crouched posture gait would be similar to the way a species that is adapted to walk with a crouched posture would walk. A better understanding of the relationship between the structure and function of the musculoskeletal system during gait can help researchers better interpret the evolution of human bipedalism. The purpose of this dissertation was to investigate the impact of morphology and posture on gait mechanics in humans and chimpanzees. Specifically, we investigated how healthy, adult human subjects perform different types of crouched walking and the degree to which human crouched posture walking converges to that of bipedal chimpanzee gait. The results from the first study of this dissertation indicate that crouched posture human gait does become more similar to chimpanzee gait, with more chimpanzee-like hip and knee flexion patterns. One important finding of this first study was that the hip was more abducted in the human crouched posture conditions, suggesting that the crouched posture itself influences the hip abduction angles measured in chimpanzee bipedal gait. However, differences between species persisted as the humans walking with a crouched posture did not have a double-peaked ground reaction force or as much pelvis transverse plane rotation. In the second study, we investigated how the major muscle groups in the lower limbs induce center of mass accelerations across different human postures. We also compared the function of muscles in human crouched posture walking to that of chimpanzee walking to try to better understand the role of morphology on muscle function during gait. Our results showed that when humans walk with a crouched posture, they rely on their gluteus maximus and vastus group to a greater extent to produce vertical accelerations than when humans walk with a normal posture. The soleus and gastrocnemius seem to have a trade-off in function between human crouched posture walking and normal walking, with the gastrocnemius inducing greater accelerations in the normal posture and the soleus inducing greater accelerations in the crouched postures. When comparing between species, we found that the chimpanzees rely less on their vastus muscle group in inducing vertical and posterior accelerations than humans walking with a crouched posture. Chimpanzees instead rely more heavily on their gluteus maximus to produce vertical accelerations than the human subjects. The distinct musculoskeletal structure between humans and chimpanzees, such as differences in

pelvis shape and muscle moment arms, likely play a key role in determining the function of muscles throughout the gait cycle. The differences between humans and chimpanzees that persist when humans walk with a crouched posture in gait kinematics, ground reaction forces, and muscle function suggest that human crouched posture walking does not approximate a gait pattern of a chimpanzee and therefore should be used with caution when trying to understand the evolution of human bipedalism.

TABLE OF CONTENTS

Page

LIST OF TABLES

Table Page

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

1.1 Introduction

Upright bipedal walking is a distinguishing feature of human evolution (Lovejoy, 1988). While birds and other primates walk on two legs (Alexander, 2004; Gatesy & Biewener, 1991), human gait uniquely features an upright posture, extended legs during stance, and a distinctly two-peaked vertical ground reaction force (GRF) (Alexander, 2004; Foster, Raichlen, & Pontzer, 2013; Grasso, Zago, & Lacquaniti, 2000). Chimpanzees, our closest living relatives, sometimes walk bipedally but do so with different pelvis motion, a flexed and abducted hind limb posture, and different GRF profiles (Elftman, 1944; Jenkins, 1972; O'Neill et al., 2015; Pontzer, Raichlen, & Rodman, 2014; Yaguramaki, Nichizawa, Adachi, & Endo, 1995). Thus, while humans and chimpanzees are closely related species, there are well documented differences in joint kinematics, center of mass motion, GRFs, and muscle stresses exerted during locomotion (Demes, Thompson, O'Neill, & Umberger, 2015; Li, Crompton, Alexander, Gunther, & Wang, 1996; O'Neill et al., 2015; Pontzer et al., 2014; Thorpe, Crompton, & Wang, 2004). These broad differences between humans and chimpanzees seen during bipedal walking are a good representation of how differences in musculoskeletal structure may influence gait mechanics. Understanding how morphology impacts gait mechanics allow us to understand both why humans walk so differently from other primates and the rest of the animal kingdom. A better understanding of the structure-function relationship within the locomotor system will provide critical information for researchers studying the evolution of hominin bipedalism.

Since the last common ancestor (LCA) of humans and chimpanzees, the hominin lineage has been defined by habitual bipedalism. However, there has been debate among researchers as to how some hominins, such as the Australopithecus or Ardipithecus species, would have walked (Crompton, Yu, Weijie, Gunther, & Savage, 1998; Lovejoy, 2005; Stern Jr. & Susman, 1983; Stern Jr., 1999; Ward, 2002). How earlier hominins and the LCA would have walked remains even more unclear in part because there is missing data in the fossil record. The interpretation of how extinct species would have walked is vitally dependent upon the fossil record of these species as well as a judgement of how the morphological features of the fossils interact to influence gait mechanics. A primary focus of the debate has been on when our hominin ancestors began to walk upright like modern humans, rather than on a flexed-limb, like chimpanzees. For example, some researchers have disagreed about how Australopithecus afarensis would have walked (upright or crouched) (Lovejoy & McCollum, 2010; Stern Jr., 1999), despite having access to the same fossil record data. Therefore, it is important to better understand how musculoskeletal features impact the gait mechanics in humans and other primates, which can impact how others interpret the fossil record of our human ancestors. This understanding is important not only for interpreting the existing fossil record, but also as more fossils are discovered from even earlier eras of the hominin lineage.

As one means to gain insight on how extinct hominins would have walked, modern investigations have often focused on comparing humans with other extant primates, such as chimpanzees and macaques (Ogihara, Makishima, & Nakatsukasa, 2010; Pontzer, Raichlen, & Sockol, 2009; Sockol, Raichlen, & Pontzer, 2007). While there is uncertainty as to whether chimpanzees or macaques are a better model of walking in the LCA, recent evidence suggests that the gait mechanics of these two primates are remarkably similar to each other (O'Neill et al., 2018). For this dissertation, we will focus on comparing humans and chimpanzees since chimpanzees are the closest living relatives of humans. The morphology of humans and chimpanzees are both distinct from the LCA, but understanding structure-function relations in the locomotor systems of chimpanzees and humans can yield important insight as to the functional significance of morphological features observed in fossil hominins.

1.2 The Influence of Morphology on Gait Mechanics

Morphology plays an essential role in shaping gait mechanics for chimpanzees and humans, as well as every other animal. Previous studies have proposed several different morphological features that may contribute to differences in gait biomechanics between humans and chimpanzees such as differences in the lumbar spine shape (Lovejoy, 2005) and pelvis shape (O'Neill, Demes, Larson, & Umberger, 2016). Unlike humans, chimpanzees have no lumbar lordosis which may prevent them from positioning their trunk vertically during locomotion (Lovejoy, 2005). This restriction in lumbar lordosis results in a center of mass location anterior to the hip joint (Sockol et al., 2007). In this case, since the center of mass is projected forward while chimpanzees walk bipedally, they may have to adopt a flexed limb posture during gait so that their base of support is underneath their center of mass (Lovejoy, 2005).

Another proposed mechanism that could account for the flexed limb posture chimpanzees adopt during gait is the shape of their pelvis, with some key differences between humans and chimpanzees in the length and orientation of the ischium, the orientation of the iliac blade, and the iliac blade height. The ischia of a chimpanzee are distally oriented, with elongated iliac blades aligned in the frontal plane, in contrast to the dorsally oriented human ischia. The shape of the chimpanzee pelvis reduces the ability of the hamstrings muscle group to produce an extensor moment when the leg is fully extended (Fleagle & Anapol, 1992). The hamstrings of a chimpanzee are in a better position to produce hip extension when the hip is flexed, which is a functional limb posture for tree climbing. Unlike chimpanzees, the hamstrings of a human are able to produce large extension moments when the leg is fully extended (Fleagle & Anapol, 1992). The function of the lesser gluteal muscles, which plays an important role in bipedal walking (Stern Jr. & Susman, 1981a), plays a different role in chimpanzee locomotion than it does in human locomotion (O'Neill et al., 2016). Recent induced acceleration analyses have demonstrated that the lesser gluteals of chimpanzees induce a forward and medially-directed acceleration of the center of mass during stance, while the lesser gluteals of humans induce an upward and medially-directed acceleration (O'Neill et al., 2016). While lumbar spine and pelvis shape may play a profound role in influencing the gait mechanics for humans and chimpanzees, it is difficult to disentangle the effects of morphology from the distinctly different postures these two species maintain during bipedal walking.

1.3 The Confounding Effects of Posture on Gait Mechanics

When analyzing animals with different habitual gait patterns, the influence of posture on preferred movement patterns needs to be considered. For this dissertation, posture will be defined as the general orientation of the trunk, pelvis, and lower/hind limbs during walking (e.g. upright vs crouched), while gait mechanics will refer more specifically to variables such as joint angles and GRFs that change over the time-course of the stride during walking. Broad changes in posture will affect the way an individual walks because individual body segments are dynamically coupled such that the orientation and motion of any one segment will have global effects on the movement of the whole body (Aminiaghdam, Rode, Muller, & Blickhan, 2017; Grasso et al., 2000). The linked-segment nature of the body means that the changing the orientation or motion at one segment or joint will often necessitate a change in how the other segments move while still achieving the objective, such as locomotion. Therefore, some of the interspecific differences in gait patterns could be explained by the upright posture in humans versus the crouched, flexed limb and forward-leaning trunk posture of chimpanzees during gait. Even simple differences in the orientation of one segment have previously been shown to impact the movement of the rest of the body. For example, a recent study showed that humans naturally adopt a more flexed leg position when walking with a forward leaning trunk (Aminiaghdam et al., 2017).

Previous studies in humans have elicited crouched limb walking by instructing their subjects to walk with a ‘bent-hip, bent-knee’ posture. While this terminology has been used in past literature, it ignores the changes that happen at the ankle and outside of the sagittal plane that occur when humans walk with these instructions. For this dissertation we will refer to this paradigm as crouched posture walking. Regardless of the description of the instructions, previous crouched posture walking studies have shown that both gait mechanics and energetics change in meaningful ways (Carey & Crompton, 2005; Foster et al., 2013; Grasso et al., 2000). Aside from documenting the obvious increase in sagittal plane hip and knee flexion and ankle dorsiflexion angles during stance (Foster et al., 2013), there are very few three-dimensional studies that examine the effect of crouched posture walking on the other degrees of freedom in the body. However, there is some evidence that the mechanics of human crouched posture walking are still distinct from chimpanzee bipedal gait. When humans are instructed to walk with a crouched posture, they tend to still maintain a vertically oriented trunk, while chimpanzees tend to have a more forward-leaning trunk during their natural bipedal gait (Foster et al., 2013; Pontzer et al., 2014). A consequence of this upright trunk angle in humans is that the GRF vector passes closer to the hip joint center of rotation in humans during crouched posture gait, while the GRF vector has a larger distance to the hip in chimpanzees during mid-stance (Foster et al., 2013; Sockol et al., 2007). This means that when humans walk with a crouched limb gait, they likely do not require the same degree of activation of muscles that contribute to hip and trunk extension as chimpanzees since the force vector passes closely to the hip joint center of rotation (Grasso et al., 2000). Therefore, it is reasonable to suggest that while some of the documented differences in gait mechanics between humans and chimpanzees (O'Neill et al., 2015) will be due to the differences in morphology, others could be due to the broad difference in posture between each species. For example, the difference in pelvis list motion between humans and chimpanzees could be due to either the morphological structure (differences in pelvis shape), or the general limb posture during stance (having a flexed limb posture impacts the frontal plane pelvis motion), or some combination of both morphology and posture.

When humans adopt new postures during gait the metabolic energy cost changes. The metabolic energy cost (including basal metabolic rate) is about 50% greater when humans adopt a crouched limb gait than in normal upright walking, and the net cost of transport (excluding basal metabolic rate) increases by about 1.7 times for similar speeds of walking (Carey & Crompton, 2005). The increase in metabolic energy expenditure during crouched limb gait seems to be due to an increase in the volume of muscle activated in the quadriceps muscle group during stance phase. The increase in activated muscle volume during crouched limb gait is due, at least in part, to a greater moment arm distance between the knee and the GRF vector during stance phase, requiring more muscle force to support body weight (Foster et al., 2013; Sockol et al., 2007; Steele, van der Krogt, Schwartz, & Delp, 2012).

Chimpanzees also consume more metabolic energy per unit of body weight when walking than humans, potentially reflecting some of the changes that are seen when humans adopt a crouched posture gait (Pontzer et al., 2009; Sockol et al., 2007). Part of this difference could be accounted for by a greater volume of muscle activated in chimpanzees during the stance phase in this flexed limb posture (Foster et al., 2013). Other explanations for this difference include the facts that chimpanzees have proportionally longer muscle fibers than humans (Thorpe, Crompton, Gunther, Ker, & McNeill Alexander, 1999) and a higher percentage of fast-twitch muscle fibers than humans (O'Neill, Umberger, Holowka, Larson, & Reiser, 2017). While these two factors may not directly impact gait mechanics, they may contribute to the greater metabolic energy cost chimpanzees experience during walking when compared with humans (Sockol et al., 2007; Taylor, Heglund, & Maloiy, 1982).

Although differences in posture are important to consider when comparing between humans and chimpanzees, broad differences in posture in humans can be observed within some clinical populations. For example, patients with cerebral palsy often walk with a crouched posture, in some ways mirroring the flexed limb posture used by chimpanzees (Wren, Rethlefsen, & Kay, 2005), which can lead to a greater metabolic cost, joint pain, and even changes in musculoskeletal structure over time (Jahnsen, Villien, Aamodt, Stanghelle, & Holm, 2004; Kerr Graham & Selber, 2003; J. Rose, Gamble, Medeiros, Burgos, & Haskell, 1989a). Furthermore, other differences related to general posture can occur in women who are pregnant with changes in both musculoskeletal structure and gait mechanics (McCrory, Chambers, Daftary, & Redfern, 2014; Segal et al., 2013). For instance, women who are pregnant often walk with greater lateral sway and anterior pelvic tilt when compared with control subjects (McCrory et al., 2014).

1.4 Purpose

There are some well documented kinematic and kinetic differences in the way humans and chimpanzees choose to walk (Jenkins, 1972; O'Neill et al., 2015). Humans tend to walk with an upright posture while chimpanzees tend to walk with a flexed, abducted hind limb when they are walking bipedally. Certainly, some of the observed differences in gait mechanics between humans and chimpanzees are a result of the differences in musculoskeletal structure, yet it is still unclear how specific morphological features affect the gait mechanics. Separately, some of the observed differences in gait mechanics could be due to the posture that each species maintains during bipedal gait. The purpose of this dissertation is to investigate how morphology and posture impact the preferred gait patterns and muscle function of humans and chimpanzees. Understanding how gait patterns depend upon morphology can help researchers further explain how the structure of the musculoskeletal system determines its function. In addition, identifying how posture influences gait mechanics in humans can help researchers discern how small changes in the motion or orientation of one or two segments impact the overall gait pattern and can be useful in several clinical settings.

1.5 Study 1: The roles of morphology and posture on gait patterns

It is likely that both morphology and posture influence preferred movement patterns during locomotion. Human posture during locomotion can be easily manipulated by giving instructions and feedback to participants, however it is much more difficult to test different walking postures in chimpanzees. While including a comparison of the gait mechanics of chimpanzees walking upright would be desirable, it is impractical. Therefore, investigating the effects of changes in posture on gait patterns can most easily be done with a human population. Manipulating posture in specific ways in a human population can give insight into how the orientation and movement at one segment can affect the movement of other segments in a dynamically-coupled system. These results will allow for the determination of what, if any, differences in walking patterns between humans and chimpanzees still exist when humans are instructed to walk with a similar posture to that of chimpanzees. The effects of morphology on gait mechanics will be tested after giving humans instructions to walk in a manner similar to chimpanzees. A series of specific instructions will be given sequentially: the first two sets of instructions will address major differences between human and chimpanzee gait in the sagittal plane, while the last instruction will address one of the primary differences in the frontal plane. Replicating the overall gait mechanics of chimpanzees as closely as possible can allow for the identification of any differences in muscle function due primarily to morphology. These methods will allow for the investigation of how species with different muscle and skeletal structures accomplish a similar movement task.

There is a need to further understand the selective advantages of maintaining an upright posture versus a crouched, flexed limb posture during gait. Comparing movement patterns between two species, such as humans and chimpanzees, may give insight into how movement patterns are influenced by morphology and how these unique patterns have evolved. The focus of this dissertation will be to determine how differences in morphology and posture affect the preferred gait patterns in humans and chimpanzees.

Aim 1: The first aim is to determine the degree to which human kinematics and GRFs converge to those of chimpanzees as humans change their posture during gait. We will compare normal walking, crouched-limb (CL), crouched-limb flexed-trunk (CLFT), and a condition with specific instructions to imitate the pelvis tilt kinematics of a chimpanzee while maintaining the CLFT posture (IMIT). We will specifically determine how the human gait mechanics compare with chimpanzees for these four conditions at two different speeds.

Hypothesis 1.1: The joint kinematics from the IMIT condition will be most similar to the chimpanzee data. In addition, the joint kinematics from the CLFT condition will be more similar to the chimpanzee data than the CL condition.

Hypothesis 1.2: The GRFs from the IMIT condition will be the most similar to the chimpanzee data. In addition, the GRFs from the CLFT condition will be more similar to the chimpanzee data than the CL condition.

1.6 Study 2: The roles of morphology and posture on muscle function

Differences in morphology and posture will change how muscles function to accelerate the body during walking. Past studies have identified the gluteus maximus, gluteus medius, vasti, hamstrings, gastrocnemius, soleus, and tibialis anterior as the muscles primarily responsible for generating horizontal and vertical accelerations of the center of mass during human gait. Previous studies within clinical populations have demonstrated that there are differences in muscle function with changes in posture (Steele, Seth, Hicks, Schwartz, & Delp, 2010; Steele, Seth, Hicks, Schwartz, & Delp, 2013); however, it is unclear whether these conclusions would transfer to an able-bodied adult population. It has been shown that when healthy humans walk with a crouched posture they must activate a greater volume of muscle fibers compared to walking with an upright posture, especially around the knee joint, to support body weight with a flexed limb (Foster et al., 2013). However, due to the differences in posture, it is still unclear how the increase in quadriceps activation to support the body may interact with anterior-posterior and medio-lateral accelerations of the center of mass. Previous work in comparative muscle function has investigated differences in estimated muscle stresses between humans and chimpanzees during locomotion. The muscles that act to extend the hip in chimpanzees exert greater muscle stresses during locomotion than humans do when walking at moderate speeds (Thorpe et al., 2004). Aside from some documented differences in the lesser gluteal function between humans and chimpanzees (O'Neill et al., 2016), the question of how morphology impacts the role of individual muscles to produce accelerations on the center of mass is still not clear. In this dissertation, muscle function is defined as the contribution of individual muscles to the three-dimensional support, progression, and sway of the center of mass. Determining how muscles contribute to the acceleration of the center of mass in different postures will provide valuable insight into how posture affects muscle function during locomotion. In addition, comparing the results in human gait to the muscle function in chimpanzee gait would give insight into how different morphological features affect the ability of muscles to produce accelerations on the center of mass while walking with similar postures. This analysis will allow for insight into how species with different morphologies accomplish similar movement objectives. It will also provide information regarding how muscle and skeletal structures influence preferred movement patterns which can help anthropologists interpret the functional significance of skeletal features within the fossil record.

Aim 2.1: The first aim of the second study is to determine how changes in posture affect muscle function during walking in humans. We will analyze how the major lower limb muscles of humans contribute to the motion of the center of mass across four different human gait postures at a fixed speed and a preferred speed from Study 1 (Normal, CL, CLFT, IMIT).

Aim 2.2: The second aim is to determine how differences in morphology between chimpanzees and humans affect muscle function. We will compare muscle function in the human condition that is most similar to chimpanzee walking with the function of analogous muscles for chimpanzees during bipedal walking.

CHAPTER 2

LITERATURE REVIEW

Animals have a broad set of movement patterns available to complete a given task, such as walking to a food source (e.g. walk forwards, walk backwards, skip, hop, etc.), yet within a species these movement patterns are relatively consistent across individuals. However, there are often obvious differences in movement patterns of different species that should be due, at least in part, to differences in morphology. Comparing movement patterns between different species can give insight into how movement patterns are influenced by morphology and how these unique patterns have evolved. Humans are the only extant primates that walk exclusively with an upright posture while chimpanzees, our closest living relatives, use a crouched posture when they walk on their hind limbs. Some of the differences in preferred walking patterns can be confounded by the fact that motion at one segment or joint can influence the motion of the other segments of the body (e.g. the motion of the hip affects the way the knee will move), such that small changes in morphology can result in broader differences in posture. For this dissertation, posture will be defined as the general orientation of the trunk, pelvis, and lower limbs during walking, such as crouched or upright. Gait mechanics will be used to describe specific joint angles and ground reaction forces which will often change throughout the course of a single stride of walking. By determining how broad changes in posture affect the gait mechanics in humans, we can provide more insight into how segments of the body interact with each other during gait. The interaction of morphology and posture on gait mechanics will also provide important information about how we can interpret the functional significance of skeletal features seen in the hominin fossil record.

2.1 Human Gait

Human gait is cyclical and is typically studied over a full stride, usually defined from a right heel strike to a subsequent right heel strike (Gage, 1990). The gait cycle is often divided into two major phases: the stance phase and swing phase. During the stance phase, the right foot is in contact with the ground, producing a force against the ground to support the body, and lasts for approximately 60% of the overall stride time. In the swing phase, the right foot is off the ground and preparing for the next heel strike, lasting for the other 40% of the overall stride time (Murray, 1967). The stance phase of walking can be further divided into two periods of double support phase and one single support phase. The double support phase occurs when both feet are in contact with the ground at the same time and the single support phase occurs when just one foot is in contact with the ground (Larsson, Odenrick, Sandlund, Weitz, & Oberg, 1980).

Typical human walking speed is between 1.2 and 1.4 m/s (Finley & Cody, 1970; Ralston, 1958; Zarrugh, Todd, & Ralston, 1974). Walking speed is equal to the person's stride length times their stride frequency. As speed increases, typically both stride length and stride frequency increase as the absolute duration of both the stance phase and swing phase decrease (Grieve & Gear, 1966; Nilsson & Thorstensson, 1987). However, there are many combinations of stride length and stride frequency that can be used to achieve a given speed. Stride length can also be influenced by the height of the individual, as taller individuals typically take longer strides (Molen, Rozendal, & Boon, 1972).

Walking produces a ground reaction force (GRF), generated between the feet and the ground according to Newton's third law of motion. Ground reaction forces during walking occur in the vertical, medial-lateral, and anterior-posterior direction. The largest component of the GRF occurs in the vertical direction and has a double-peaked pattern separated by a minima during mid-stance phase (Alexander, 2004; Winter, 1990). Peak vertical GRFs scale with body weight and are approximately 110% of body weight when walking at a comfortable speed (J. Rose & Gamble, 2005). The first vertical GRF peak occurs shortly after initial heel strike due to the loading response as the center of mass (COM) is decelerated in the first half of stance phase. The vertical GRF minima occurs during mid-stance as the COM rises over the stance foot. The second peak occurs during the second half of stance, as the stance leg pushes off against the ground to accelerate the COM forward (J. Rose & Gamble, 2005). The anterior-posterior GRF is typically the second largest GRF component in magnitude, but typically less than 25% of body weight (Andriacchi, Ogle, & Galante, 1977). The anterior-posterior GRFs consist of a negative, braking force during the first half of stance, and a positive, propulsive force during the second half of stance. Lastly, the medial-lateral GRF make up the lowest component of the GRF, peaking at about 5% of body weight (J. Rose & Gamble, 2005).

During the stride, the COM moves in a sinusoidal pattern in the vertical direction (Saunders, Inman, & Eberhart, 1953). The COM is highest during the mid-stance phase when the stance leg is extended and lowest during the double support phase. The vertical oscillation of the COM arises from the lower limb acting as an inverted pendulum during the single support phase of walking (Cavagna, Thys, & Zamboni, 1976; Kuo, Donelan, & Ruina, 2005). The sinusoidal pattern of the COM allows for the recovery of potential and kinetic energy and is thought to make walking more economical (Cavagna, Heglund, & Taylor, 1977; Gordon, Ferris, & Kuo, 2009).

Humans are capable of walking up to about 2 m/s, although changing speed will have an effect on the resultant joint kinematics, GRFs, and muscle activation patterns (Hof, Elzinga, Grimmius, & Halbertsma, 2002; Kwon, Son, & Lee, 2015; Schwartz, Rozumalski, & Trost, 2008). Faster walking speeds result in larger ranges of motion at both the hip and knee in the sagittal plane (Murray, Mollinger, Gardner, & Sepic, 1984). Faster walking also will result in greater peak vertical GRFs (~130% body weight) and lesser GRFs during mid-stance (~60% of body weight). The peak anterior-posterior GRFs will also be greater at fast speeds (Schwartz et al., 2008). Walking at different speeds typically does not alter the phasing of the muscle activation patterns. However, there are significant differences in muscle activation amplitude across different speeds of walking, especially in the rectus femoris, biceps femoris, and tibialis anterior (den Otter, Geurts, Mulder, & Duysens, 2004).

Center of mass mechanics and joint motion during gait are largely driven by muscle forces, so understanding muscle function is an important piece of understanding the control and mechanics of locomotion. Muscle function during human gait has been evaluated using electromyography to measure the electrical activity of muscles during gait. Electromyography provides access to the timing and amplitude of muscle activation during gait (Ounpuu & Winter, 1989; Winter, 1990). However, electromyography does present some challenges in determining how muscles contribute to motion, since all that is recorded is the electrical activity within the muscle. This electrical activity is thought to be a surrogate measure for the magnitude of muscle force, but there are still several processing steps and assumptions that must be made before an estimate of how a single muscle accelerates a joint could be obtained.

A more direct way to evaluate muscle function is to use musculoskeletal modeling to evaluate how muscles contribute to COM motion (Anderson & Pandy, 2003; Zajac & Gordon, 1989). Several studies have shown how the major lower limb muscle groups contribute to the support and progression of the COM during walking in humans using an induced acceleration analysis (Zajac & Gordon, 1989). This type of analysis allows for insight into how each muscle would contribute to the acceleration of the COM. Induced acceleration has shown the gluteus maximus, vasti, and dorsiflexors slow the progression of the COM during early stance, and the gluteus medius, soleus, and gastrocnemicus positively accelerate the COM during late stance phase (Liu, Anderson, Pandy, & Delp, 2006). Further studies have shown that the vasti group and the soleus muscles are particularly sensitive to walking speed with the induced acceleration analysis (Liu, Anderson, Schwartz, & Delp, 2008a). In the mediolateral direction, the hip abductors play an important role in generating medial GRFs, and the knee extensors, plantar flexors, and adductors play important roles in generating lateral GRFs (John, Seth, Schwartz, & Delp, 2012a).

The recent developments in musculoskeletal modeling and simulation techniques allow for further insight into how muscles function during dynamic movements like gait, without invasive surgery. Utilizing these techniques for this dissertation will allow us to understand how individual muscles accelerate the center of mass for different postures in humans. These techniques will also be used to study how muscles act to accelerate the center of mass in chimpanzee bipedal gait. While general differences in gait mechanics between humans and chimpanzees can easily be observed and have been reported for over 70 years (Elftman, 1944), it is only recently that 3-D joint kinematics in humans have been directly compared with chimpanzee data (O'Neill et al., 2015). In the next section, the walking gait of chimpanzees will be compared with that of humans.

2.2 Chimpanzee Gait

In nature, chimpanzees have been observed to walk with both quadrupedal and bipedal postures. While quadrupedal walking time is more abundant, adult chimpanzees in the wild may spend about 2-6% of their locomotor time walking bipedally (M. D. Rose, 1991; Sarringhaus, MacLatchy, & Mitani, 2014). Typical walking speeds for chimpanzees in the wild range from 0.67 – 1.34 m/s (Hunt, 1992), although chimpanzees in laboratory environments have been recorded walking up to 1.79 m/s (Pontzer et al., 2014). Unlike the upright, straight-legged posture humans adopt when walking bipedally, chimpanzees walk with an abducted and flexed limb posture and different pelvis motion (Elftman, 1944; Jenkins, 1972; O'Neill et al., 2015). There are also differences in morphology between humans and chimpanzees, such as differences in lumbar spine shape and pelvis shape that have been proposed to directly affect gait mechanics (Lovejoy, 2005; O'Neill et al., 2016). These differences in posture and morphology may contribute to differences in ground reaction forces (GRFs), joint kinematics, and metabolic energy expenditure when comparing chimpanzees to humans during bipedal walking.

The vertical GRFs in chimpanzee bipedal walking typically do not have the distinguishing two-peak pattern common in typical human gait (Yaguramaki et al., 1995), instead they produce a one-peaked GRF. However, some chimpanzees have been reported to produce double-peaked GRFs during gait trials, however even in these trials the amplitude of the peaks is small and the GRF trace is relatively flat (Pontzer et al., 2014). The relatively monophasic vertical GRF pattern is related to a reduction in the recovery of potential and kinetic energy in chimpanzees when compared to normal human walking (Crompton et al., 1998; Demes et al., 2015). The medial-lateral GRFs are greater in chimpanzee bipedal walking when compared to normal human walking (Li et al., 1996).

The motion of the COM during chimpanzee walking displays some degree of pendular action, however they do not have the same degree of recovery of mechanical energy that humans achieve (Demes et al., 2015). Like normal human walking, when chimpanzees walk the maximum height of the COM occurs during single-support phase and the minimum height occurs during double-support phase (Demes et al., 2015). However, the pathway of the COM displays larger variability in chimpanzees when compared to human walking (Demes et al., 2015). The pelvis segment (Figure 2.1) and hind-limb (Figure 2.2) mechanics of chimpanzee bipedal gait differs from that of normal human walking (Elftman, 1944; Jenkins, 1972). When chimpanzees walk bipedally, they tend to adopt a crouched posture where both the hip and knee are more flexed and the ankle is more dorsiflexed throughout the stance phase (Figure 2.2) (Elftman, 1944; Jenkins, 1972; O'Neill et al., 2015). In the frontal plane, the pelvis list and hip adduction angles and patterns are different between humans and chimpanzees. In humans, the pelvis drops downward toward the limb swing side during midstance, but in chimpanzees the pelvis is elevated upward on the swing side (Figure 2.1). The chimpanzee lacks a significant bicondylar angle at the knee joint (Jenkins, 1972), which could contributes to the difference in pelvic tilt sequence during gait in chimpanzees compared with humans (O'Neill et al., 2015). Due to the lack of the bicondylar angle and more hip abduction during stance in the chimpanzee, the pelvis elevation on the swing side will move the center of mass towards the stance side foot which will have a more lateral position in the chimpanzees than it would in humans. This pelvic tilt pattern allows the chimpanzee to place their trunk over the stance foot and to aid in swing-leg foot-ground clearance (O'Neill et al., 2015).

Chimpanzees consumes more metabolic energy during walking than what would be expected for a species with their body mass, while human walking is less expensive than what should be expected (Sockol et al., 2007; Taylor et al., 1982). Two significant determinants of the cost of locomotion is volume of activated muscle and contact time during bipedal and quadrupedal walking (Kram & Taylor, 1990; Roberts, Chen, & Taylor, 1998). The higher metabolic cost in chimpanzees could be related to the flexed-limb gait mechanics of chimpanzees which requires more activated muscle volume to support body weight than humans during walking (Figure 2.3B) (Sockol et al., 2007). In addition, in this study the chimpanzees had a shorter contact time with the ground, which often is associated with a greater metabolic cost, than humans during bipedal walking (Figure 2.3C) (Sockol et al., 2007). Within chimpanzee gait, walking either bipedally or quadrupedally results in a similar metabolic cost (Sockol et al., 2007; Taylor & Rowntree, 1973), although there is some variance between individual chimpanzees (Pontzer et al., 2014). Some chimpanzees display a higher metabolic cost during bipedal walking while other chimpanzees had a higher metabolic cost during quadrupedal walking. However, the variability between subjects averaged out such that the metabolic costs across subjects was similar between the conditions (Pontzer et al., 2014). It was also demonstrated that the thigh and knee angles of some chimpanzees may be correlated to the metabolic energy expenditure, suggesting that even small increases in extension of the lower limbs may result in significant energetic savings (Sockol et al., 2007).

Another factor that may contribute to the difference in metabolic energy expenditure during locomotion is the proportionally longer muscle fibers in chimpanzees compared with humans (Thorpe et al., 1999). The longer muscle fibers would contribute to a greater energy expenditure due to a greater volume of muscle activated per cross sectional area. For a given force, longer muscle fibers would consumer a greater amount of metabolic energy since active muscle volume is proportional to the product of muscle force and muscle fascicle length (Roberts et al., 1998). Seemingly paradoxical, but another potential cause of the greater cost of locomotion in chimpanzees could be due to a shorter lower limb length (Steudel-Numbers & Tilkens, 2004). The volume of activated muscle may be counterbalanced in a longer limb by increasing the time with which the foot is in contact with the ground for each step due to a lower stride frequency for a given speed. Saving metabolic energy may be an important selection factor in the evolution of modern human bipedalism. Reducing the cost of transport would have given early humans a selective advantage while foraging for food (Rodman & McHenry, 1980).

The muscle stresses of the chimpanzee hindlimb during locomotion have shown that training status of the chimpanzee may play a large role in the mechanics of gait. The peak stress in the triceps surae muscles were lower during late stance for an untrained chimpanzee subject when compared to trained chimpanzees. This was probably due to the untrained chimpanzee keeping the GRF vector closer to the ankle joint instead of moving the GRF vector closer to the toes, as seen in the trained chimpanzees. A larger peak muscle stress was found in the untrained chimpanzee for the quadriceps and hip extensor muscles (Thorpe et al., 2004).

Unlike the research on human gait and muscle function, information on how individual muscles accelerate the center of mass during chimpanzee gait is relatively unknown. Some initial research using induced acceleration to investigate muscle function between humans and chimpanzees has shown some differences in how the lesser gluteal muscles accelerate the center of mass, while there were no differences in the function of the hamstrings between these species (O'Neill et al., 2016). In this study, the humans walked with their self-selected gait patterns while matching the speed of the chimpanzees. Therefore, it is still unknown if the difference in gluteal function between humans and chimpanzees is a consequence of the differences in morphology, the difference in broad posture during locomotion, or some combination of morphology and posture. This dissertation will expand upon the number of muscles analyzed as well as include a number of different human postures to compare with the chimpanzee data in order to tease apart how morphology and posture independently affect muscle function. The next section will highlight specific differences in morphology that are thought to contribute to the differences in gait mechanics between humans and chimpanzees.

2.3 Effects of Morphology on Gait Mechanics

Determining specifically how the muscle and skeletal structure of organisms affects movement patterns is challenging since it is usually not possible to purposefully manipulate morphology within an organism. This means that comparing between groups with cross-sectional studies is the most feasible way to study differences in morphology. Humans and chimpanzees have relatively similar morphological features when compared to the broad, diverse animal kingdom. The morphological similarity exists because humans and chimpanzees have a “relatively” recent common ancestor, diverging from a common ancestor about 7-10 million years ago (White et al., 2009). Now, while humans and chimpanzees have some degree of morphological similarity, there are some important post-cranial structure differences that probably play important roles in influencing the patterns of movements such as gait.

2.3.1 Morphology of chimpanzees and humans

The lumbar spine of humans has an inward lordotic curvature and is fairly mobile compared to chimpanzees (Lovejoy, 2005). The lordosis curve in the lumbar spine in humans allows them to position their trunk vertically when standing upright (Aiello & Dean, 2002). Chimpanzees have rather immobile lower spines, due in part to a shorter free lumbar column length than in humans. The distance between the iliac crests and thorax is small in chimpanzees, which results in an inflexible lower back (Lovejoy, 2005). Since chimpanzees have no lumbar lordosis, this may prevent them from positioning their trunk vertically during locomotion (Lovejoy, 2005). This restriction in lumbar lordosis results in a COM location anterior to the hip joint (Sockol et al., 2007). Since the COM is projected forward during chimpanzee bipedal walking, chimpanzees might have to adopt a crouched posture during gait so that their base of support is underneath the COM (Lovejoy, 2005). Some authors believe the lack of lumbar lordosis in chimpanzees is the sole, or at least primary, reason that chimpanzees walk with a crouched posture (Lovejoy, 2005; Lovejoy & McCollum, 2010). However, the specific shape of the lumbar spine is not the only morphological feature that has been proposed to contribute to differences in gait between humans and chimpanzees.

In addition to differences in the lumber spine, another primary difference between the morphology of chimpanzees and humans is in the shape of the pelvis. The human pelvis has a greater angle between the ilium and the ischium, which may also contribute to the ability of the human to orient their trunk vertically while standing. The hamstrings muscle moment arms are very small when the chimpanzee extends the hip, so keeping a flexed hip posture allows the muscle moment arm for the hamstrings to be large and capable of producing large hip extension moments (Aiello & Dean, 2002; Fleagle & Anapol, 1992). The pelvis of the chimpanzee also has elongated, anteriorly directed iliac blades. Due to the differences in pelvis structure, there are differences in how some of the hip muscles contribute to either hip extension or hip abduction between humans and chimpanzees. The anteriorly directed iliac blades affect the way the gluteal muscles contribute to hip extension and adduction, with muscles like the gluteus medius contributing to substantially to hip extension in chimpanzees but being more of a hip abductor in humans (Aiello & Dean, 2002).

Moving distally, at the knee, humans typically have a frontal plane angle between their thigh and shank of about 10 degrees (Lovejoy, 2007). This angle allows for the foot to be easily placed underneath the center of mass during walking in humans. This frontal plane angle between the femur and the tibia is called the bicondylar angle, and it forms in humans as a response to skeletal loading during locomotion during early childhood (Shefelbine, Tardieu, & Carter, 2002). The bicondylar angle is so specialized to locomotion that it is absent in nonambulatory and low ambulatory humans (Tardieu & Trinkaus, 1994). However, the same bicondylar angle does not exist in chimpanzees, this means their legs are much straighter and makes it more difficult for them to place their feet underneath their center of mass during bipedal walking (O'Neill et al., 2015).

Lastly, the foot structure of humans and chimpanzees is different. Humans have a thick plantar aponeurosis that is utilized during push-off, which stiffens the mid-foot and elevates the longitudinal arch (Caravaggi, Pataky, Gunther, Savage, & Crompton, 2010; J. H. Hicks, 1954). Humans also have an adducted hallux that is unable to oppose the other toes. In contrast, chimpanzees have an abducted, opposable hallux, and their phalanges are long and curved which can be advantageous during climbing and grasping (Fernandez, Holowka, Demes, & Jungers, 2016). During human push-off phase, the midfoot appears to remain rigid which provides a stable lever for the ankle plantar flexors to use during push-off (Bojsen-MÃ¸ller, 1979). However, during chimpanzee gait, the foot dorsiflexes about the midfoot following heel lift, a kinematic pattern that has been called the ‘midtarsal break’ (Susman, 1983). Although some of these morphological differences predict that the chimpanzee would have a more flexible foot during locomotion and that this would be a disadvantage during bipedal walking, recent research has demonstrated that humans have a greater range of motion in the midfoot over the stance phase (Holowka, O'Neill, Thompson, & Demes, 2017). Therefore, humans are able to utilize both stiffness and mobility in the midfoot during the stance phase, and this complex longitudinal arch in humans complements other adaptions for efficient and habitual bipedal walking.

Many of these morphological differences between humans and chimpanzees are likely to influence the preferred gait patterns and contribute to differences in gait mechanics observed between these species. However, a confounding factor in evaluating the differences in gait mechanics due to morphology between humans and chimpanzees is that each species has a broadly different posture during locomotion. This is an important factor to consider as even small changes in the motion of one joint can affect the way other joints move during gait and the metabolic energy expenditure. This next section will highlight some of the ways posture can influence gait mechanics and metabolic energy expenditure for both humans and chimpanzees.

2.4 Effects of Posture on Gait Mechanics

It is challenging or impossible to systematically test different walking patterns with chimpanzees or other species since it is hard to instruct them to walk with different postures. However, experimenters can successfully instruct humans to move in a variety of "non-preferred" conditions, allowing researchers to manipulate different gait characteristics such as speed, stride length, stride frequency (see section 2.1). Researchers can also instruct human subjects to walk with different postures, including postures that imitate the habitual posture of chimpanzees (Yaguramaki et al., 1995). When humans are instructed to walk more like a chimpanzee does, the subjects in these studies have been able to imitate several main features of chimpanzee gait including sagittal plane joint kinematics at the hip and knee as well as vertical GRFs (Foster et al., 2013; Yaguramaki et al., 1995). However, whether these similar sagittal-plane joint kinematics are also seen in the frontal and transverse planes, after giving humans instructions to walk like chimpanzees, is still unknown. Manipulating posture in humans allows for insight into both the flexibility of the human system to varying movement patterns and how different muscle and skeletal structures accomplish a similar movement task.

The mechanics and energetics of gait change when humans walk with different postures, such as a flexed-limb posture. Previous studies have manipulated the posture of humans during gait by instructing them to walk with a ‘bent-hip, bent-knee’ (BHBK) gait (Carey & Crompton, 2005; Crompton et al., 1998; Foster et al., 2013). In BHBK gait, the metabolic energy cost increases by about 50 % when compared with normal, upright walking (Carey & Crompton, 2005). Additionally, the net cost of transport increases by about 1.7 times for similar speeds of walking when humans walk in a BHBK posture compared with a normal posture. Core temperature, lactate production, oxygen consumption, and heart rate all increase after humans adopt a BHBK posture during gait (Carey & Crompton, 2005). The estimated minimum net cost of transport occurred at about 1.4 m/s for BHBK walking, while the minimum net cost of transport for upright walking is about 1.2 - 1.3 m/s (Carey & Crompton, 2005; Johanson et al., 1982; Ralston, 1958).

The increase in metabolic energy in BHBK gait seems to be due to an increase in the volume of muscle activated during stance phase. The increase in activated muscle volume during BHBK gait is due to an increase in the moment arm distance between the knee and the GRF vector during stance phase (Foster et al., 2013; Sockol et al., 2007; Steele et al., 2012). While the gait kinematics at the hip and knee become more similar to chimpanzees, some gait mechanics in human crouched-gait are still different from chimpanzee gait. When humans are instructed to walk with a BHBK gait, they will keep their trunk oriented vertically, while the chimpanzees have their trunk projected forward (Foster et al., 2013; Sockol et al., 2007). One consequence of the trunk being oriented vertically is that the GRF vector passes close to the hip joint center of rotation in humans.

In chimpanzees, the GRF vector has a larger distance to both the hip and the knee (Sockol et al., 2007) (Figure 2.2a). When humans walk upright, the largest GRF vector moment arm is around the ankle, where the muscle fibers that contribute to plantarflexion are relatively short (Neptune, Kautz, & Zajac, 2001). This allows for upright walking in humans to be very efficient.

Another potential area of inefficiency in BHBK gait is due to motion of the COM. The recovery rate of the potential energy is much lower when humans walk with a BHBK gait (Wang, Crompton, Li, & Gunther, 2003). Normally, the out-of-phase fluctuations of the potential and kinetic energies of the COM during walking make for an efficient system. However, in human BHBK gait and chimpanzee gait, the fluctuations are less out-of-phase (Demes et al., 2015; Wang et al., 2003). The recovery of energy has been shown to be between 55% and 70% for humans walking normally (Cavagna et al., 1976; Wang et al., 2003), 27% for humans walking with a BHBK gait (Wang et al., 2003), and as low as 15% for chimpanzees walking (Demes et al., 2015). The lower rate of recovery in chimpanzees and humans walking BHBK is a result of the flatter trajectory of the COM and the single-peak of the vertical GRF profile during stance phase.

One area that requires further research is a full three-dimensional analysis comparing human flexed-limb gait to chimpanzee bipedal gait. Understanding more about the joint-level mechanics between these conditions would help elucidate how the morphology of different species affects preferred movement patterns while walking with similar postures. Although specifying the posture of a human during the gait task infers some inherent qualities in the movement (the hip and knee will necessarily be more flexed during BHBK gait), still other features of gait may be different due to morphological features of the human and chimpanzee. One such difference between human flexed-limb and chimpanzee gait may lie in the frontal and transverse plane motion. Chimpanzees rotate at the pelvis and trunk differently than humans (Demes et al., 2015; Thompson, Demes, O'Neill, Holowka, & Larson, 2015). For example, as highlighted in Section 2.2, humans and chimpanzees have very different pelvis list patterns. In addition, chimpanzees have an in-phase rotation of the pelvic and thoracic motion while humans have an out-of-phase pattern (Thompson et al., 2015). Any differences in the gait mechanics that still exist have instructing humans to walk more like a chimpanzee may give more information about why the metabolic cost is greater in chimpanzees than in humans, beyond the difference in activated muscle volume and time of contact (Sockol et al., 2007).

The inclination of the trunk has been shown to be an important determinant of joint kinematics and ground reaction forces during gait. Recent studies compared human bipedal walking to the walking mechanics of birds, although the effects of a forward-leaning trunk can be viewed with respect to the natural inclination of the trunk in chimpanzee bipedal walking. As it does with chimpanzees, a forward-leaning trunk would reposition the COM forward, in front of the hips (Alexander, 2004; Aminiaghdam et al., 2017; Blickhan, Andrada, Muller, Rode, & Ogihara, 2015). An earlier 2-dimensional study found that with a forward-inclined trunk, the knees became more extended slight more extended, although not significantly different (Yaguramaki et al., 1995). However, two more recent studies found a forward-leaning trunk angle induced more flexion at the hips and knees and more dorsiflexion during stance at the ankle (Aminiaghdam et al., 2017; Saha, Gard, & Fatone, 2008). The forward-leaning trunk also results in an increase in the 1st vertical GRF peak when compared to regular walking (Aminiaghdam et al., 2017; Saha et al., 2008; Yaguramaki et al., 1995). A rightward shift in the horizontal GRF profile was also demonstrated in the forward-leaning trunk gait (Aminiaghdam et al., 2017). When instructed to walk with a forward-leaning trunk, it is interesting that the sagittal plane joint kinematics at the hip, knee, and ankle appear to be more similar to the sagittal plane joint kinematics seen in chimpanzee bipedal gait (Aminiaghdam et al., 2017; O'Neill et al., 2015; Saha et al., 2008). However, the GRFs during human gait with a forward-leaning trunk still have a semi-typical double-peaked profile rather than a monophasic GRF profile as typically seen in chimpanzee gait (Aminiaghdam et al., 2017; Pontzer et al., 2014).

Another study focused more specifically on how the trunk orientation changes the control of flexed-limb, or BHBK, walking (Grasso et al., 2000). This study had three conditions: an erect posture condition, a BHBK condition, and a BHBK condition where the subjects were instructed to lean forward during gait. This study reported a change in electromyography (EMG) magnitude during each of these conditions. A shift in EMG activity from the knee joint to the hip joint associated with a change in trunk orientation during BHBK gait suggests that the reorientation of the trunk does change the GRF vector moment arms to the knee and hip joints. Taken altogether, these studies demonstrate that the orientation of the trunk plays an important role in the control of gait mechanics and should be included in any investigation of the effects of posture on locomotion.

While in healthy populations, humans can be instructed to walk with many different types of postures, in certain clinical populations, such as individuals affected by cerebral palsy, their natural gait is in a flexed limb gait posture (J. Rose, Gamble, Medeiros, Burgos, & Haskell, 1989b). This gait pathology has been studied in a variety of scenarios for this population, including musculoskeletal computer modeling simulation (J. L. Hicks, Schwartz, Arnold, & Delp, 2008; Steele et al., 2010; Steele, Demers, Schwartz, & Delp, 2012; Steele et al., 2013). In individuals that walk with a more severe crouch gait, the compressive tibiofemoral forces are much greater than in unimpaired walking (Steele et al., 2012). An induced acceleration analysis on children affected by cerebral palsy shows that they have less passive skeletal support during stance and therefore must use higher muscle forces to walk when compared to unimpaired children (Steele et al., 2010). Furthermore, many of the same muscles relied on for healthy human walking are responsible for supporting and accelerating the COM during stance, but a crouched gait relies more heavily on the gluteus medius and hamstrings muscles to accelerate the COM forward (Steele et al., 2010). During crouch gait, the quadriceps and plantar flexors produce opposing anterior-posterior forces during stance, which may contribute to some of the metabolic inefficiency of crouch gait (Steele et al., 2013). Lastly, in crouch gait the gluteus medius may not be able to support the COM as well as in unimpaired gait (Steele et al., 2013). Since these studies are done in children affected by cerebral palsy, it is unclear whether these conclusions would transfer to a healthy, adult population walking with a flexed-limb posture.

In addition to the studies in humans that systematically manipulate posture during gait, there is some evidence that broad postural changes can have a meaningful effect in chimpanzee gait. Sockol, et al. (2007) reports single individual chimpanzee, analyzed separately from the sample of five chimpanzees in the subject population. This individual maintained a slightly more extended limb during stance, and accompanied by a longer foot contact time, had a lower metabolic energy expenditure during bipedal walking than quadrupedal walking. While this is a single individual within a highly trained chimpanzee population, this data seems to suggest that small changes in posture can have an effect on the overall metabolic energy expenditure (Sockol et al., 2007).

Investigating the influence of both morphology and posture does present some challenges, due to the potential for these two factors to interact with each other. The habitual posture of an individual and the long-term loading of the musculoskeletal system can influence the shape and structure of the skeleton, an argument based on Wolff's Law that states loading patterns influence the trabecular structure (Wolff, 1986). To highlight just one example of how posture and morphology can interact, Section 2.3 discussed how the bicondylar angle of the knee forms during early childhood, once the individual begins to walk (Shefelbine et al., 2002; Tardieu & Trinkaus, 1994). Although posture and morphology can interact in many ways, one newer and developing method of analysis that can help tease apart some of the interactions is through musculoskeletal modeling. The next section will explain some of the potential for musculoskeletal modeling within biomechanics research studies.

2.5 Musculoskeletal Modeling and Simulation

Musculoskeletal modeling and simulation present a unique opportunity to perform integrated studies combining experimentally collected data with computer models of a musculoskeletal system. These types of studies are well suited for studies where some of the data are hard or impossible to obtain *in vivo* for a variety of reasons, including invasive measurement techniques or the impossibility of isolating certain variables. In order to circumvent these obstacles, computer models have been developed to isolate variables such as joint loading, muscle fiber force or power, and elastic energy storage and return in tendons. Computer models are also helpful in simplifying the analysis of certain movements to make predictions. For example, simple pendulum models have been developed to analyze the basic mechanics of human walking (Kuo, 2001; Saunders et al., 1953). Early models of walking used a simple inverted pendulum model to describe the exchange of potential and kinetic energy during the walking cycle (Mochon & McMahon, 1980). These simple models present many advantages for analyzing complex movement tasks. However, they also have many disadvantages, as these models assume that a person walks with straight knees which is obviously not the case.

The next level of complexity in computer models for human gait account for knee flexion with dynamically linked compound pendulums and have been used to predict walking over a wide range of terrain (McGeer, 1990). Actively powered models pendular models have been used to model the relationship between speed and step length in humans (Kuo, 2001). This model allowed for the investigation of different hypothesized determinants of metabolic costs, such as the cost of performing work (Cavagna & Kaneko, 1977; Donelan, Kram, & Kuo, 2002) or the cost of generating force (Griffin, Roberts, & Kram, 2003; Kram & Taylor, 1990), and how each of these might determine how humans choose to walk at a particular speed and step frequency. This model also predicted that other metabolic cost hypotheses such as the integral of force over time (impulse) and showed that swing leg work and peak force do not make reliable predictions for walking either (Kuo, 2001).

Other simple models and equations have been developed to predict the mechanics of walking and associated metabolic cost. Preferred stride frequency can be predicted from a force-driven harmonic oscillator, which counteracts the effects of gravitational, damping, and stiffness forces using a periodic forcing function to maintain its oscillation (Holt, Hamill, & Andres, 1991). This suggests that the goal of locomotion is self-optimization, or to reduce the muscular requirements or metabolic energy utilizing the resonant frequency of the legs to achieve these minimums. The metabolic cost of walking has also been predicted using equations of varying complexity. Early equations to predict metabolic energy expenditure used only the gait speed to predict the metabolic expenditure (Ralston, 1958). Later on, equations were developed to account for step length and step frequency, as well as walking speed, in predicting the metabolic energy expenditure (Zarrugh & Radcliffe, 1978). These simple models are useful in many contexts, but do not allow for insight into how individual muscle actions contribute to the mechanics and energetics of walking.

Inverse dynamics is another type of model used in biomechanics research to evaluate the net joint moments during walking. Inverse dynamics calculates the net joint moment based on joint kinematics, external forces (such as GRFs), and segment inertial properties. After calculating the joint moments, joint mechanical work and power can be calculated. These values are useful in evaluating the correlation between mechanical work and total metabolic energy expenditure. Inverse dynamics has some limitations as well, including the assumption that all the segments act as rigid bodies, that the joints are frictionless, and ignores the effects of ligaments. Inverse dynamics also only can calculate a net joint moment, which makes it impossible to calculate muscle forces due to the redundancy of the system ignores potential co-contraction (Kuo, 1998).

Complex musculoskeletal models have been developed recently to analyze muscle coordination (Zajac, Neptune, & Kautz, 2002), metabolic energy expenditure (Umberger, Gerritsen, & Martin, 2003), mechanical work done by individual muscles (Neptune et al., 2001), and potential injury mechanisms (Thelen & Anderson, 2006). It has also been used to investigate the effect of walking speed on muscle function and mechanical energetics (Neptune, Sasaki, & Kautz, 2008). Computer simulations of normal walking have allowed for the identification of the actions of specific muscles that would be impossible with experimental methods. One advantage of these complex musculoskeletal models is that they allow for the direct representation of the morphology of the individual or population being studied. The ability to create and modify the musculoskeletal structure within a model has previously been adopted in clinical research to investigate how changes in morphology, like a tendon transfer or tendon lengthening surgeries, could affect the functional outcomes in clinical populations (Delp & Zajac, 1992; Montgomery, Balasubramanian, Mardula, & Allan, 2013).

In most musculoskeletal models, a Hill-type muscle model is used to evaluate how muscles contribute to the overall motion (Hill, 1938). In a Hill-type muscle model, there are three components associated with each musculotendon unit. The contractile element in the model is the only component that can actively produce force when a stimulus acts upon it and is generally thought to best represent the muscle fibers in the musculotendon unit. The contractile element produces force based on four relationships: excitation-activation, force-activation, force-velocity, and force-length. Excitation-activation relates the neuronal input of the muscle (excitation) to the output of the muscle (activation). The excitation-activation relationship encapsulates the delay in muscle activation due to the time it takes for calcium to be distributed throughout the muscle. Force-activation scales the peak force the contractile element can produce on a scale from 0 to 100 percent. It is a direct, linear relationship where, for example, 50 percent activation will result in the contractile element producing 50 percent of its current maximal force. The current maximal force that the contractile element can produce is based on the force-velocity and force-length relationships. The force-velocity relationship determines how the peak force of the contractile element is dependent upon the velocity of the contractile element. When the contractile element shortens, it will not be able to produce as much peak force as if it were isometric, and when the contractile element is lengthened it will be able to produce more force than if it were isometric. The force-length relationship determines how much force a contractile element will produce based on the current length. Muscles will have an optimal length where the force will be largest, and lengths that are either longer or shorter will produce less force. The shape of this relationship is an inverted parabola where the force produced will fall to zero when the contractile element gets too long or too short.

The series elastic element is a passive spring in series with the contractile element and is generally thought to represent the tendon and aponeurosis or the musculotendon unit. The last component is the parallel elastic element and it also acts as a spring but acts in parallel to the contractile element and series elastic element. The parallel elastic element can produce force without any activation of the contractile element. Both the series elastic element and the parallel elastic element have stiffness parameters which define their force production for a given amount of extension. The parallel elastic element will only produce force when the musculotendon unit is relatively long. The threshold length at which the parallel elastic element will produce force varies from muscle to muscle.

Modeling techniques allow for the estimation of individual muscle forces using either static optimization (SO) or dynamic optimization (Anderson & Pandy, 2001). Both of these processes utilize a cost function in order to solve the redundancy problem associated with multiple muscles crossing single joints. There are different cost functions that have been utilized including minimizing muscle stresses, minimizing muscle activations, minimizing metabolic energy, or maximizing some aspect of the movement such as jump height. Static optimization is less computationally expensive; however, it does not account for the muscle activation dynamics like dynamic optimization. Even taking into account these limitations of SO, it has been shown to be sufficient for estimating muscle forces during walking (Lin, Dorn, Schache, & Pandy, 2012). Static optimization solves for muscle forces for each time point throughout the movement, where each time point is independent of the others so the solution at one point in time does not influence the solution at the next point. Because SO solves for muscle force at each time point independently, a cost function that requires the analysis of the whole movement, such as maximizing jump height or minimizing metabolic cost, cannot be used. Therefore, SO typically uses muscle activations or muscle stresses within the cost function.

Dynamic optimization uses the whole motion when solving the cost function, so it use a cost function that minimizes the overall metabolic energy. Dynamic optimization allows for simulations to account for activation dynamics, force-length, and force-velocity relationships. Unlike SO, it does not require experimental tracking data to solve the problem. This means that simulations of movements where there is no experimental data are possible. If experimental data do exist, the optimization problem can attempt to reproduce the experimental data as closely as possible (Erdemir, McLean, Herzog, & van den Bogert, 2007).

In all, there are a variety of different modeling tools and applications that have been used to tackle questions in biomechanics, some of which depend on experimental data and others that predict motion without any experimental data available. This dissertation will use musculoskeletal modeling techniques to predict how muscles produce an acceleration on the center of mass. This research will rely upon the software package, OpenSim, to perform gait simulations in order to estimate the contribution of each muscle to accelerate the center of mass throughout a full gait cycle. The next section will describe the specifics of OpenSim in more detail.

2.5.1 OpenSim

OpenSim is a commonly used open-source application used in musculoskeletal modeling and simulation (Delp et al., 1990; Delp & Loan, 1995; Delp et al., 2007). It consists of a collection of low-level computational tools that can be accessed through either a graphical user interface or programming software such as Python or MATLAB. OpenSim uses a dynamics engine called Simbody, an open-source, extendable toolkit for multibody mechanics (Sherman, Seth, & Delp, 2011). The OpenSim platform has a number of tools for analyzing musculoskeletal models and generating simulations of movements. Different tools for use with various musculoskeletal models include: scaling, inverse kinematics, reduce residuals, inverse dynamics, computed muscle control, static optimization, forward dynamics, and induced acceleration.

Scaling is done as a first step before most other types of analyses are possible. A generic musculoskeletal model is scaled to match the anthropometry of a particular subject. Each segment of the model is scaled based on the relative distances between pairs of markers placed on the subject during a data collection. The next step that is commonly used is the tool for inverse kinematics. This tool determines the joint angles and translations for the scaled model that will reproduce the experimental data by solving a least-squares problem that minimizes the differences between the measured marker locations and the locations of the markers on the model subject to joint constraints (Lu & O'Connor, 1999). The reduce residuals tool is used to compensate for experimental errors and modeling assumptions to make the motion of the model dynamically consistent with the ground reaction forces. This tool makes small adjustments to the motion of the model and mass parameters to reduce the residual forces and moments that would be required for a dynamically consistent motion according to Newton’s second law (Hamner, Seth, & Delp, 2010; Kuo, 1998).

The inverse dynamics tool calculates the net joint moments for each joint in the model during a movement. The kinematics from either inverse kinematics or reduce residuals tools can be used for this step along with the external loads, like ground reaction forces, measured from experimental data. The inverse dynamics tool solves the equations of motions to calculate the net forces and torques for each joint. Static optimization and computed muscle control are two different tools to estimate muscle forces and activations during a movement. Static optimization is an extension of the inverse dynamics tool that can further resolve net joint moments into individual muscle forces at each time point. Computed muscle control is a type of dynamic optimization that can compute muscle excitations that could drive a musculoskeletal model to reproduce a desired set of kinematics (Thelen & Anderson, 2006). Forward dynamics takes muscle excitations as input and drives a forward simulation of a musculoskeletal model by integrating differential equations that define the dynamics of the system. The forward dynamics tool is one tool within OpenSim does not require experimental data to track and can be used in predictive solutions to given perturbations.

The induced acceleration tool is used for computing the accelerations that each individual muscle would cause on a given model. For example, the tool could be used to estimate how each individual muscle force contributes to the acceleration of the center of mass or knee angle. The inputs for this tool include the kinematics from either the reduce residuals tool or inverse kinematics and the ground reaction forces (Hamner et al., 2010; Hamner, Seth, Steele, & Delp, 2013; Steele et al., 2013). The induced acceleration tool uses kinematic constraints on the foot in order to make the analysis computationally efficient. A rolling constraint has been shown to be the most effective in reproducing ground reaction forces and moments (Hamner et al., 2013). The rolling constraint combines four individual constraints: a unilateral non-penetrating constraint where the foot cannot penetrate the ground, plus a fore-aft no-slip constraint, medial-lateral no-slip constraint, and a vertical no-twist constraint combine to define a pure rolling constraint. For this dissertation, induced acceleration analysis will be used to determine how individual muscles accelerate the center of mass for both human and chimpanzee gait.

2.5.2 Predictive Simulation

Musculoskeletal modeling and simulation can often be a complementary component of experimental studies. Unfortunately, some types of experimental data are hard or impossible to collect due to either the invasive nature of a measurement or the lack of availability of subjects within the population of interest. Once situation where subjects are unavailable for a data collection is when the species is now extinct, as is the case for early hominins and thus performing experimental studies on these species are impossible (Nagano, Umberger, Marzke, & Gerritsen, 2005; Sellers, Cain, Wang, & Crompton, 2005). However, performing predictive simulations on extinct species is one way to begin to understand how species that no longer exist would have walked. These predictive simulations employ a variety of techniques, all driven by the desire to understand how the morphological features of extinct hominins would have influence gait strategies.

Predictive simulation of human locomotion dates back to the early 1970s with two-dimensional models and a reduced set of muscle or torque actuation (Chow & Jacobson, 1971; Hatze, 1976). More recent predictive simulations have used three-dimensional musculoskeletal models to simulate human gait by minimizing the predicted metabolic energy expenditure (Anderson & Pandy, 2001). Further studies have evaluated different objective functions for human gait, and highlight the sensitivity of the predictive results to the objective function (Ackermann & van den Bogert, 2010; Miller, 2014). Predictive simulation techniques have become increasingly feasible as computational methods get faster with better algorithms and faster computers (Ackermann & van den Bogert, 2010; Lee & Umberger, 2016). Using computer models can allow for insight into the effects of morphology on gait mechanics because morphology can be directly represented and changed.

In addition to numerous human musculoskeletal models, musculoskeletal models of other species have been developed through the SIMM (Delp & Loan, 1995) and OpenSim (Delp et al., 2007) software packages. For example, models of the rat (Johnson, Jindrich, Roy, & Edgerton, 2008), mouse (Charles, Cappellari, Spence, Wells, & Hutchinson, 2016), and tyrannosaurus rex (Hutchinson, Anderson, Blemker, & Delp, 2005) have been established within OpenSim to use in musculoskeletal modeling and predictive simulations. A computer model of the chimpanzee was developed and is available on OpenSim as well (O'Neill et al., 2013). Thus far, this musculoskeletal model of the chimpanzee has not been used in any predictive studies, however some initial induced acceleration analysis has been done with this model and has demonstrated that there are differences in how the lesser gluteal muscles function between humans and chimpanzees due to differences in musculoskeletal structure and gait kinematics (O'Neill et al., 2016).

Recent studies have begun to take advantage of the power of predictive simulations to investigate how early hominins may have walked. Detailed musculoskeletal models of Australopithecus afarensis have been developed and used to evaluate whether this species could have walked like a modern-day human without a greater predicted metabolic cost than humans (Nagano et al., 2005). The musculoskeletal properties of A. afarensis were integrated into a computer model using 3D bone scans and combined with predicted muscle pathways based on modern human anatomy. The results of this study predict that early hominins could have walked in a similar manner to that of modern-day humans, with only minor differences in muscle recruitment patterns. Other research has used the principles of evolutionary robotics to attempt to predict an energy-efficient gait of A. afarensis based on its skeletal dimensions and fossil footprints hardened in volcanic ash deposits (Sellers et al., 2005). This study predicted that A. afarensis was an excellent bipedal walker capable of walking at speeds up to 1.3 m s^{-1}.

Although predictive simulation is not directly a part of this dissertation, this technique does provide an exciting opportunity to answer questions about the effects of morphology and posture on gait mechanics. For example, since the musculoskeletal model is completely digitized within the computer it can therefore be directly manipulated to evaluate how specific changes in morphology could affect preferred gait mechanics. As discussed above, predictive simulation previously been used within the context of evolutionary biomechanics, the next section will elaborate on how this dissertation can inform questions about the driving factors that contributed to the gait mechanics in modern day humans and chimpanzees.

2.6 Evolution of Human Bipedalism

Bipedalism seems to be one of the important drivers in the history of human evolution (Alexander, 2004; Lovejoy, 1988). Hominin skeletal remains, such as the famous Australopithecus afarensis (A.L. 288-1) skeleton often referred to as “Lucy” (Johanson & Taieb, 1976; Johanson et al., 1982), have been a prominent part of the debate over the biomechanics of gait in our ancestors. Some researchers have argued that individuals with Lucy’s skeletal structure would have walked with a flexed-limb posture (Stern Jr. & Susman, 1983; Susman, Stern Jr., & Jungers, 1984), while others argue that she would have been a fully upright biped, walking with an erect posture in much of the same way that modern humans do (Carey & Crompton, 2005; Lovejoy, 2005). The argument for a flexed-limb gait is based on certain functional interpretations of Lucy's anatomy such as: the orientation of the iliac blades, the shape of the acetabulum, and a posteriorly tilted surface of the tibia (Stern Jr., 1999).

Some of the anatomic arguments supporting a fully upright walking style include the tibial plateau angle relative to the tibiotalar joint surface, the contour of femoral condyles, a pronounced lumbar lordosis, and a high femoral carrying angle (Barak et al., 2013). Furthermore, since the metabolic energy of humans walking with a BHBK posture increases by almost double when compared to an upright gait (Carey & Crompton, 2005), these researchers argue the metabolic energy required of a flexed-limb gait would have prohibited Lucy from walking any great distance with this posture. Trabecular evidence has also been used to support the upright walking hypothesis in Australopithecus afarensis (Barak et al., 2013). There are similarities in trabecular structure in the distal end of the tibia between modern humans and early hominins, but both are different from the trabecular structure in the tibia of chimpanzees. This argument is based on Wolff's Law, that loading patterns during locomotion influence the trabecular structure of lower limb bones (Wolff, 1986).

Many researchers have compared humans with chimpanzees or other living primates to gain insight regarding how the human-chimpanzee last common ancestor would have walked (Ogihara et al., 2010; Pontzer et al., 2009; Sockol et al., 2007). This has been done because the fossils of our human ancestors share skeletal features of both humans and other primates. However, a more recent discovery of an Ardipithecus ramidus fossil has shown that some skeletal features of our ancestors are shared by neither humans nor other primates (Lovejoy, 2009; White et al., 2009). While no existing species has the same musculoskeletal features as our human ancestor (of course), comparing the structure and function of the musculoskeletal systems for humans and chimpanzees while walking will allow for further insight into why humans generally walk with an upright posture and a straight leg during stance while chimpanzees walk with a flexed, abducted limb. Understanding how morphology impacts the decision to walk with an upright or crouched posture can further inform other studies seeking to interpret the factors underlying the evolution of human bipedal walking. There has also been some debate as to whether chimpanzees or macaques are better living representatives of the last common ancestor, but a recent study shows that these two species walk remarkably similar to each other (O'Neill et al., 2018). For this dissertation, we have focused on comparing humans with chimpanzees since the chimpanzee is the closest living relative for humans. Many of the questions about how early hominins would have walked remain unanswered. One significant application of studying healthy human flexed-limb gait and comparing the results to that from normal chimpanzee walking is it would allow for further discussion as to how early hominis would have walked, based on the morphological features in these species. Furthermore, manipulating the posture within our human subjects will provide important information about how the motion of one joint or segment can affect the motion of the other joints and segments during gait.

2.7 Summary

Humans and chimpanzees walk bipedally with different postures. Humans maintain an upright trunk and a relatively straight leg during stance phase while chimpanzees walk with a forward-leaning trunk and a flexed-limb during stance. Previous literature has established these differences in joint kinematics, as well as demonstrating that there are differences in ground reaction forces and muscle stresses. These differences in gait mechanics are greatly influenced by the differences in morphology that exist between chimpanzees and humans, but some differences in gait mechanics that are observed could be due to the constraints of a dynamically linked system. These constraints mean that changes in the motion of one joint could have broad effects on how the rest of the system moves during gait. Although it is difficult to manipulate the posture in chimpanzees, many studies have manipulated the posture of humans during gait for various purposes. Manipulating the posture in humans during gait allows for insight into the flexibility of the human body to various instructions and allows for the investigation of how one system can achieve different movement objectives. Musculoskeletal modeling and simulation techniques allow for the estimation of data that is difficult or impossible to obtain experimentally. These computer models can aid in the determination of how morphology and posture influence muscle function in different species. The goal of this dissertation is to tease apart the independent effects of posture and morphology in humans and chimpanzees during locomotion. By providing insight into the specific roles that morphology and posture play on the mechanics of bipedal walking, we can provide a stronger foundation for interpreting the functional significance of features seen in the fossil hominin record.

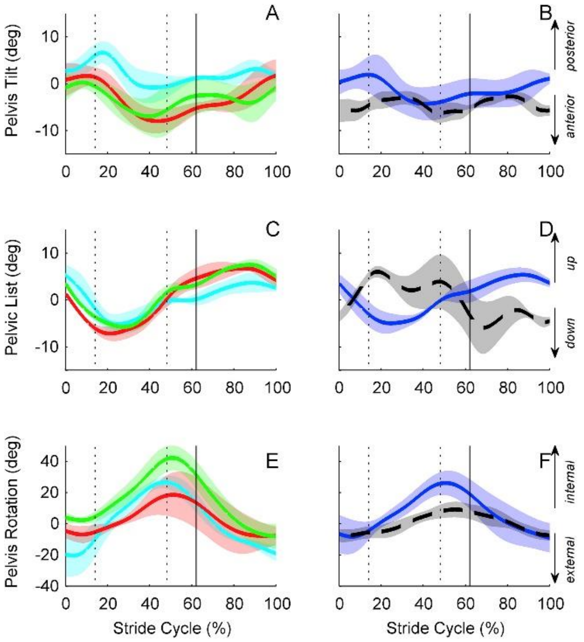


Figure 2.1: Pelvis tilt (A-B), list (C-D), and rotation (E-F) over a walking stride for three chimpanzees (left column) and chimpanzees (solid blue line) and humans (dashed black line) averaged across groups (right column). The dashed vertical lines show where toe off and heel strike occur for the contralateral limb and the solid vertical lines show were toe off occurs for the ipsilateral limb (O'Neill et al, 2015).

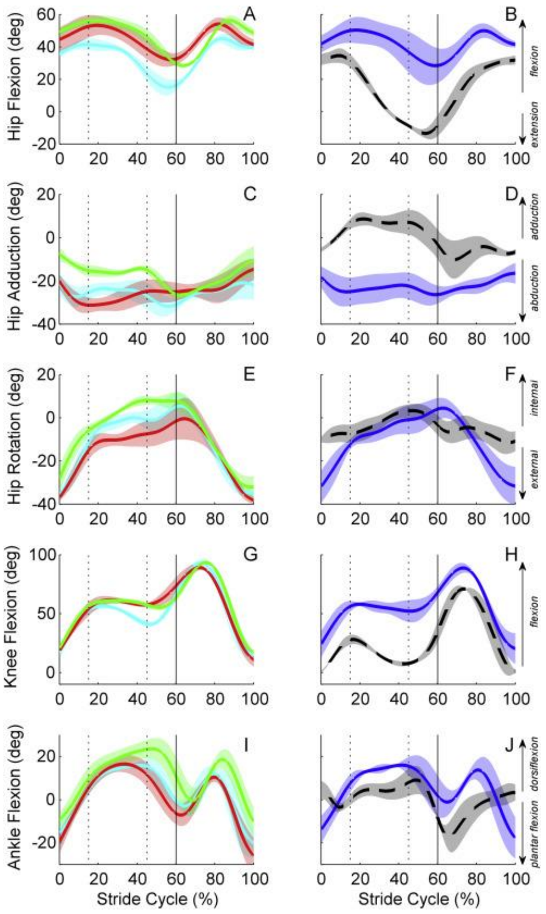


Figure 2.2: Hip flexion (A-B), hip adduction (C-D), hip rotation (E-F), knee flexion (G-H), and ankle flexion (I-J) for a stride for three chimpanzees (left column), and chimpanzees (solid blue line) and humans (dashed black line) averaged across groups (right column). The dashed vertical lines show where toe off and heel strike occur for the contralateral limb and the solid vertical line shows where toe off occurs for the ipsilateral limb (O'Neill et al, 2015).

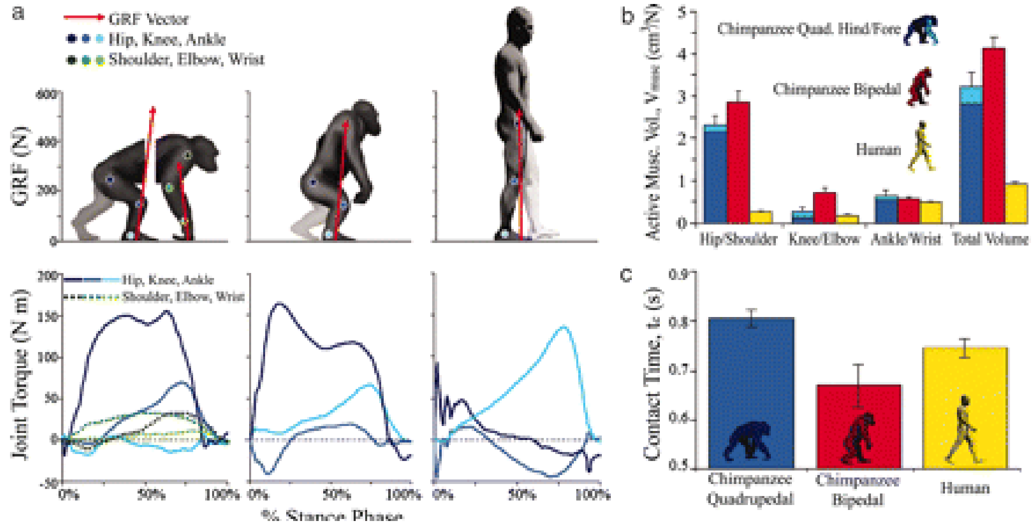


Figure 2.3: A) The top row shows a comparison of the walking postures for quadrupedal and bipedal chimpanzee gait and human upright gait, along with the ground reaction force vector relative to each joint. The bottom row depicts the joint torques at the hip, knee, and ankle for chimpanzees and humans. Note the much greater hip joint torque in chimpanzees compared with humans. B) Estimated activated muscle volume during gait for chimpanzees and humans. C) Mean contact time during walking in chimpanzees and humans.

CHAPTER 3

METHODS

The purpose of this dissertation is to further understand the roles of morphology and posture on gait mechanics in humans and chimpanzees. While humans and chimpanzees are both able to walk bipedally, and do so naturally to varying extents, the gait patterns each species uses to achieve bipedal walking are quite different. Human walking is characterized by extended legs during mid-stance, a double-peaked GRF, and an upright posture. Chimpanzees accomplish bipedal walking with a flexed-limb posture. Differences in gait mechanics between humans and chimpanzees occur in somewhat obvious ways in the sagittal plane, but there are also important differences in the frontal and transverse planes, including the range of motion in pelvis list and hip rotation as well as mean hip adduction angle. What is unknown is whether the differences in frontal and transverse plane motion are simply a consequence of the flexed limb posture adopted by the chimpanzees, or rather reflect the interspecific differences in morphology. One of the goals of this dissertation is to tease apart whether the differences in gait mechanics are due primarily to either the morphological features or the broad posture differences between species. Some of the differences in gait mechanics will be due to differences in morphology between these species, such as differences in pelvis shape, lumbar spine, and muscle-tendon design. However, some differences in gait mechanics between species may simply be due to the different postures used in walking and should be reduced when humans walk with a crouched posture similar to chimpanzees. In order to better understand the influence of posture on bipedal gait mechanics while controlling for morphology, human subjects will walk with a variety of different postures using instructions that induce differences, not only in the sagittal plane, but also the frontal and transverse planes. The gait mechanics for each of the different human postures will be compared to the chimpanzee gait results to analyze which of the human postures most closely replicates chimpanzee gait. These results will allow us to determine what, if any, differences in gait mechanics still exist when humans are instructed to walk with a similar posture to that of chimpanzees. The remaining differences in gait mechanics could demonstrate the limitations placed on gait mechanics by the morphology of humans. Additionally, even if the gait kinematics and GRFs produced by the human subjects in one or more of the postural conditions matches closely with chimpanzee results, there will still be differences in muscle function and coordination between the two species due to the differences in musculoskeletal structure. By providing insight into the specific roles that morphology and posture play on the mechanics of bipedal walking we can provide a stronger foundation for interpreting the functional significance of features seen in the fossil hominin record.

3.1 Study 1: The Roles of Morphology and Posture on Gait Patterns

The focus of this first study is to determine the effects of posture and morphology on joint kinematics and GRFs during gait. Ten human participants will be recruited for one lab visit. During the visit, each subject will be instructed to walk with different postures over four conditions while kinematic and GRF data are collected. The four human posture conditions will be used to determine the effects of posture on gait mechanics. For the morphology comparison, the human subject data will be compared with chimpanzee bipedal gait data from previously published literature (Demes et al., 2015; O'Neill et al., 2015; O'Neill et al., 2016). The comparisons between postures and between species will be evaluated using cross-correlation coefficients and root-mean-square differences. The results of this first study will provide insights into the roles of morphology and posture on preferred gait patterns. The results from this study will further serve as inputs into the second study of this dissertation project.

3.1.1 Human Subjects

Ten human subjects (5 male, 5 female) between the ages of 21-40 will be recruited. Each subject will have no gait pathologies that would affect the way they walk, and subjects must be in good health with no cardiovascular disease, neurological disease, or orthopedic problems that would affect how the subject walks. In addition, they will currently meet the national physical activity guidelines of 150 minutes of moderate to vigorous exercise each week (Garber et al., 2011). Each subject will be screened for age, health status, and self-reported physical activity level before being enrolled in the study. Before participating, subjects will complete a Physical Activity Readiness Questionnaire (PAR-Q) to assess their readiness to complete the study. The subjects will also read and sign an informed consent document to satisfy the requirements of the University of Massachusetts Amherst institutional review board.

3.1.2 Experimental Protocol

Each subject will have their weight, height, age and lower-limb length recorded. Subjects will wear lab-supplied tight-fitting clothing and will walk barefooted, since the chimpanzees also did not wear shoes during the data collection. Retro-reflective markers will be attached bilaterally to the lower limbs, pelvis, trunk, and head. The markers will be placed on the following locations: top of the head, manubrium of the sternum, 7th cervical vertebra, sacrum, right and left acromion processes, medial and lateral epicondyles of the elbow, medial and lateral aspects of the wrist, anterior superior iliac spines (ASIS), posterior superior iliac spines (PSIS), iliac crests, greater trochanters, lateral and medial epicondyles of the knee, lateral and medial malleoli, 1st and 5th metatarsal heads, and 2nd phalanges of the feet. In addition, clusters consisting of four markers will be placed on the lateral aspects of the right and left thigh and shank segments and clusters of three markers will be placed on each heel.

A static, standing calibration trial will be recorded prior to collecting the overground walking trials. Following the standing calibration, each subject will walk overground at two speeds: a preferred speed and a fixed speed of 1.09 m s^{-1} (± 3%) using four different postural conditions. The fixed speed is matched to the average, absolute walking speed for the previously-collected chimpanzee bipedal gait data (O'Neill et al., 2015). Preferred walking speed will be measured while having subjects walk back and forth along a 25-meter walkway. Subjects will be instructed to walk, without stopping, back and forth around two cones set up at either end of the walkway at a comfortable pace until they are asked to stop. Photoelectric sensors placed six meters apart will measure the time it takes for the subject to cover six meters in the middle of the walkway. After the subject completes two laps around the walkway they will be informed that the measurement has ended, with the average six-meter walking speed recorded four total times. The preferred walking speed will be calculated as the average of these four trials (Plotnik et al., 2015).

The four human postural conditions are (1) Normal, (2) Crouched-limb (CL), (3) Crouched-limb flexed-trunk (CLFT), and (4) human imitation of chimpanzee (IMIT). These conditions will be performed sequentially, due to the additive nature of the instructions, with the two speeds presented in a random order for each subject. For example, if the fixed speed is presented first, the order of the eight conditions will be: (1) Normal at fixed speed, (2) Normal at preferred speed, (3) CL at fixed speed, (4) CL at preferred speed, (5) CLFT at fixed speed, (6) CLFT at preferred speed, (7) IMIT at fixed speed, (8) IMIT at preferred speed. Half of the subjects will have the fixed speed presented first and half of the subjects will have the preferred speed presented first, with the order of the postural conditions remaining the same.

In the Normal condition, subjects will be instructed to "walk normally at the given speed." Before the CL condition, subjects will assume a static squat with 50^o of hip flexion and 30^o of knee flexion as measured by a goniometer, to match earlier human crouched-gait studies (Foster et al., 2013). The shoulder height of the subjects in this posture will be recorded. The measured shoulder height will be used as a target height for the subjects to follow for each of the CL gait trials, using a stiff wire stretched across the lab walkway. In the CL condition, subjects will be instructed to "walk while bending at the hips and knees to match the target height across the walkway at the given speed." Before the CLFT condition, subjects will assume a static squat with 30^o of trunk flexion, 50^o of hip flexion, and 30^o of knee flexion. The target trunk flexion angle of 30^o is set to match with bipedal chimpanzee data (Pontzer et al., 2014). The target height will be adjusted to match this new posture. In the CLFT condition, subjects will be instructed to "walk while bending at the trunk, hips, and knees to match the target height at the given speed." For the last condition (IMIT), each subject will be instructed to "walk like you did in the previous condition, but now focus on pitching your trunk and pelvis over the supporting limb during the swing phase." In addition, subjects will view a short, animated video of a chimpanzee walking bipedally and will be asked to imitate the motion of the chimpanzee. The imitation condition is similar to the CLFT condition, but with the specific instruction to modify frontal plane motion to match with how chimpanzees walk. For each of the eight conditions, subjects will have the opportunity to ask questions about the instructions and will practice the motion before trials are recorded. Before each condition, the subject will be asked to practice by walking overground across the force platforms using the prescribed posture and speed five times. From pilot testing, five practice trials were sufficient to allow the subject to feel comfortable with the new posture.

After sufficient time to practice and ask questions about the specific posture condition, subjects will walk overground across the walkway with three embedded force plates (AMTI, Watertown, MA, USA) while GRFs are recorded at 1200 Hz. Kinematic data will be collected at 240 Hz using an eleven-camera motion analysis system (Qualysis Track Manager, Gothenburg, Sweden). Overground speed will be measured using infrared photoelectric timing sensors placed six meters apart along the walkway. Three acceptable trials from each condition will be collected. A trial will be considered acceptable if the speed was within ± 3% of the given speed, the feet strike the force plates in the correct sequence, and the subject maintained the target posture throughout the trial.

3.1.3 Kinematics and Kinetics

A three-dimensional model of the human musculoskeletal system will be used to analyze the human gait patterns in this study within the OpenSim software package. The model has 23 mechanical degrees of freedom and is actuated by 80 muscle paths representing 76 muscles of the lower extremities and trunk (Anderson & Pandy, 1999; Delp et al., 2007; Lai, Arnold, & Wakeling, 2017). The head, arms, and trunk are modeled as a single rigid body that articulates with the pelvis via a ball-and-socket joint. Each hip is also modeled as a ball-and-socket joint. The knee is represented as a modified hinge joint with translations of the tibia relative to the femur that are coupled to knee flexion and extension (i.e. to better match the mobility of the human knee joint) (Yamaguchi & Zajac, 1989). The ankle-subtalar complex is represented as a universal joint, and the metatarsophalangeal joint is modeled as a hinge joint.

Joint kinematics will be calculated in OpenSim for each of the ten human subjects. For each subject, the generic musculoskeletal model will be scaled to match the anthropometrics of the subject based on the locations of the markers during the standing calibration trial. The generic model is scaled so that virtual markers on the model match the positions of the measured marker coordinates from the standing calibration. This subject-specific, scaled model is used to determine the generalized coordinates of the model during the walking trials using an inverse kinematics algorithm (Delp et al., 2007; Lu & O'Connor, 1999). The inverse kinematics algorithm minimizes the distance between the experimental markers and the virtual markers in order to evaluate the joint angles for each subject over every trial for each condition. Joint moments will also be calculated in OpenSim for each of the ten human subjects. The inverse dynamics tool built into OpenSim calculates joint moments based on the kinematics, the inertial properties of the model, and the measured ground reaction forces (Delp et al., 2007; Kuo, 1998).

3.1.4 Chimpanzee Data Collection Protocol

The chimpanzee kinematic and GRF data are drawn from previously published studied (O’Neill et al., 2015; Demes et al., 2015) with the methods summarized here for completeness. Three male common chimpanzees (age: 5.5 ± 0.2 years; mass: 26.5 ± 6.7 kg) walked across an 11-meter rigid, level walkway while three-dimensional kinematic data were collected at 150 Hz (O'Neill et al., 2015). Each chimpanzee was trained to walk bipedally using a food reward and positive reinforcement for at least 6 months before data collection began. The chimpanzees walked at self-selected speeds while following an animal trainer offering a food reward. An individually-scaled chimpanzee musculoskeletal model (O'Neill et al., 2013) was used to calculate joint angles using the same inverse kinematics approach in OpenSim described in section 3.1.3. The chimpanzee musculoskeletal model has 20 mechanical degrees of freedom and 88 muscles paths representing 70 muscles of the lower limbs and trunk (O'Neill et al., 2013). The musculoskeletal model was scaled to each of the three individuals using a short series of video frames obtained during the double-support phase of a stride. The GRFs for each trial were recorded at 1500 Hz (Demes et al., 2015). Joint moments will be calculated in OpenSim following the same procedure described in section 3.1.3.

3.1.5 Statistical Analyses

The pelvis tilt, pelvis list, pelvis rotation, hip flexion, hip adduction, hip rotation, knee flexion, and ankle flexion joint angles as well as the vertical, anterior-posterior, and medial-lateral GRFs will be compared across the different human postures and between species. The data will be time normalized to the stride time of each trial and the group average will be calculated for each condition. The following sets of analyses will be performed in two ways: first, the analyses will be performed using three human male subjects from the subject pool to match the number and sex of the chimpanzee subject pool, then the same set of analyses will be performed using all ten human subjects from the subject pool.

The adjusted coefficient of multiple correlation (CMC) will be calculated to compare the stride-to-stride and intraspecific variation of the pelvis and lower limb joint angles for each of the eight human posture conditions. The CMC calculation will be used to evaluate the correlation of the segment and joint motion for each individual and among individuals. The CMC values range from 0 to 1, with a value of 1 indicating that the data is perfectly correlated. The values calculated for the human data will be compared to previously published CMC data from the chimpanzee data set for an interspecific comparison between the two species (O'Neill et al., 2015).

Similarities in pattern and differences in magnitude for joint kinematics and GRFs will be evaluated using the group average data by calculating zero-lag cross-correlations (r) and root-mean-square differences (RMSD). The cross-correlation coefficient is a measurement of the similarity in pattern of joint kinematics and GRFs and will be calculated for each variable for each of the human conditions versus the chimpanzee data set. The cross-correlation coefficient (r) is calculated by

$$r = \frac{1}{\sqrt{R_{xx}R_{yy}}} R_{xy}$$

where x is an output variable from one condition (e.g. chimpanzee hip flexion angle) and y is the same output variable (e.g. human hip flexion angle in the Normal posture) from a second condition. R_{xx} is the dot product of x and x, R_{yy} is the dot product of y and y, and R_{xy} is the dot product of x and y. Cross-correlation coefficients range from -1 to 1, where a coefficient of 1 means the two output variables are identical and a coefficient of -1 means the output variables are reflected about the x-axis. Generally, a greater cross-correlation coefficient indicates the two variables are more similar to each other.

The RMSD value is a measurement of mean differences in the magnitudes of the joint kinematics and GRFs between conditions and between species. RMSD is calculated by

$$RMSD = \sqrt{\frac{1}{N} * \sum_{t=1}^{N} (x_t - y_t)^2}$$

where N is the number of time points (usually 101), x_t is the time series of an output variable for one condition (e.g. chimpanzee hip flexion), and y_t is the time series of an output variable for a second condition (e.g. human hip flexion in the Normal posture). The minimum value for the RMSD measurement is 0, which would indicate the two variables perfectly overlap with each other, while greater RMSD values give an indication of the amount of difference that exists between the two variables.

Similarities (using *r*) and differences (using RMSD) in joint kinematics and GRFs across postures will be evaluated by three comparisons for the four human conditions at each of the two speeds: Normal vs. CL, Normal vs. CLFT, and Normal vs. IMIT. Similarities and differences in gait mechanics due to differences in morphology will be evaluated by four comparisons using *r* and RMSD for joint angles and GRFs between: Chimpanzee vs. Normal, Chimpanzee vs. CL, Chimpanzee vs. CLFT, and Chimpanzee vs. IMIT for each of the two speeds.

For each comparison, the *r* and RMSD values will be computed for eight joint angles and the three orthogonal components of the GRF. To accommodate the large number of variables compared with each of the two statistics, four unique outcome measures will be computed. The two sums of the *r* and RMSD for the eight joint angles and the two sums of the *r* and RMSD for the three GRFs for each human versus chimpanzee comparison will be calculated. The human condition that has lowest value of RMSD and the highest value of *r* will be determined to be the most similar to the chimpanzee data set.

3.2 Study 2: The Roles of Morphology and Posture on Muscle Function

The focus of the second study will be to determine the effects of morphology and posture on the biomechanical function of muscles. In this study, muscle function is defined as the contribution of individual muscles, or in some cases muscle groups, to the acceleration of the whole-body center of mass in the vertical, anterior-posterior, and medial-lateral directions. The kinematic and GRF data from Study 1 will be used as the basis for the induced acceleration analysis. The results from the induced acceleration analysis will be compared by testing for differences in the relative contribution of each major muscle group to the anterior-posterior, medial-lateral, and vertical accelerations of the center of mass. The results of this study will provide insights as to how changes in posture and differences in morphology influence muscle function in bipedal walking.

3.2.1 Subjects and Experimental Protocol

The subjects and protocol from Study 1 will be used for Study 2.

3.2.2 Muscle Level Analysis

The joint kinematics and GRFs from Study 1 will be used to perform an analysis of the center of mass accelerations that are induced by the major lower limb muscles of humans and chimpanzees during level, bipedal walking (Zajac & Gordon, 1989). For both the human data and the chimpanzee data, the following procedure will be used.

Once the joint kinematics are computed from inverse kinematics, residual forces will be reduced by performing a residual reduction analysis (RRA) within OpenSim. RRA makes minor adjustments to joint kinematics and model segment inertial properties in order to reduce dynamic inconsistencies between the motion and the measured GRFs (Delp et al., 2007). RRA will be performed on each trial for each subject. The performance of RRA will be evaluated by its ability to reduce peak residual forces to below 10 N and average residual forces to below 5 N without changing the average joint kinematics by more than 2-5 degrees. With these new joint kinematic results, muscle forces will be predicted for each trial by performing a static optimization procedure within OpenSim.

Static optimization solves for muscle forces at each time point during the stride independently of any previous or subsequent time points, thereby making this procedure computationally efficient. Static optimization is based on inverse dynamics, and uses the calculated joint torques to solve a muscle load sharing problem. There are numerous muscles that cross each joint in the body which creates a redundancy problem in solving for muscle forces. Static optimization solves for muscle forces by minimizing the sum of squared muscle activations at each point in the gait cycle (Erdemir et al., 2007). Static optimization is solved within the OpenSim by minimizing the objective junction

$$J = \sum_{m=1}^{n} (a_m)^2$$

while solving the equations of motion for the joint torques subject to the muscle activation-to-force condition:

$$\sum_{m=1}^{n} (a_m F_m^0) r_{m,j} = \tau_j$$

where n is the number of muscles, $a_m$is the activation level of muscle m at a discrete time step, F_m^0 is its maximum isometric force, $r_{m,j}$ is its moment arm around the j^th^ joint axis, τ_j is the generalized force acting around the j^th^ joint. Predicted muscle activations from static optimization will be compared to published literature values to assure that the predicted muscle forces are reasonable before proceeding to the induced acceleration analysis.

An induced acceleration analysis (IAA) will be performed within OpenSim to determine how each muscle accelerates the whole body center of mass in the vertical, anterior-posterior, and medial-lateral directions for the human and chimpanzee data (Hamner et al., 2010; Steele et al., 2013; Zajac & Gordon, 1989). In complex movements that involve multiple muscles and many joints, it becomes difficult to identify how individual muscle forces influence the kinematics. IAA is able to establish the effect of a muscle force on the motion of the whole body, based on the magnitude of the muscle force and the orientation of the body at each time point. The acceleration potentials induced by unit muscle forces will be multiplied by the predicted muscle forces from static optimization to obtain the center of mass accelerations induced by each muscle. The induced acceleration, *IAA*, of muscle *j* is defined as the contribution of muscle *j* to all system accelerations according to:

$$IAA_j = M(q)^{-1} R^{(j)}(q) F_{MT_j}$$

where $R^{(j)}(q)$ is the jth column of the muscular moment arm matrix *R*(*q*), $M(q)^{-1}$ is the inverse of the system mass matrix, and F_{MT_j} is the force of the j^th^ muscle. The calculated induced accelerations will be verified by checking the sum of the constraint reaction forces computed during the induced acceleration analyses closely match the measured GRFs (Hamner et al., 2013).

3.2.3 Statistical Analysis

The following statistical tests will be performed in two ways: first, the analyses will be performed using three human male subjects from the subject pool, then the same set of analyses will be performed using all ten human subjects from the subject pool (See section 3.1.5). The contributions of each of nine major muscles or muscle groups to anterior-posterior, medial-lateral, and vertical COM accelerations will be evaluated for each of the different human postures at both speeds and between the two species. The gluteus maximus, gluteus medius, iliopsoas, hamstrings group, vasti group, rectus femoris, gastrocnemius, soleus, and tibialis anterior muscles will be the primary muscles analyzed. These muscles have been selected as they have been shown to be the principle muscles utilized to accelerate the COM during human walking (Anderson & Pandy, 2003; Liu et al., 2008a). Beyond the primary muscles, the induced accelerations for all muscles that are included in the human (80 total muscles) and chimpanzee (88 total muscles) models will be analyzed, and if there are any other muscles that make a major contribution to the acceleration of the COM those muscles will be included for comparison as well. For each muscle and species, the average contribution to anterior-posterior, medial-lateral, and vertical COM accelerations will be calculated for each trial (Steele et al., 2013). Differences in muscle function across postures will be evaluated by determining the differences in the average contribution of each muscle to the induced acceleration of the COM between the human posture conditions using a two-way ANOVA, with speed and posture as the two factors. Differences in muscle function due to differences in morphology will be evaluated by comparing the chimpanzee induced acceleration results to the most similar human posture condition evaluated from Study 1 using a t-test (based on the *r* and RMSD results).

CHAPTER 4

PROPOSAL AMENDMENTS: AMENDEMENTS TO THE PROPOSED METHODS

This chapter describes the modifications made to the experiments and analyses between the proposal stage and the final document. The studies maintained all of the originally proposed experimental protocols, however some changes to the proposed analyses were necessary.

The three male humans versus three male chimpanzee comparisons proposed for Study 1 are presented in an appendix (Appendix 1). Overall, these results did not show any distinctive trends when compared with the ten humans versus three chimpanzee comparisons, and where it did show some moderate effect, the results were sensitive to which of the three male humans were input into the analyses. In addition, the three male human versus three male chimpanzee comparison was not done for study 2 because of the lack of distinction showed with this comparison in study 1.

In study 1 (Chapter 5), I originally proposed to present coefficients of multiple correlation for each of the human posture conditions to compare with the coefficients of multiple correlation presented in O’Neill et. al. (O'Neill et al., 2015). However, these results are not presented in this document. The equations used to calculate the coefficients of multiple correlation can give negative numbers inside a square root, ultimately resulting in imaginary numbers. Imaginary numbers were found in our analyses for several of the output variables, and as such this analysis is not presented. Future work will be done to try to more accurately account for variability between human postural conditions.

There were slight modifications made to the statistical methods for study 2 (Chapter 6). In addition to the two-way repeated measures ANOVA performed on the muscle analyses, I then used a false discovery rate procedure (Benjamini & Hochberg, 1995) to test for differences between posture conditions.

CHAPTER 5

STUDY ONE

5.1 Introduction

Upright, bipedal walking is a distinguishing feature of human evolution, setting humans apart from other primates (Lovejoy, 1988). Human gait is characterized by extended limbs during stance phase, a vertically oriented trunk, and a distinctly two-peaked vertical ground reaction force (GRF) (Alexander, 2004; Foster et al., 2013; Grasso et al., 2000). Our closest living relatives, chimpanzees, being facultative bipeds, can walk on their hind limbs, but they do so with a flexed and abducted hind limb, a forward-projected trunk, and pelvis motion distinctly different from humans (Elftman, 1944; Jenkins, 1972; O'Neill et al., 2015; Pontzer et al., 2014). While musculoskeletal morphology likely plays a key role driving the differences in bipedal gait mechanics, it is also likely that the distinct habitual postures used by each species also impacts their unique gait mechanics. For this study, we define posture as the general orientation of the trunk, pelvis, and lower/hind limbs during walking (e.g., upright versus crouched), and the term gait mechanics refers to specific variables such as joint angles and GRFs that change over the course of the stride during gait. Understanding how musculoskeletal morphology and posture impact gait mechanics can allow researchers to better understand why humans walk differently from chimpanzees and other facultative bipeds and can help researchers interpret how bipedalism evolved in the hominin fossil record.

While it is known how modern humans and chimpanzees walk, it remains unclear how our hominin ancestors would have walked. There has been much debate about the gait kinematics of earlier hominins, such as *Australopithecus afarensis* or *Ardipithecus ramidus* (Crompton et al., 1998; Lovejoy, 2005; Stern Jr. & Susman, 1983; Stern Jr., 1999; Ward, 2002). Given that these species are extinct, it is not possible to observe and measure how earlier hominins walked. Therefore, the interpretation of how these extinct species walked is crucially dependent upon the fossil record, and a judgement of how specific traits preserved in the fossil record would have influenced posture and gait mechanics. A primary question in evolutionary biomechanics is when our hominin ancestors began to walk with an upright posture like modern humans, rather than on flexed limbs like modern chimpanzees (O'Neill, Demes, Thompson, & Umberger, 2018). Researchers have disagreed about how *Ar. Ramidus* and *Au. afarensis* walked (upright or crouched) despite having access to the same fossil materials (Lovejoy & McCollum, 2010; Stern Jr., 1999). Therefore, it is important to better understand how morphology impacts gait mechanics in humans and other primates, which can help researchers better interpret the hominin fossil record. While the morphologies of humans and chimpanzees are both distinct from their last common ancestor and other hominins, understanding the structure-function relationship in humans and chimpanzees can yield insight into how specific morphological features impact gait mechanics.

There are several differences in musculoskeletal morphology between humans and chimpanzees that are thought to contribute to their unique gait mechanics (Figure 5.1). The shape of the lumbar column and pelvis have been proposed to be strong determinants of the distinct gait mechanics between humans and chimpanzees (Lovejoy, 2005). Chimpanzees lack a lumbar lordosis, which might make it more difficult to orient their trunk vertically during bipedal walking; instead their trunk is projected forward. One hypothesis is chimpanzees walk with a flexed-limb posture to place their base of support underneath their whole-body center of mass as a compensation for a forward leaning trunk (Lovejoy, 2005).

Another morphological feature that could account for the flexed limb posture chimpanzees adopt during gait is the shape of their pelvis, with some important differences between humans and chimpanzees in the length and orientation of the ischium, the orientation of the iliac blade, and the iliac blade height (Fleagle & Anapol, 1992). These skeletal features affect the muscle paths and muscle moment arms of the hip extensors and hip abductors (Kozma et al., 2018; McHenry, 1975). Chimpanzees can produce large hip extension moments when their hip is flexed due to a large muscle moment arm at the hamstrings in this position (O'Neill et al., 2013), which is a functional limb posture for climbing. However, chimpanzees are unable to produce large hip extension moments when their leg is fully extended due to a much smaller hamstrings moment arm. Therefore, chimpanzees may walk with a flexed-limb posture to take advantage of the greater hamstring moment arm in this flexed position (Fleagle & Anapol, 1992; Kozma et al., 2018).

There are several other musculoskeletal differences between humans and chimpanzees that could also play an important role in shaping gait mechanics, including differences in foot structure which may affect the push-off phase of walking (Caravaggi et al., 2010; Fernandez et al., 2016; Holowka et al., 2017), bicondylar knee valgus angle which may help humans place their feet underneath their center of mass (Lovejoy, 2007; Shefelbine et al., 2002), and muscle-tendon architecture including a greater percentage of fast-twitch muscle fibers in the lower limbs of chimpanzees (O'Neill et al., 2017). The sum of all of these morphological differences likely drives some of the observed differences in preferred gait mechanics in humans and chimpanzees; however, a confounding factor in evaluating these musculoskeletal effects is the difference in habitual posture between these species, as humans walk upright with extended limbs and chimpanzees use a crouched posture.

Broad changes in posture will affect the way an individual walks because individual body segments are dynamically coupled, such that the orientation and motion of any one segment will have global effects on the movement of the whole body (Aminiaghdam et al., 2017; Grasso et al., 2000). The linked-segment nature of the body means that changing the orientation or motion at one segment or joint will often necessitate a change in how the other segments move while still achieving the movement objective, such as locomotion. Therefore, some of the interspecific differences in gait mechanics observed between humans and chimpanzees could be explained by the upright posture in humans, versus the crouched posture of chimpanzees, and may be independent of morphology.

Since it is not possible to collect experimental data on extinct hominin species, one avenue for studying the evolution of bipedalism has been to instruct humans to walk with a crouched posture to investigate factors, such as metabolic energy expenditure and muscle force production, that may influence preferred gait patterns (Carey & Crompton, 2005; Foster et al., 2013). These studies then make inferences on how our hominin ancestors might have walked (upright or crouched) based on how modern humans perform crouched-posture walking. For example, concluding that if modern humans have difficulty performing crouched gait, then our hominin ancestors would have not used a crouched posture (Carey & Crompton, 2005). However, it is unclear if the way that modern humans walk with a crouched posture would be similar to the way a species adapted to crouched-posture walking would. Since chimpanzees are facultative bipeds, it is possible to compare humans walking with crouched postures directly to chimpanzees, but until recently (O'Neill et al. 2015) there were no 3-D kinematic data for chimpanzees on which to base a comparison. There is some evidence to suggest that human crouched posture walking is distinct from chimpanzee bipedal gait, as previous studies have documented that humans maintain a more upright, vertically-aligned trunk segment when asked to walk with a crouched-limb posture (Foster et al., 2013), rather than the forward-projected chimpanzee trunk. In addition, there are documented differences in center of mass mechanics between bipedal chimpanzees and humans walking with a crouched posture (Demes et al., 2015). The remaining differences in gait mechanics when humans walk with a crouched posture are important to document because they can have consequences for how the muscles of the lower limbs function (Foster et al., 2013; Sockol et al., 2007) and can have implications for interpreting the gait mechanics of hominin ancestors (Crompton et al., 1998).

It is likely that both morphology and posture play important roles in determining gait mechanics. Unlike the case with chimpanzees, human posture during locomotion can be easily manipulated by giving instructions and feedback to participants. Manipulating human posture in ways that imitate chimpanzee gait allow for the determination of what, if any, differences in gait kinematics and ground reaction forces still exist when humans are instructed to walk in a manner similar to that of a chimpanzee. The remaining differences in gait mechanics may be due to constraints associated with musculoskeletal morphology, preventing humans from fully reproducing chimpanzee-like gait mechanics.

Additionally, comparing different human posture conditions can give insight into how the orientation and motion at one segment can affect the movement of other segments in a dynamically-coupled system. Comparing the similarities and differences of human and chimpanzee gait mechanics may provide insight into how gait mechanics are influenced by morphology and how these unique patterns have evolved. Therefore, the *aim of this study* was to determine the degree to which human kinematics and GRFs converge to those of chimpanzees as humans walk with different crouched postures. We instructed humans to walk with four different instructions: normal walking, crouched-limb (CL) walking, crouched-limb flexed-trunk (CLFT) walking, and a condition with specific instructions to imitate the pelvis tilt kinematics of a chimpanzee during walking while maintaining the CLFT posture (IMIT). The CL and CLFT conditions were given sequentially to produce chimpanzee-like kinematic motion in the sagittal plane. Following these conditions, the IMIT condition was then given as a way to produce chimpanzee-like frontal plane motion at the pelvis. These human posture conditions were compared to normal chimpanzee bipedal walking collected and published in O’Neill et al. (O'Neill et al., 2015). We *hypothesized* that the joint kinematics and GRFs from the IMIT condition would be most similar to the chimpanzee data. In addition, the joint kinematics and GRFs from the CLFT condition would be more similar to the chimpanzee data than the CL condition.

5.2 Methods

5.2.1 Human Experimental Protocol

Ten healthy, recreationally-active human subjects [5 male/5 female; age: 27 ± 5 years; height: 1.70 ± 0.08 m; mass: 68 ± 11 kg; leg length: 0.88 ± 0.04 m] were recruited for this study. Each subject had no history of gait pathologies and was in good health with no known cardiovascular disease, neurological disease, or orthopedic problems that would affect how the subject walked. Subjects self-reported that they met the American College of Sports Medicine physical activity recommendations by exercising at least 150 minutes per week at a moderate to vigorous level (Garber et al., 2011). Before participating, subjects read and signed an informed consent document approved by the University of Massachusetts Amherst institutional review board. Subjects also completed a Physical Activity Readiness Questionnaire to assess their readiness to complete the study.

After recording each subject's mass, height, age, and lower-limb length, retro-reflective markers were attached bilaterally to the lower limbs, pelvis, trunk, and head of each subject (Figure 5.1). Subjects then walked at a comfortable speed for five laps back and forth in the lab (20 m length) covering a total of 200 meters to assess preferred walking speed. Walking speed was measured using two photoelectric timing sensors placed six meters apart in the middle of the walkway. This 6-meter speed was recorded during the last four laps of the 200-meter walk and averaged across the four trials to calculate preferred walking speed for each subject.

There were four human postural conditions: (1) normal (Norm), (2) crouched-limb (CL), (3) crouched-limb flexed-trunk (CLFT), and (4) human imitation of chimpanzee (IMIT). These conditions were performed sequentially due to the additive nature of the instructions. Subjects performed each postural condition at two different speeds; their preferred walking speed and at a speed that matched the average, absolute walking speed for previously collected chimpanzee bipedal gait data (fixed speed; 1.09

m/s) (O'Neill et al., 2015). While the order of the postural conditions was performed sequentially, the order of the two speeds was presented randomly among subjects.

In the Normal condition, subjects were instructed to “walk normally at the given speed.” The CL condition was designed to mimic, as best as possible, the study designs from previous crouched posture research (Carey & Crompton, 2005; Foster et al., 2013). Before the CL condition, subjects assumed a static squat with 50^o of hip flexion and 30^o of knee flexion as measured by a goniometer, to match earlier human crouched-gait studies (Foster et al., 2013). The measured shoulder height in this static posture was used as a target height for the subjects to follow for each of the CL trials, using a rope stretched across the lab walkway at the measured shoulder height. In the CL condition, subjects were instructed to “walk while bending at the hips and knees to match the target height across the walkway at the given speed.” The CLFT condition was intended to target the difference in trunk angle between humans and chimpanzees during bipedal walking, and was based on the chimpanzee trunk angle from Pontzer et al. (Foster et al., 2013; Grasso et al., 2000; Pontzer et al., 2014). Before the CLFT condition, subjects assumed a static squat with 30^o of trunk flexion, 50^o of hip flexion, and 30^o of knee flexion. The target trunk flexion angle of 30^o was set to match with bipedal chimpanzee data (Pontzer et al., 2014). The target rope height was adjusted to match this new posture. In the CLFT condition, subjects were instructed to “walk while bending at the trunk, hips, and knees to match the target height at the given speed.” For the last condition (IMIT), each subject was instructed to “walk like you did in the previous condition, but now focus on pitching your trunk and pelvis over the supporting limb during the swing phase.” In addition, subjects viewed a short, animated video of a chimpanzee walking bipedally and were asked to imitate the overall motion of the chimpanzee. The IMIT condition was similar to the CLFT condition, but with the specific instruction to modify frontal plane pelvis motion to match with how chimpanzees walk. This condition was designed to specially address one of the important frontal plane differences in normal gait kinematics measured in humans and chimpanzees (O'Neill et al., 2015).

At the beginning of the data collection, a static calibration trial was recorded prior to collecting any of the overground walking trials. For each of the eight conditions (four postures times two speeds), subjects walked overground across a walkway with three embedded force plates (AMTI, Watertown MA, USA) while GRFs were recorded at 1200 Hz. Kinematic data were collected simultaneously at 240 Hz using an eleven-camera motion capture system (Qualisys Track Manager, Gothenburg, Sweden). Overground speed was measured using the two photoelectric timing sensors placed six meters apart in the middle of the walkway. Before each of the conditions, subjects practiced the motion for no less than three walking bouts and had the opportunity to ask questions about the instructions before trials were recorded. Three acceptable trials were recorded for each of the eight conditions. A trial was considered acceptable if: the speed was within ± 3% of the target speed, the feet cleanly struck each of the three force plates in the correct sequence, and the subject maintained the target posture throughout the trial. Maintenance of the target posture was assessed visually, with the help of the rope stretched along the walkway.

A three-dimensional model of the human musculoskeletal system from the OpenSim software package was used to analyze the kinematic patterns for each human condition (Delp et al., 2007; Lai et al., 2017). The model has 21 mechanical degrees of freedom, with the head, arms and trunk segment modeled as a single rigid body that articulates via a ball-and-socket joint with a six degree-of-freedom pelvis segment. The hip was modeled as a ball-and-socket joint and the knee was represented as a modified hinge joint with translations of the tibia relative to the femur that are coupled to knee flexion and extension (i.e. to better match the mobility of the human knee joint) (Yamaguchi & Zajac, 1989). The ankle and metatarsophalangeal joints were each modeled as hinge joints. For each of the ten subjects, a generic model was scaled to best match the anthropometrics of the individual subject based on a static, standing calibration trial. The scaled model was then used to determine the generalized coordinates for each trial using the inverse kinematics algorithm in OpenSim (Delp et al., 2007; Lu & O'Connor, 1999). The results from the inverse kinematics tool were then used as inputs for all subsequent analyses.

5.2.2 Chimpanzee Experimental Protocol

The chimpanzee kinematic and GRF data were drawn from previously published studies (Demes et al., 2015; O'Neill et al., 2015) with the methods briefly presented here. Three male common chimpanzees (age: 5.5 ± 0.2 years; mass: 26.5 ± 6.7 kg; hind limb length: 0.39 ± 0.02 m) walked overground while three-dimensional kinematic data were recorded at 150 Hz and GRF data were recorded at 1500 Hz. Each chimpanzee was trained to walk bipedally using a food reward and positive reinforcement for at least six months before data collection began. The chimpanzees walked at self-selected speeds while following an animal trainer offering a food reward. A generic chimpanzee musculoskeletal model (O'Neill et al., 2013) was scaled to each individual chimpanzee using a short series of video frames obtained during the double support phase. The chimpanzee musculoskeletal model has 16 mechanical degrees of freedom representing the hind limbs and pelvis segments. The mechanical degrees of freedom in the chimpanzee model were consistent with the human model for the pelvis, hips, knees, and ankles. However, unlike the human model, the chimpanzee model did not have a separate segment for the trunk and did not have a metatarsophalangeal joint in the foot. The individually-scaled models were used to calculate joint angles using the inverse kinematics approach in OpenSim.

5.2.3 Statistical Analysis

The pelvis tilt, pelvis list, pelvis rotation, hip flexion, hip adduction, hip rotation, knee flexion, and ankle flexion joint angles as well as the vertical, anterior-posterior (AP), and medial-lateral (ML) components of the GRF were compared for each of the eight different human posture conditions to the chimpanzee normal walking condition. The data for each trial were time normalized to the stride time, averaged across trials for each condition within each subject, and then was averaged across conditions within each group. Each of the following analyses and comparisons were performed using the ten human subjects and the three male chimpanzees.

Similarities in pattern and differences in magnitude for joint kinematics and GRFs were evaluated using the group average data by calculating zero-lag cross-correlations (*r*) and root-mean-square differences (RMSD). The cross-correlation coefficient is a measurement of the similarity in pattern of joint kinematics and GRFs between humans and chimpanzees, and was calculated for each variable for each of the human conditions versus the chimpanzee data set. The *r* was calculated with zero lag so that the similarity in pattern for each variable was relative to the timing of the gait cycle. Generally, a greater *r* (closer to 1) indicates the two variables are more similar to each other in pattern. The RMSD value is a measurement of mean differences in the magnitudes of the joint kinematics and GRFs for each human condition compared with the chimpanzee data. The minimum value for the RMSD measurement is 0, which would indicate the variable perfectly overlaps between species, while greater RMSD values give an indication of the amount of difference in magnitude that exists in that variable between the two species.

Similarities and differences in gait mechanics were compared between species by calculating the *r* and RMSD for each joint angle and GRF variable between the bipedal chimpanzee data and each of the eight human posture conditions: Chimpanzee vs. Normal, Chimpanzee vs. CL, Chimpanzee vs. CLFT, and Chimpanzee vs. IMIT for the both the preferred and fixed human walking speeds. For each comparison, the *r* and RMSD values were computed for the three pelvis segment angles, five joint angles, and the three orthogonal components of the GRF. To accommodate the large number of variables computed, four unique outcome measures were computed for each human versus chimpanzee comparison. The average of the *r* and the average of the RMSD for the eight kinematic variables were calculated to broadly compare the kinematics between species. The average of the *r* and the average of the RMSD for the three GRFs were also calculated to broadly compare the kinetics between species. The human condition that had lowest value of RMSD and the highest value of *r* was determined to be the most similar to the chimpanzee data set.

5.3 Results

The average preferred walking speed for the ten human subjects was 1.30 ± 0.15 m s^{-1}. During the human fixed speed conditions, the human subjects were able to closely match (1.10 ± 0.02 m s^{-1}) the average chimpanzee bipedal walking speed (1.09 m s^{-1}; Table 5.1). The human subjects took longer and quicker strides during the faster, preferred speed conditions than during the fixed speed conditions (Table 5.1). The chimpanzee strides were shorter and quicker than the human strides for both the preferred and fixed conditions (Table 5.1). There were only small differences in kinematics and GRFs between the two human speeds for each postural condition, therefore results for the two human speeds will be discussed together in the following paragraphs.

5.3.1 Pelvis Kinematics

Pelvis angles were calculated in the global reference frame relative to a neutral position for both the human and chimpanzee gait data. On average, in the normal human conditions (both fixed speed and preferred speed conditions), the pelvis was tilted forward between 5 and 10 degrees throughout the gait cycle (Figure 5.2A). In the chimpanzee bipedal gait trials, the pelvis was oriented in a relatively neutral position throughout the gait cycle. The pelvis tilt angle was similar for the normal human conditions and the chimpanzee bipedal gait (Table 5.2). However, each of the human crouched posture conditions resulted in greater pelvis tilt angles (between 10 – 20 degrees) than in chimpanzee gait (Table 5.3).

In the frontal plane during the normal human walking conditions, the pelvis is listed downwards towards the swing-side limb; however, chimpanzees raise their pelvis on the swing-side (Figure 5.2B). This results in these two pelvis list patterns being out-of-phase with each other as shown by the negative *r* values in Table 5.2. The human crouched postures, especially the IMIT condition, resulted in the pelvis list pattern and magnitude to become more chimpanzee-like, but it did not closely match the chimpanzee pattern, with the greatest *r* value being less than 0.5 (Tables 5.2 and 5.3).

Both the human and chimpanzee subjects internally rotated their pelvis during the first half of the gait cycle, followed by external pelvis rotation during the second half of the gait cycle (Figure 5.2C). However, the chimpanzees had a greater pelvis rotation range of motion during gait than for any of the human conditions (Table A.5). There were some subtle differences in pelvis rotation between the human posture conditions, however the normal human posture conditions produced the most similar pelvis rotation motion in both pattern (Table 5.2) and magnitude (Table 5.3), but was still quite different from the chimpanzee motion.

5.3.2 Hind-limb Kinematics

The human hip flexion angle was more extended throughout stance phase during the normal human posture conditions (for both speeds) compared to normal chimpanzee hip flexion (Figure 5.2D). There was a greater hip flexion angle during the human crouched posture conditions than the normal conditions, consistent with the instructions for these conditions. These human crouched posture conditions produce a hip flexion motion that is more similar in both pattern (Table 5.2) and magnitude (Table 5.3) to the chimpanzees than the normal human conditions. There were only small differences in hip flexion motion between the different human crouched posture conditions. The most chimpanzee-like hip flexion patterns occurred during the CLFT and IMIT conditions (Table 5.2). While the most similar hip flexion magnitude occurred in the CL conditions, the CLFT and IMIT conditions were relatively similar to the CL condition in hip flexion magnitude (Table 5.3).

In the normal human conditions, the hip begins the gait cycle in an abducted position, adducts during the early part of stance phase, and then abducts during late stance (Figure 5.2E). In contrast, chimpanzees have greater hip abduction angles throughout the stance and swing phases. During the human crouched-posture conditions, the hip is abducted for the entire gait cycle, but to a lesser amount than in chimpanzees. The additional instructions provided during the IMIT condition produced the most similar frontal plane hip motion in pattern (Table 5.2) and magnitude (Table 5.3). However, while the magnitude of the human hip abduction angle during the crouched-posture conditions approaches the magnitude of the chimpanzees, it peaks at about 15 degrees instead of reaching a magnitude of 20-25 degrees.

Both humans and chimpanzees internally rotate their hip during stance phase and externally rotate their hip during swing phase, however the chimpanzees have a greater range of motion in this direction than any of the human conditions (Appendix A.5; Figure 5.2F). There were only small differences in hip rotation between the human posture conditions, with the IMIT conditions producing the most chimpanzee-like hip rotation pattern (Table 5.2), while the normal conditions had the most chimpanzee-like hip rotation magnitude (Table 5.3).

During the normal human conditions, the knee angle had a more extended position than the chimpanzee knee angle (Figure 5.2G). Providing the humans with instructions to walk with a crouched posture produced a knee flexion motion that was more similar in pattern (Table 5.2) and magnitude (Table 5.3) to the chimpanzee knee flexion than normal human conditions. The pattern of knee motion was more similar to chimpanzees during each of the crouched posture conditions compared to the normal condition, and the IMIT condition had the greatest *r* value. While there were only small differences in knee flexion magnitude between the human crouched posture conditions, the CL condition produced the smallest knee flexion RMSD value.

For the human conditions, during early stance phase the ankle was rapidly plantar flexed, then gradually dorsiflexed throughout midstance followed by a rapid plantar flexion motion during the push-off phase. During the human crouched posture conditions, the ankle joint maintained a more dorsiflexed position when compared to the normal human conditions, with a pattern of motion that was similar to the normal conditions. When comparing the motion of the human ankle to the chimpanzee ankle, the *r* values were relatively similar among the different posture conditions (Table 5.2). However, the normal human conditions produced an ankle motion that was most similar in magnitude to the chimpanzees (Table 5.3).

5.3.3 Ground Reaction Forces

The humans and chimpanzees both produced a negative, braking AP GRF during the first half of stance and then a positive, propulsive AP GRF during the second part of stance (Figure 5.3A). The most notable difference between the human and chimpanzee AP GRF occurred during late-stance, where the peak positive AP GRF for the human conditions was greater than the chimpanzees. When compared with the normal human conditions, the human crouched posture conditions produced only slightly more chimpanzee-like AP GRF patterns (Table 5.4) and magnitude (Table 5.5).

The normal human condition resulted in a double-peaked vertical GRF pattern (Figure 5.3B). During the crouched posture conditions, the vertical GRF still had a two-peaked shape but had a lesser second peak in each of the human crouched postures than was seen in normal human gait. The chimpanzee vertical GRF had only one distinct peak and the peak occurred before mid-stance. The vertical GRFs during the human crouched posture conditions were more similar in pattern (Table 5.4) and magnitude (Table 5.5) to the chimpanzee vertical GRF, with only subtle differences in pattern among the different human crouched posture conditions.

In the human conditions, the ML GRF had a positive, medial peak during early stance and then maintained a negative, lateral GRF during mid-stance (Figure 5.3C). The human crouched posture conditions produced greater lateral GRFs during mid-stance than the normal human conditions. When compared to any of the human conditions, the chimpanzees produced greater magnitude lateral GRFs throughout the middle of stance phase. The human crouched posture conditions resulted in ML GRFs that were more similar in pattern to the chimpanzee ML GRFs (Table 5.4), and the human IMIT preferred condition had the least deviation from the chimpanzee ML GRFs (Table 5.5).

5.3.4 Zero-lag Cross Correlation (r) and Root-Mean-Square Difference (RMSD) Averages for Kinematics and GRFs

Overall, when evaluating the kinematics and ground reaction force patterns using the average *r* between the humans and chimpanzees, the IMIT conditions produced the most chimpanzee-like kinematic (Table 5.2) and GRF (Table 5.4) patterns. The CL and CLFT conditions produced average *r* kinematics values that fell between the normal and IMIT conditions, but contrary to our hypothesis, the CLFT conditions did not result in a more chimpanzee-like gait pattern than the CL conditions. The ground reaction forces among the three human crouched postures were similar in pattern when evaluated using the cross-correlation coefficients. In comparing the magnitude differences between the human conditions and the chimpanzee gait based on the RMSD values, there was a distinction between the normal human conditions and the set of crouched posture conditions. The average RMSD value was greater in the normal human condition than in the human crouched posture conditions, but the RMSD values between each of the crouched posture conditions were broadly similar to each other for both the kinematic and ground reaction force data.

In assessing which of the human posture conditions was the closest match to the chimpanzee gait kinematics and ground reaction forces, it was determined that the IMIT preferred speed condition was the most similar to chimpanzee bipedal gait. The IMIT preferred speed condition was determined to be the most “chimpanzee-like” because it had the greatest average kinematic *r* value when compared to the other human posture conditions, and had a similar value in the other three metrics (GRF *r* and both RMSD averages) to other crouched posture conditions. The six human crouched posture conditions were relatively similar using the other metrics: average GRF *r*, average kinematic RMSD, and average GRF RMSD.

5.4 Discussion

Our hypothesis was that the instructions given during the CL, CLFT, and IMIT conditions would result in gait kinematics and GRFs that were more chimpanzee-like than normal human walking. Our results indicate that the instructions did result in a more chimpanzee-like gait, however there was not a clear, stepwise improvement in the chimpanzee-like gait mechanics with additional instructions. On average, there was no difference between the CL and CLFT posture conditions in gait kinematic patterns. The IMIT condition resulted in the most chimpanzee-like kinematic pattern (as measured by *r*), but the GRF pattern and the magnitudes of the kinematics and GRFs (as measured by RMSD) were similar among the six crouched posture conditions. The greater average kinematic *r* value in the IMIT conditions compared to the CL or CLFT conditions was mostly driven by a more chimpanzee-like pelvis list pattern, in direct response to the instructions to modify the pelvis list motion for the IMIT conditions. When comparing the human crouched posture conditions to the chimpanzee bipedal gait, some substantial differences in gait mechanics remained. Unlike the chimpanzees, the human subjects maintained a double-peaked GRF, had distinctly different pelvis motion, and did not abduct their hip to the same magnitude as was seen in the chimpanzees.

5.4.1 Kinematics

Although the human CL and CLFT instructions only targeted sagittal plane motion, these conditions also resulted in altered frontal plane kinematics. When humans walked with these crouched postures, they employed a different pelvis list pattern and had an abducted hip throughout stance phase. The frontal plane pelvis and hip motion in these posture conditions were more similar to chimpanzee-like kinematics than the normal human conditions. This suggests that the crouched posture itself contributes to why chimpanzees and other non-human primates elevate their pelvis on the swing side and walk with an abducted hind limb (Jenkins, 1972; O'Neill et al., 2015; O'Neill et al., 2018). Elevating the pelvis on the swing side is likely performed to aid with foot clearance as the leg is swung forward in preparation for the next step, this helps the foot to clear the ground in combination with greater hip and knee flexion during the crouched posture conditions.

While the human crouched posture conditions resulted in greater hip abduction during stance phase than the normal human posture conditions, the magnitude of hip abduction angle was still less than that of the chimpanzees. One potential explanation for this remaining difference in the magnitude of the hip abduction angle is the presence of a frontal plane, bicondylar knee angle of about 8-14 degrees in humans, whereas in chimpanzees this angle is close to 0 degrees (Shefelbine et al., 2002; Tardieu & Trinkaus, 1994). The human bicondylar angle allows humans to place their foot underneath the center of mass throughout the stance phase while maintaining an adducted hip position. Chimpanzees, lacking this same frontal plane angle, must abduct their hip to place their center of mass over their stance foot. The differences in knee alignment may allow the human subjects in this study to perform the crouched posture conditions with a lesser amount of hip abduction than the chimpanzees have during bipedal gait.

There were only minor differences in the kinematics between the CL and CLFT conditions, indicating that the orientation of the trunk does not exert a substantial impact the gait kinematics of human crouched posture walking. However, one difference between these conditions was the human subjects had greater hip flexion angles throughout the gait cycle in the CLFT condition than the CL condition. This was likely caused by a greater forward tilt of the pelvis during the CLFT condition than the CL condition, as when we instructed the human subjects to flex forward at the trunk, they achieved this by flexing forward with both the pelvis and trunk segments. The lack of broad differences in kinematics between CL and CLFT conditions agrees with Grasso et al. (Grasso et al., 2000). However, other researchers that have isolated the effect of trunk orientation on gait mechanics have found that trunk angle can affect the sagittal plane angles of the knee and ankle (Aminiaghdam et al., 2017). Given the focus on the structure of the lumbar spine in evolutionary biomechanics research (Lovejoy & McCollum, 2010), the results of this study provide some evidence that the orientation of the trunk is just one factor, among many, that could impact 3-D gait kinematics (O’Neill et al., 2018). Future work using musculoskeletal computer modeling techniques could further test the importance of the structure and orientation of the trunk segment in influencing gait kinematics.

One of the important kinematic differences that remained between humans and chimpanzees was the difference in the range of motion for the pelvis and hip transverse plane rotations. Chimpanzees have approximately a 40-degree range of motion for both pelvis rotation and hip rotation, but the humans in the crouched posture conditions had a range of motion of about 15 degrees (Table A.5). One possible explanation for this difference is that chimpanzees have shorter legs than humans in both an absolute and relative sense, so they may rotate their pelvis throughout the gait cycle to increase their overall stride length. Increasing the pelvis rotation as a compensation for shorter legs has been observed in humans when comparing females with males (Whitcome, Miller, & Burns, 2017). Another potential reason for the greater pelvis and hip rotations in chimpanzees than humans could be based on a more posterior orientation of the iliac blades in chimpanzees, which could affect the role of the hip extensors and abductors (O'Neill et al., 2015; Stern Jr. & Susman, 1981a).

5.4.2 Ground Reaction Forces

Along with differences in kinematics, the human crouched posture conditions also resulted in more chimpanzee-like GRFs compared to the normal human conditions. The crouched posture GRF results compare favorably with the GRFs from other crouched posture studies (Aminiaghdam et al., 2017; Grasso et al., 2000), with a greater first peak in the vertical GRF compared to the second peak and a less prominent dip in force during mid-stance. When compared to the normal human conditions, the human crouched posture conditions resulted in a lesser second vertical GRF peak and greater lateral GRFs during mid-stance. However, the GRF patterns in each of the human conditions were still distinct from the GRF patterns in chimpanzees, indicating that the crouched posture alone does not account for the monophasic vertical GRF or a reduced AP GRF peak patterns measured in chimpanzees.

The differences in GRF patterns between the human crouched posture conditions and chimpanzees are in agreement with previous research showing a difference in center of mass motion between these two species (Demes et al., 2015). In human gait, the second vertical GRF peak and positive AP GRF peak are dominated by plantar flexor activity (Liu, Anderson, Schwartz, & Delp, 2008b; Winter, 1983). Since the chimpanzee GRF patterns do not have human-like peaks it is possible that chimpanzees rely less heavily than humans on their plantar flexor muscles when walking bipedally. Muscle-level analyses of chimpanzee and human crouched posture gait focusing on the role of the plantar flexor muscle group could allow us to better understand the determinants of the shape of the GRF patterns in humans and chimpanzees.

5.4.3 Limitations

One potential limitation of this study was that the human subjects were given only a few minutes to practice each of the crouched posture conditions. A relatively short practice time was given in part because humans can readily walk with crouched postures, but the task does lead to muscle fatigue (Carey & Crompton, 2005) and we did not want our subjects to become fatigued during the testing session. Since the crouched posture conditions were not common tasks for the human subjects, it is possible that other modifications in gait mechanics would occur with a longer practice session (Selgrade, Thajchayapong, Lee, Toney, & Chang, 2017). Future studies could address this limitation with multiple practice sessions with the crouched posture gait.

This study built upon previous work by including instructions to modify human gait towards that of a chimpanzee in both the sagittal and frontal planes. However, it is possible that different types of feedback or instruction could be provided to the subjects to guide them towards an even more chimpanzee-like gait than what was seen here. Specific instructions to human participants to increase pelvis and hip rotation or hip abduction angle could further reduce differences in kinematics between humans and chimpanzees. However, additional instructions might be overwhelming to subjects because they would have to pay attention to many different things at once. Future studies could try to implement real-time visual feedback to further modify specific features of the kinematics or ground reaction forces in human crouched posture walking.

Another potential limitation of this study is that human subjects walked at two speeds (fixed speed to match the average chimpanzee speed, and the preferred speed of the human subjects); however, the human subjects did not walk at the same relative (dimensionless) speed as the chimpanzees based on the differences in leg length. Given the differences in hind-limb length (Humans: 0.88 ± 0.04 m; Chimpanzees: 0.39 ± 0.02 m), a relative speed condition would have required the human subjects to walk at approximately 1.65 m s^{-1}. During pilot testing, it was found that human subjects had difficulty performing the crouched postures conditions while walking at this faster, relative speed. However, there were only minor differences between the fixed (1.1 m s^{-1}) and preferred (1.3 m s^{-1}) speed conditions in this study, and human kinematics have been shown to be broadly similar for the fixed and relative speeds cited above (O'Neill et al., 2015). Thus, we expect the general conclusions in this study would hold for a range of normal human walking speeds.

5.4.4 Implications for studying the evolution of bipedal walking

While the human crouched posture instructions prompted the subjects to walk with a more chimpanzee-like pelvis list, hip flexion and abduction, and knee flexion motion, these postures failed to reproduce other important aspects of the gait mechanics of chimpanzees (e.g. pelvis and hip transverse plane rotations, ankle flexion angle, vertical GRFs). These remaining differences in kinematic and ground reaction force patterns agree with previous research documenting differences in center of mass mechanics between humans walking with crouched postures and chimpanzee bipedal gait (Demes et al., 2015). When compared with previous human crouched posture studies, we provided more specific instructions to the human subjects to attempt to imitate the chimpanzee gait, yet the differences in gait mechanics between species persisted. The previous studies have used human crouched posture conditions to try to better understand the metabolic economy and muscle force requirement in these postures (Carey & Crompton, 2005; Foster et al., 2013), with implications for how our human ancestors walked. However, as there are important remaining differences in gait mechanics between human crouched posture gait and chimpanzee gait, and the morphologies of both humans and chimpanzees are distinct from the morphology of species like *Au. afarensis*, investigating how modern-day humans walk with a crouched posture may not approximate how our human ancestors walked. Therefore, using humans walking with a crouched posture as a model to study the evolution of human walking should be approached with caution.

Since experimental locomotion studies in extinct species are not possible, comparing bipedal locomotion data from humans and non-human primates may still be a fruitful path for explore questions of the evolution of habitual bipedalism. To better understand when in time our human ancestors began to walk upright instead of with a crouched posture, it will be helpful to gain further insight into the musculoskeletal traits that drive the crouched postures adopted by chimpanzees during bipedal gait. Specifically, a better understanding of how the muscles in the hind limb of the chimpanzee function throughout the gait cycle will help researchers better understand why chimpanzees walk the way they do and what changes in musculoskeletal morphology are necessary to permit an upright, striding bipedal gait.

5.4.5 Conclusion

While the human crouched posture conditions produced a more chimpanzee-like gait than normal human walking, some substantial differences remained between these species. The remaining differences between humans and chimpanzees in both gait kinematics and GRFs may be reflective of the stark differences in morphology between these two species. Given these results, it is clear that morphology and posture both play important roles in influencing the gait mechanics. In addition to musculoskeletal morphology and habitual posture, other factors likely play important roles in determining gait mechanics such as the neural control of motion, metabolic energy expenditure, or stability of gait. Altogether, this study demonstrates some of the limitations of making inferences about early hominin walking by instructing humans to walk with crouched postures.

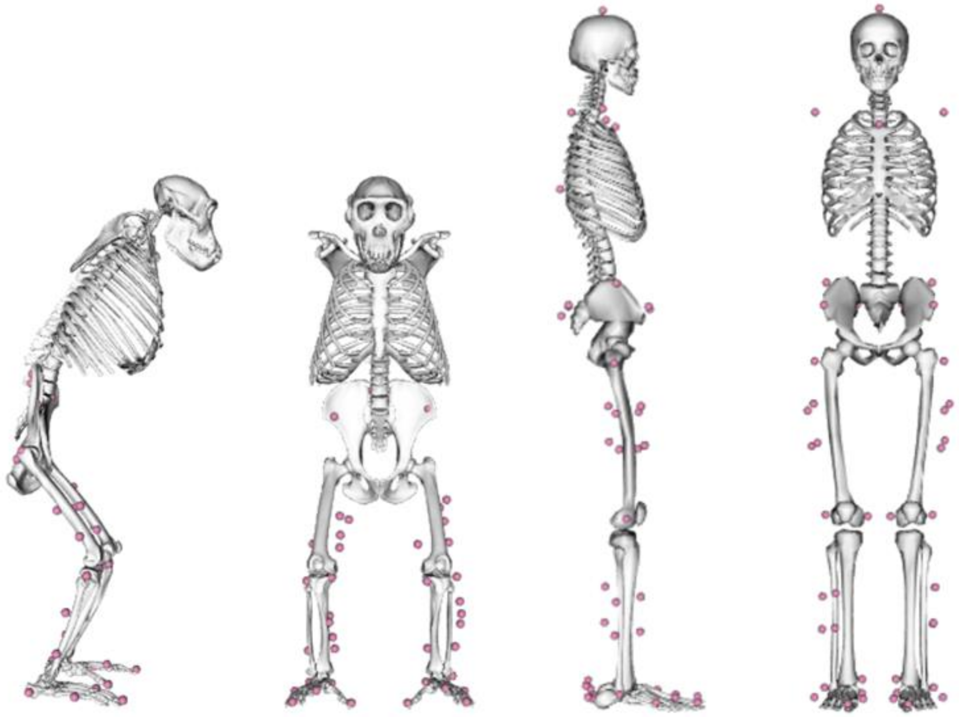


Figure 5.1: Representations of the skeletal morphology for the (A) chimpanzee and (B) human in OpenSim. The anatomical markers and segment marker clusters are depicted with pink dots.

Table 5.1: Spatial-temporal results for the eight human conditions and one chimpanzee bipedal walking condition.

	Stride Time (s)	Stride Length (m)	Speed (m/s)
Human Norm Fixed	1.12 ± 0.04	1.24 ± 0.05	1.10 ± 0.02
Human Norm Preferred	1.02 ± 0.08	1.33 ± 0.08	1.31 ± 0.14
Human CL Fixed	1.12 ± 0.07	1.23 ± 0.06	1.10 ± 0.02
Human CL Preferred	1.01 ± 0.09	1.29 ± 0.07	1.29 ± 0.15
Human CLFT Fixed	1.12 ± 0.06	1.23 ± 0.06	1.10 ± 0.02
Human CLFT Preferred	0.99 ± 0.08	1.29 ± 0.07	1.31 ± 0.15
Human IMIT Fixed	1.16 ± 0.09	1.27 ± 0.10	1.10 ± 0.02
Human IMIT Preferred	1.04 ± 0.12	1.35 ± 0.13	1.31 ± 0.14
Chimpanzee Normal	0.70 ± 0.12	0.78 ± 0.07	1.09 ± 0.10

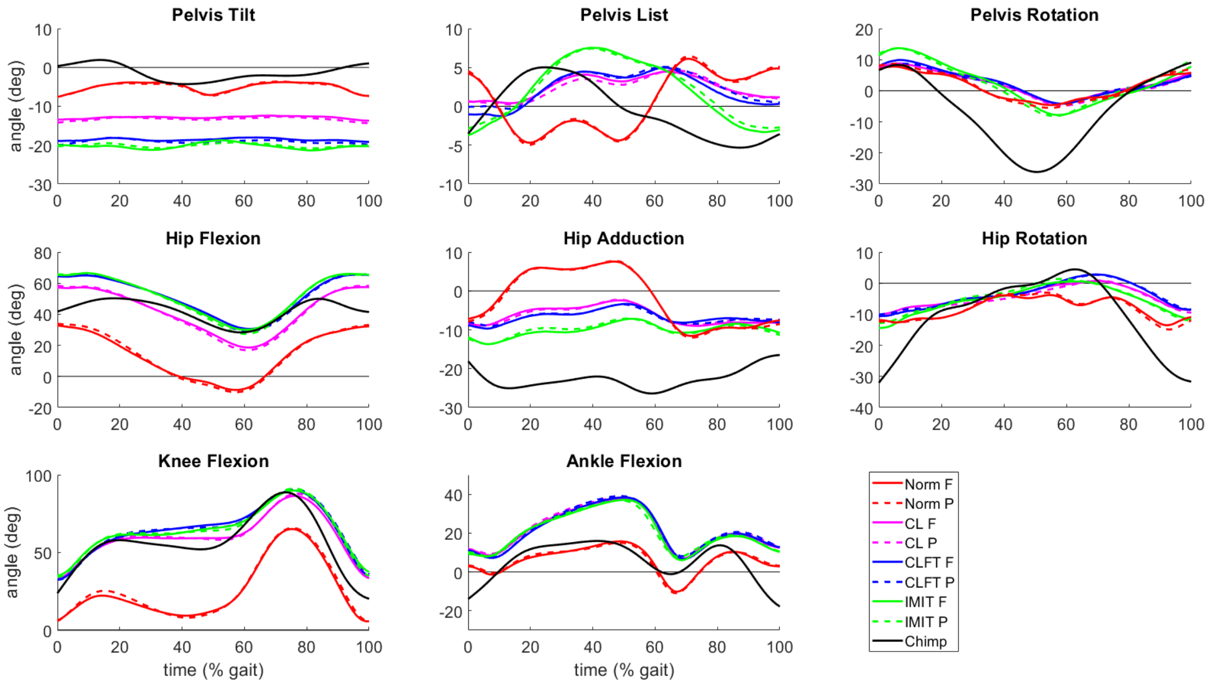


Figure 5.2: Segment and joint kinematics for the eight human conditions and one chimpanzee bipedal walking condition. Solid lines show the results of the 1.09 m s^{-1} gait speed (human fixed speed (F) and chimpanzee gait (Chimp)), while dashed lines show the results of the humans preferred speed (P).

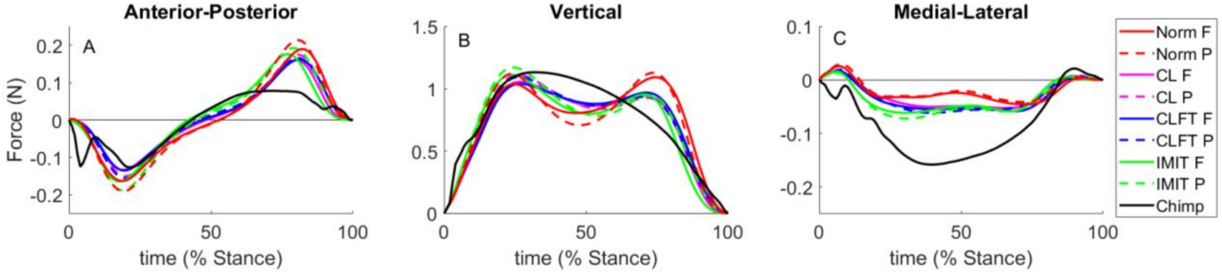


Figure 5.3: Ground reaction forces in the anterior-posterior (A), vertical (B), and medial-lateral (C) for the eight human conditions and one chimpanzee bipedal walking condition. Solid lines show the results of the 1.09 m s^{-1} gait speed (human fixed speed (F) and chimpanzee gait (Chimp)), while dashed lines show the results of the humans preferred speed (P).

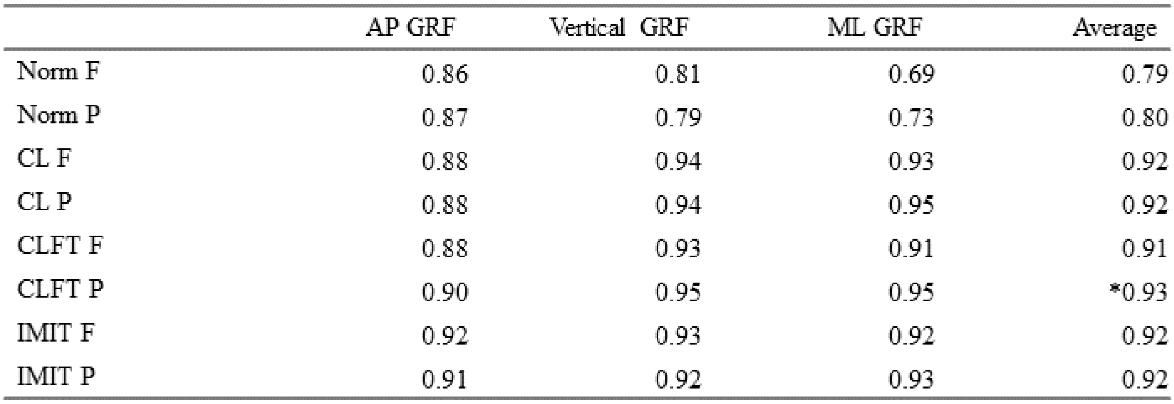
Table 5.2: Zero-lag cross-correlation coefficients for each human posture versus chimpanzee for each kinematic variable. Greater, positive values indicate more similar, in-phase kinematic patterns. Asterisks note the variable that matches best with the chimpanzee data.

	Pelvis Tilt	Pelvis List	Pelvis Rot	Hip Flex	Hip Add	Hip Rot	Knee Flex	Ankle Flex	Average
Norm F	-0.15	-0.85	*0.92	0.76	-0.39	0.85	0.82	0.62	0.32
Norm P	-0.10	-0.84	0.91	0.77	-0.41	0.88	0.80	0.58	0.33
CL F	-0.44	0.02	0.78	0.85	-0.37	0.80	0.93	0.68	0.41
CL P	-0.36	-0.15	0.68	0.85	-0.27	0.74	0.89	0.68	0.38
CLFT F	-0.08	0.16	0.70	0.85	-0.30	0.72	0.92	0.65	0.45
CLFT P	*0.26	0.05	0.75	0.85	-0.18	0.70	0.90	0.67	0.50
IMIT F	-0.20	*0.59	0.77	0.87	*-0.01	0.90	0.92	0.71	0.57
IMIT P	0.14	0.53	0.87	*0.88	-0.12	*0.93	*0.94	*0.74	*0.61

Table 5.3: Root-mean-square-differences for each human posture versus chimpanzee for each kinematic variable. The minimum value for the RMSD measurement is 0, which would indicate the two variables perfectly overlap with each other, while greater RMSD values give an indication of the amount of difference in magnitude that exists between the two variables. Asterisks note the variable that matches best with the chimpanzee data.

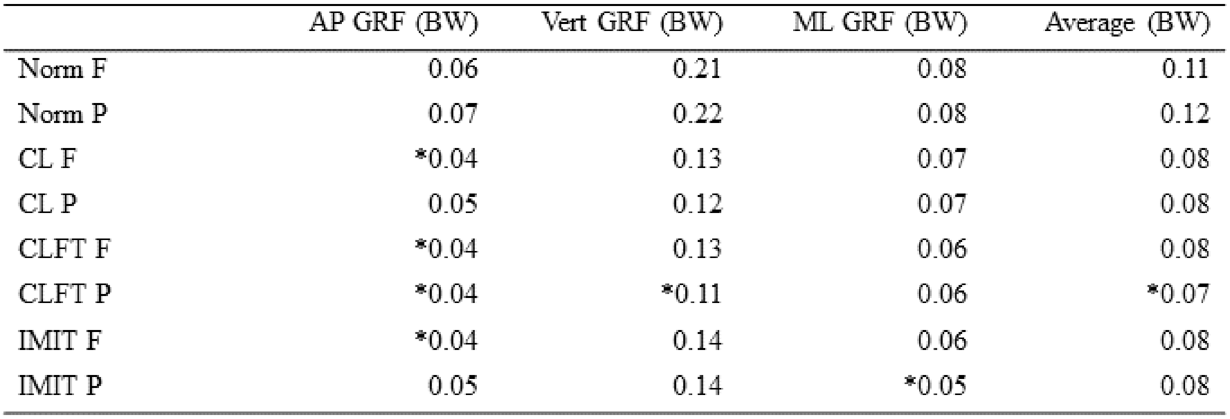
	Pelvis Tilt (°)	Pelvis List (°)	Pelvis Rot (°)	Hip Flex (°)	Hip Add (°)	Hip Rot (°)	Knee Flex (°)	Ankle Flex (°)	Avg. (°)
Norm F	*2.6	7.0	11.6	33.7	22.3	8.8	33.0	*7.5	15.8
Norm P	*2.6	7.0	*11.2	33.8	22.2	*8.2	32.4	7.8	15.6
CL F	9.1	5.1	12.7	*9.3	16.6	10.7	*8.0	18.8	*11.3
CL P	9.5	5.1	12.7	10.3	16.6	10.5	9.4	19.1	11.7
CLFT F	14.8	4.8	13.0	9.7	16.2	11.0	10.7	18.7	12.4
CLFT P	15.3	5.1	12.8	10.0	16.1	11.2	11.3	19.2	12.6
IMIT F	16.5	*4.4	11.9	10.3	*12.8	9.1	10.7	17.7	11.7
IMIT P	16.3	4.5	11.3	10.4	12.9	9.2	10.1	17.6	11.5

Table 5.4: Zero-lag cross-correlation coefficients for each human posture versus chimpanzee for each ground reaction force variable. Greater, positive values indicate more similar, in-phase ground reaction force patterns. Asterisks note the variable that matches best with the



	AP GRF	Vertical GRF	ML GRF	Average
Norm F	0.86	0.81	0.69	0.79
Norm P	0.87	0.79	0.73	0.80
CL F	0.88	0.94	0.93	0.92
CL P	0.88	0.94	0.95	0.92
CLFT F	0.88	0.93	0.91	0.91
CLFT P	0.90	0.95	0.95	*0.93
IMIT F	0.92	0.93	0.92	0.92
IMIT P	0.91	0.92	0.93	0.92

Table 5.5: Root-mean-square-differences for each human posture versus chimpanzee for each ground reaction force variable. Asterisks note the variable that matches best with the chimpanzee data.



	AP GRF (BW)	Vert GRF (BW)	ML GRF (BW)	Average (BW)
Norm F	0.06	0.21	0.08	0.11
Norm P	0.07	0.22	0.08	0.12
CL F	*0.04	0.13	0.07	0.08
CL P	0.05	0.12	0.07	0.08
CLFT F	*0.04	0.13	0.06	0.08
CLFT P	*0.04	*0.11	0.06	*0.07
IMIT F	*0.04	0.14	0.06	0.08
IMIT P	0.05	0.14	*0.05	0.08

CHAPTER 6

STUDY TWO

6.1 Introduction

Human gait mechanics are unique among other primates (O'Neill et al., 2018), featuring an upright trunk and extended lower limbs during stance phase (Alexander, 2004). The closest living relatives to humans, chimpanzees, sometimes walk bipedally but do so with a forward-leaning trunk and flexed, abducted hind limbs (O'Neill et al., 2015). While the distinct musculoskeletal morphology of these two species likely accounts for some of the observed differences in bipedal gait mechanics, it is also possible that the different habitual postures used by each species contributes to their unique gait mechanics. For this study, we define posture as the general orientation of the trunk, pelvis, and lower/hind limbs during walking (e.g., upright versus crouched), and the term gait mechanics refers to the group of variables, including joint angles and GRFs, that change over the course of the stride during walking.

The upright posture of normal human gait is considered a defining aspect of human evolution (Lovejoy, 1988; Ward, 2002). A fundamental question in human evolution is when our hominin ancestors, such as *Australopithecus afarensis* (~3.4 MYA) or *Ardipithecus ramidus* (~4.4 MYA), began walking in a modern human-like manner, on two limbs with an upright posture (Crompton et al., 1998; Lovejoy & McCollum, 2010; Stern Jr., 1999; Susman et al., 1984). Given that these species are now extinct, and their walking patterns cannot be observed, evolutionary biomechanists have compared human gait to that of other primates to try to better understand the way extinct hominins walked (Foster et al., 2013; O'Neill et al., 2015; Pontzer et al., 2009).

In considering how extinct species walked, researchers have relied on the fossil record of these species, along with an assessment of how specific traits of their musculoskeletal morphology would have influenced their posture and gait mechanics. However, while the skeletal structure of these extinct species is preserved in the fossil record to varying degrees, the muscular system is not preserved beyond bony landmarks indicating the insertion or origin points of muscles. The lack of a preserved muscular system, and therefore an incomplete understanding of how muscles would have functioned to produce gait in these species, further complicates the interpretation of the fossil record. While no existing species has the same musculoskeletal features as our human ancestors, comparing the structure and function of the musculoskeletal systems for humans and closely related species such as chimpanzees during gait can allow for insight as to why humans evolved to walk with an upright posture and a straight leg during stance, while chimpanzees walk with a flexed, abducted hind limb. Further insight into the effect of morphology on gait mechanics can help us understand why chimpanzees walk with a crouched posture, even though crouched walking is considered less economical (Carey & Crompton, 2005), with implications for understanding the evolution of hominin bipedalism.

Although there are many potential reasons why modern humans and chimpanzees walk differently, the distinct morphology of each species likely plays an important role in their different gait mechanics (Lovejoy, 2005; O'Neill et al., 2015; Sockol et al., 2007). The lack of a lumbar lordosis and a morphology that favors producing large hip extensor moments when the hip is in a flexed position (e.g., as during climbing) are some potential reasons why chimpanzees may walk with a flexed limb posture (Fleagle & Anapol, 1992;

Kozma et al., 2018; Lovejoy, 2005; McHenry, 1975). These morphological differences will influence how muscle forces in the lower/hind limbs act to accelerate the body during walking. In addition, the difference in posture used by these two species will also impact how muscles function during the gait cycle. Previous research on humans walking with a crouched posture have reported that humans walk with greater muscle activation (Foster et al., 2013). In addition, there are differences in how a muscle induces an acceleration on the center of mass in clinical populations who walk with crouched postures (Steele et al., 2013), although it is unclear if this would translate to an able-bodied population. A more complete understanding of the independent effects of morphology and posture on muscle function can provide useful information regarding how muscle and skeletal structures influence the preferred movement patterns in primates, which can help anthropologists interpret the functional significance of skeletal features within the fossil record.

The *first aim* of this study was to determine how changes in posture affect muscle function during walking in humans. Muscle function will be operationally defined in this study as the contribution of individual muscles to the three-dimensional support, progression, and sway of the whole-body center of mass. We analyzed how the major lower limb muscles of humans contribute to the motion of the center of mass across four different human upright and crouched postures. These analyses were performed at the fixed human speed (matched to the average, absolute speed of the chimpanzees) and at the preferred walking speed for each human subject. We instructed humans to walk with four different instructions: normal walking (Figure 6.1A), crouched-limb (CL) walking, crouched-limb flexed-trunk (CLFT) walking, and a condition with specific instructions to imitate the pelvis tilt kinematics of a chimpanzee during walking while maintaining the CLFT posture (IMIT; Figure 6.1B).

The *second aim* was to determine how differences in morphology between chimpanzees and humans affect muscle function. We compared muscle function in the human condition that was most similar to chimpanzee walking (IMIT preferred speed; see Study 1) with the function of analogous muscles in chimpanzees during bipedal walking (Figure 6.1C). The comparisons among the human posture conditions were used to determine the effect of walking with a crouched posture, rather than an upright posture, on muscle function. The comparisons between the human crouched posture condition and the chimpanzee crouched posture condition were used to try to understand the effect that different morphologies have on muscle function when different species walk with similar gait mechanics.

6.2 Methods

Ten healthy, recreationally active human subjects [5 male/5 female; age: 27 ± 5 years; height: 1.70 ± 0.08 m; mass: 68 ± 11 kg; leg length: 0.88 ± 0.04 m] with no history of gait pathologies or orthopedic issues were recruited for this study. All human subjects read and signed an informed consent document before participating in the study approved by the University of Massachusetts Amherst institutional review board. Kinematic and kinetic data were collected as the human subjects walked overground with the following four postures: (1) normal (Norm), (2) crouched-limb (CL; walk while bending at the hips and knees), (3) crouched-limb, flexed trunk (CLFT; CL condition plus forward trunk flexion), and (4) human imitation of chimpanzee gait (IMIT; CLFT plus a frontal plane instruction to focus on elevating the pelvis on the swing side). Each of these four posture conditions were performed at the preferred speed for each subject (1.30 ± 0.15 m s^{-1}), and at a speed that matched the average, absolute speed of the previously collected bipedal chimpanzee gait data (Fixed speed; 1.10 ± 0.02 m s^{-1}). Subjects performed three trials for each condition for each speed. For further description of the human subjects protocol, the reader is referred to Section 5.2 of this dissertation.

The kinematics and kinetics for the chimpanzee bipedal gait data were drawn from previously published studies (Demes et al., 2015; O'Neill et al., 2015) with the methods briefly presented here. Overground bipedal gait data were collected on three male common chimpanzees *P. troglodytes* (age: 5.5 ± 0.2 years; mass: 26.5 ± 6.7 kg) as the chimpanzees walked across a walkway at self-selected speeds (1.09 ± 0.10 m s^{-1}) following an animal trainer (O'Neill et al., 2015). The data collections were performed with the approval of the Stony Brook University Institutional Animal Care and Use Committee. Each chimpanzee was trained to walk on its hind limbs for at least six months prior to the beginning of the data collection using food rewards and positive reinforcement.

The kinematic and GRF data for both humans and chimpanzees were then used to perform an analysis of the center of mass accelerations that were induced by the major lower/hind limb muscles for each species (Zajac & Gordon, 1989). The human musculoskeletal model had 21 mechanical degrees of freedom and was actuated by 80 muscle paths representing 76 muscles of the lower limbs (Anderson & Pandy, 1999; Delp et al., 2007; Lai et al., 2017). The head, arms, and trunk were modeled as a single rigid-body segment that articulated with the pelvis via a ball-and-socket joint at the L5-S1 level. Each hip also articulated with the pelvis segment with a ball-and-socket joint. The knee was represented as a modified hinge joint with translations of the tibia relative to the femur that were coupled to knee flexion and extension, to better match the mobility of the knee joint (Lai et al., 2017; Yamaguchi & Zajac, 1989). The ankle and metatarsophalangeal joint were modeled as hinge joints.

The chimpanzee musculoskeletal model had 23 mechanical degrees of freedom and 88 muscle paths representing 70 muscles of the hind limbs (O'Neill et al., 2013). Each degree-of-freedom was modeled the same way as the human musculoskeletal model, except for the first tarsometatarsal joint, which was included in the chimpanzee musculoskeletal model and accounted for the two additional degrees-of-freedom relative to the human model. The chimpanzee model from O’Neill et al. (O'Neill et al., 2013) was modified for this study to include a rigid head, arms, and trunk segment representing the segment inertial parameters for the upper body of the chimpanzee. The location of the ball-and-socket joint between the head, arms, and trunk segment and the pelvis segment was at the L2/L3 level (instead of the lumbar-sacral level as in the human model). The locations of the lumbar joint were different between the human and chimpanzee models because chimpanzees are thought to have limited mobility in their lower lumbar region due to their tall iliac blades, narrow sacrum, and transverse lumbar processes, which “entrap” the lower lumbar spine and reduce flexibility (McCollum, Rosenman, Suwa, Meindl, & Lovejoy, 2010; O'Neill et al., 2018).

For both the human and chimpanzee bipedal data, the following procedures were used. The generic musculoskeletal model (human or chimpanzee) was first scaled to the linear dimensions and mass of each subject. The generalized kinematic coordinates were then computed using inverse kinematics (Lu & O'Connor, 1999) and were used as inputs into a residual reduction analysis (RRA) within OpenSim in an effort to enhance the dynamic consistency of the model-based results. (Delp et al., 2007). RRA makes minor adjustments to the kinematics and model segment inertial parameters to reduce the dynamic inconsistencies between the computed kinematics and the measured GRFs (Hamner et al., 2013). RRA was first performed on a single, normal condition trial to create a new musculoskeletal model with adjustments to the model segment inertial parameters. The newly created model was then used to perform RRA on the remaining trials for that subject, adjusting the kinematics without further adjustments to model segment inertial parameters. RRA was evaluated based on its ability to reduce the residual forces on the pelvis segment, while changing the kinematics by a root-mean-square difference of less than 2-5 degrees (when compared with the result from inverse kinematics). The kinematic results from RRA were then used as inputs for both static optimization and the induced acceleration analysis.

Static optimization is a computationally efficient way to estimate muscle forces at every time point throughout the gait cycle for every trial for every subject (Lin et al., 2012). Static optimization uses calculated joint torques to solve the muscle load sharing problem by minimizing the sum of squared muscle activations at each point in the gait cycle (Erdemir et al., 2007). Static optimization was solved within OpenSim by minimizing the objective function

$$J = \sum_{m=1}^{n} (a_m)^2$$

while solving the equations of motion for the joint torques subject to the muscle activation-to-force condition:

$$\sum_{m=1}^{n}(a_m F_m^0) r_{m,j} = \tau_j$$

where n is the number of muscles, $a_m$is the activation level of muscle m at a discrete time step, F_m^0 is its maximum isometric force, $r_{m,j}$ is its moment arm around the jth joint axis, τ_j is the generalized force acting around the jth joint.

An induced acceleration analysis (IAA) was then performed within OpenSim to determine how each muscle accelerates the whole-body COM in the vertical (support of body weight), anterior-posterior (braking and propulsion), and medial-lateral (side-to-side sway) directions for the human and chimpanzee data (Hamner et al., 2013; Steele et al., 2013; Zajac, 1989). For complex movements such as walking, involving multiple muscles and many degrees-of-freedom, it becomes difficult to identify how individual muscle forces impact the motion of the whole body. IAA seeks to establish the effect of a specific muscle force on whole-body kinematics based on the computed muscle force and configuration of the body segment at each point in time during the gait cycle. The induced acceleration of muscle *j* is defined as the contribution of muscle *j* to all system accelerations according to:

$$\ddot{q}_J = M(q)^{-1} R^{(j)}(q) F_{MT_j}$$

Where $\ddot{q}_J$ is a vector of all the accelerations in the system, $R^{(j)}(q)$ is the jth column of the muscular moment arm matrix *R*(*q*), $M(q)^{-1}$ is the inverse of the system mass matrix, and F_{MT_j} is the force of the jth muscle. IAA calculates the acceleration potentials for each muscle in the model based on 1 N of muscle force, and then these acceleration potentials are multiplied by the muscle forces obtained via static optimization to compute the COM accelerations induced by each muscle.

The contributions of each of nine major muscle groups to the vertical, anterior-posterior, and medial-lateral COM accelerations were evaluated for each of the different human posture conditions at both speeds, and for the chimpanzee walking data. The nine major muscles or muscle groups that were evaluated were gluteus maximus, gluteus medius, iliopsoas, hamstrings (biceps femoris long head, semimembranosus, and semitendinosus), rectus femoris, vasti (vastus medialis, vastus lateralis, and vastus intermedius), gastrocnemii (medial and lateral), soleus, and tibialis anterior. These muscles were identified as muscles primarily responsible for generating vertical, anterior-posterior, and medial-lateral accelerations of the center of mass during gait (John, Seth, Schwartz, & Delp, 2012b; Lim, Lin, & Pandy, 2017; Liu et al., 2006; Liu et al., 2008a).

For each muscle, the average contribution to the vertical, anterior-posterior, and medial-lateral COM accelerations were calculated for each trial (Steele et al., 2013). Differences in muscle function between the human posture conditions were evaluated using a two-way repeated-measures ANOVA, with speed and posture as the two factors (alpha = 0.05) using SPSS. In the event of significant main effects, the false discovery rate procedure (Benjamini & Hochberg, 1995) was used for multiple comparison testing among postures using MATLAB. The within-human comparisons directly tested the effects of posture, with morphology held constant. In an effort to try to understand how morphology impacts muscle function for walking with similar postures, the IAA results from the chimpanzees were compared with the human condition that was most similar to the chimpanzee gait mechanics, as described in Chapter 5 of this dissertation. Differences in muscle function between humans and chimpanzees were evaluated using an unpaired t-test. The human posture condition that was most similar to the chimpanzee was determined to be the IMIT Preferred condition (based on *r* and RMSD; see Chapter 5), wherein the human subjects were asked to walk while bending forward at the trunk, hips, and knees, while also listing their pelvis up on the swing side.

6.3 Results

The kinematic and ground reaction force results were reported in Chapter 5 and can be found in Figures 5.2 and 5.3. The estimated muscle forces throughout the gait cycle for each human condition and the chimpanzee bipedal gait are shown for each of the nine muscle groups in Figure 6.2. The overall timing and magnitude of the muscle force production for the muscle groups are different between the human crouched postures and the normal conditions. The gluteus maximus (Figure 6.2A) and vastus group (Figure 6.2D) were active in the first half of stance phase in the normal condition but were active throughout most of stance phase in the human crouched posture conditions which was more like the chimpanzee patterns in these muscles. There were greater forces produced by the gastrocnemius (Figure 6.2G) in the normal conditions than the human crouched posture conditions, opposite of the soleus (Figure 6.2H) muscle which had greater forces in the human crouched posture conditions than the normal conditions. Muscle forces normalized to species body weight are presented in Figure 6.3. Normalized to body weight, the force produced by the gluteus maximus in the human crouched posture conditions was similar to the chimpanzees (Figure 6.3A). However, importantly, the normalized muscle force of the vastus group is greater in the human crouched postures compared to the chimpanzees (Figure 6.3D).

6.3.1 Vertical Induced Accelerations across Human Postures

The time series data for the vertical induced accelerations, averaged for each condition, for each of the muscle groups are shown in Figure 6.4. There was a significant effect of posture on the average acceleration induced by the gluteus maximus (Figure 6.5A; $p < 0.01$). There were greater accelerations induced by gluteus maximus in the CLFT than the CL and IMIT conditions, and the accelerations induced by gluteus maximus for all crouched posture conditions were greater than the normal conditions. Posture had a significant effect on the gluteus medius (Figure 6.5B; $p < 0.01$), with greater acceleration induced by the gluteus medius in the normal condition than the human crouched posture conditions, and the least acceleration induced in the IMIT condition compared with the other human crouched posture conditions. There was a significant effect of posture on the iliopsoas (Figure 6.5C; $p = 0.03$) muscle group, although the magnitudes of acceleration induced were small.

The vertical accelerations induced by the vastus group (Figure 6.5D; $p < 0.01$) were greater in each of the human crouched posture conditions than in the normal conditions. The vertical accelerations induced by hamstrings (Figure 6.5E; $p < 0.01$) muscle group was greater in the CLFT conditions than the IMIT conditions, but the magnitudes of acceleration were small. Posture had a significant effect on the rectus femoris (Figure 6.5F; $p < 0.01$), with greater vertical acceleration induced by this muscle group in the normal conditions than the human crouched conditions. Among the crouched posture conditions, the average accelerations induced by the rectus femoris in the CLFT condition were negative (downward) and was significantly different from the average accelerations induced in the CL and IMIT conditions which were both positive.

There was a greater vertical acceleration induced by the gastrocnemius in the normal conditions than in the human crouched posture conditions (Figure 6.5G; $p < 0.01$). Among the crouched posture conditions, the accelerations induced by the gastrocnemius in the CLFT condition were less than those induced in either the CL or IMIT conditions. Greater vertical accelerations were induced by the soleus in the human crouched posture conditions than the normal conditions (Figure 6.5H; $p < 0.01$), with the IMIT condition resulting in greater accelerations induced by the soleus than the CL or CLFT conditions. There were no statistically significant effects of posture on the vertical accelerations induced by the tibialis anterior (Figure 6.5I; $p = 0.06$).

There was a significant effect of speed on the gluteus maximus ($p < 0.01$), gluteus medius ($p < 0.01$), and vastus group ($p = 0.01$). There were greater vertical accelerations induced by the gluteus maximus and vastus group in the preferred speed conditions compared to the fixed speed. Whereas there was a lesser vertical acceleration induced by gluteus medius in the preferred speed conditions compared to the fixed speed.

6.3.2 Anterior-Posterior Induced Accelerations across Human Postures

The induced accelerations in the AP direction averaged for each condition, for each muscle over time for both the human and chimpanzee bipedal gait are presented in Figure 6.6. The average anterior acceleration induced by the gluteus maximus was greater in the crouched posture conditions than in the normal human conditions, and the acceleration induced in the CLFT condition were greater than in the CL condition (Figure 6.7A; $p < 0.01$). There was a significant effect of posture on both the gluteus medius (Figure 6.7B; $p < 0.01$) and iliopsoas (Figure 6.7C; $p < 0.01$) but the magnitudes of average AP acceleration were close to zero in each of these muscles among all human conditions.

The posterior acceleration induced by the vastus group was greater in the human crouched posture conditions than the normal conditions (Figure 6.7D; $p < 0.01$). Posture also had a significant step-wise relationship on the AP accelerations induced by the hamstrings (Figure 6.7E; $p < 0.01$), with the least anterior acceleration in the normal conditions, greater in the CL conditions, greater in the CLFT, and greatest anterior acceleration in the IMIT conditions. There were greater posterior accelerations induced by the rectus femoris in the normal conditions than in the crouched posture conditions (Figure 6.7F; $p < 0.01$), and it had a greater posterior acceleration in the CL than the CLFT conditions.

Similar to the vertical direction, the anterior acceleration induced gastrocnemius was greater in the normal conditions than in the crouched posture conditions (Figure 6.7G; $p < 0.01$) while the anterior acceleration induced by the soleus was greater in the crouched posture conditions than the normal conditions (Figure 6.7H; $p < 0.01$). Among the crouched posture conditions there were greater accelerations induced by the gastrocnemius in the CL conditions compared to the CLFT conditions, and greater accelerations induced by the soleus in the IMIT conditions than the CLFT conditions. There were greater posterior accelerations induced by the tibialis anterior in the normal conditions than the crouched posture conditions (Figure 6.7I; $p < 0.01$).

The vastus group was the only muscle that had a statistically significant effect of speed on the AP induced acceleration ($p = 0.04$). The posterior acceleration induced by the vastus group was greater in the preferred speed conditions than in the fixed speed conditions.

6.3.3 Medial-Lateral Induced Accelerations across Human Postures

The time series data for the induced accelerations in the ML direction averaged for each condition, for each muscle for both the human and chimpanzee bipedal gait are presented in Figure 6.8. There was a greater average lateral acceleration induced by the gluteus maximus (Figure 6.9A; $p < 0.01$) in the human crouched postures than the normal human conditions, and greater lateral accelerations in the CLFT and IMIT conditions compared to the CL conditions. There was a significant effect of posture on the lateral acceleration induced by the gluteus medius (Figure 6.9B; $p< 0.01$), however there was not a clear difference between the human crouched postures and the normal conditions. The average lateral acceleration induced by the gluteus medius had the smallest magnitude in the IMIT condition. The medial acceleration induced by the iliopsoas was greater in the normal conditions than the human crouched posture conditions, although the magnitude was small (Figure 6.9C; $p < 0.01$).

There was a lateral acceleration induced, on average, by the vastus group in the human crouched postures, however there was a medial acceleration induced, on average, by the vastus group in the normal conditions (Figure 6.9D; $p < 0.01$). Among the posture conditions, the lateral acceleration induced by the vastus group was greater in the IMIT conditions that either the CL or CLFT conditions. There was no significant effect of posture on the ML accelerations induced by the hamstrings (Figure 6.9E; $p = 0.10$). There was a significant effect of posture on lateral acceleration induced by the rectus femoris

(Figure 6.9F; $p = 0.02$), with greater lateral acceleration induced by the rectus femoris in the IMIT than in the other conditions.

The medial acceleration induced by the gastrocnemius was greater in the normal conditions than in the human crouched postures (Figure 6.9G; $p < 0.01$). This seemed to offset the soleus muscle function, as the medial acceleration induced by the soleus was greater in the human crouched postures than in the normal conditions (Figure 6.9H; $p < 0.01$). There was also a significant effect of posture on the lateral acceleration induced by the tibialis anterior (Figure 6.9I, $p = 0.03$), with smaller medial acceleration induced by the tibialis anterior in the IMIT condition than in the CL or CLFT conditions.

There was a significant effect of speed on the ML accelerations induced by gluteus medius ($p = 0.02$), hamstrings ($p = 0.01$), and rectus femoris ($p < 0.01$). The lateral accelerations induced by the gluteus medius were greater in the fixed speed conditions than the preferred speed conditions. There were greater medial accelerations induced by the hamstrings in the preferred speed conditions than in the fixed speed. Lastly, there were greater lateral accelerations induced by rectus femoris in the preferred speed conditions than the fixed speed.

6.3.4 Between-species Induced Accelerations

When comparing the vertical acceleration induced by the major muscle groups between the human IMIT preferred condition and the chimpanzee condition, there were significant differences in gluteus maximus (Figure 6.10A; $p < 0.01$), glutes medius (Figure 6.10B; $p < 0.01$), vastus group (Figure 6.10D; $p < 0.01$), and gastrocnemius (Figure 6.10G; $p = 0.03$). There were greater average vertical accelerations induced by gluteus maximus and gastrocnemius in the chimpanzees than in the human IMIT preferred condition. There was a greater vertical acceleration induced by the vastus group in the human IMIT preferred condition than in the chimpanzees. There was a negative (downward) vertical acceleration induced by the gluteus medius in the chimpanzees, while in the human IMIT condition the gluteus medius induced an upward vertical acceleration.

Between the two species, there were significantly different AP accelerations induced by gluteus maximus (Figure 6.11A; $p < 0.01$), vastus group (Figure 6.11D; $p < 0.01$), hamstrings (Figure 6.11E; $p = 0.04$), rectus femoris (Figure 6.11F; $p < 0.01$), soleus (Figure 6.11H; $p < 0.01$), and tibialis anterior (Figure 6.11I; $p = 0.03$) muscles. There were greater anterior accelerations induced by the hamstrings and soleus muscles in the human IMIT condition than the chimpanzees. There were greater posterior accelerations induced by the vastus group, rectus femoris, and tibialis anterior muscles in the human IMIT than the chimpanzees. In the human IMIT condition, there was an average anterior acceleration induced by the gluteus maximus, but there was an average posterior acceleration induced by the same muscle group in the chimpanzees.

In the ML direction, there were significant differences between species for the accelerations induced by the gluteus maximus (Figure 6.12A; $p < 0.01$), rectus femoris (Figure 6.12F; $p < 0.01$), gastrocnemius (Figure 6.12G; $p < 0.01$), soleus (Figure 12H; $p < 0.01$), and tibialis anterior (Figure 6.12I; $p < 0.01$). When compared to the chimpanzees, there were greater lateral accelerations induced by the gluteus maximus, rectus femoris, and tibialis anterior muscles in the human IMIT conditions. In the human IMIT condition, there were average medial accelerations induced by the gastrocnemius and soleus muscles, but in the chimpanzees these muscles induced lateral accelerations.

6.3.5 Summary

Instructing human subjects to walk with different crouched postures resulted in differences in muscle functions for almost every muscle group we investigated. In some cases, such as the ML acceleration induced by the vastus group, the crouched posture resulted in the muscle function switching the direction that it accelerated the center of mass (i.e., from medial acceleration to lateral acceleration). When comparing between species, even though the postures of the two species were broadly similar (see Chapter 5) there were still many differences found in how the major muscle groups accelerated the center of mass. Many of these were differences in magnitude, but there were also some cases of opposite directions of muscle function between species.

6.4 Discussion

In this study, we used an induced acceleration analysis to investigate muscle function during gait in humans walking with different postures, as well as in chimpanzees walking bipedally. Muscle function was defined as the acceleration induced on the whole-body center of mass by an individual muscle or muscle group. The different human postures had a significant effect on the function of each of the nine major muscles or muscle groups we investigated in this study. The speed with which the humans performed the different gaits also had a significant effect, but only in muscles that crossed the hip or the knee joint. There were also significant differences in muscle function between humans walking with a chimpanzee-like gait and chimpanzees walking bipedally. Thus, even when walking with broadly similar kinematics, there were interspecific differences in how muscles produced accelerations of the center of mass.

The differences in muscle function are likely due to the substantial differences in musculoskeletal morphology between humans and chimpanzees.

The overall timing and magnitude of muscle force production in the gluteus maximus, vastus group, biceps femoris, and rectus femoris muscles agree qualitatively with previously published electromyography results from human crouched posture walking (Grasso et al., 2000). However, the timing and general magnitude of muscle forces estimated for gastrocnemius muscle among the human crouched posture conditions were different from what was reported in Grasso et al. It is unclear if the reason for the discrepancy is due to the static optimization procedure alone, but it is possible that the subjects in this study walked with a different muscle recruitment pattern than what was measured in the single subject reported in Grasso et al. (Grasso et al., 2000).

6.4.1 The Effect of Posture on Muscle Function During Gait

There were many differences in muscle function among the different human posture conditions; however, the crouched postures were more similar to each other in both pattern and magnitude of induced accelerations, than they were to the normal human gait. For many muscle groups investigated, such as the gastrocnemius, soleus, and gluteus maximus, the magnitudes of the induced accelerations were vastly different between human crouched posture conditions and normal conditions. In the case of medial-lateral acceleration induced by the vastus group, there was a reversal in the direction of the average acceleration between the human crouched postures and the normal human posture. Among the three different human crouched postures, the patterns of induced accelerations were generally similar. In some cases, there were differences in the magnitude of average accelerations among the human crouched postures, but these differences were more subtle than the differences between the human crouched postures and the normal human posture. This aligns with the differences in kinematics and ground reaction forces among the different human postures, with the three crouched postures being relatively similar to each other while the normal posture was distinct from the crouched postures (see Chapter 5).

The gastrocnemius and soleus muscles are good examples of how both magnitude of the muscle forces and the orientation of body segments affect the accelerations induced on the whole-body center of mass by muscles (Zajac & Gordon, 1989) The peak muscle force during push-off in the gastrocnemius for normal human walking was three times greater than the peak muscle forces in the crouched posture conditions (Figure 6.2G). Yet the differences in the peak accelerations induced by the gastrocnemius were six times greater in the normal condition than the crouched postures in the vertical direction (Figure 6.4G), and only two times greater in the normal condition than the crouched postures in the horizontal direction (Figure 6.6G). Essentially, the potential for gastrocnemius to produce center of mass acceleration was reduced in the vertical direction and enhanced in the anterior-posterior direction when humans walked with a crouched posture compared with the normal condition (Figures A.1 and A.2). A similar effect of the orientation of body segments was seen in the soleus muscle, except the muscle force was greater in the crouched postures than in the normal postures. These results demonstrate the limitation of evaluating muscle function based only on muscle force magnitudes, especially when the conditions being compared have different body segment configurations.

For the CLFT and IMIT conditions, where the subjects were instructed to walk with a forward-leaning trunk, the human subjects also tilted their pelvis further forward in these conditions when compared to the CL condition. The greater forward pelvis tilt angle for the CLFT and IMIT conditions meant that the hip joint was also more flexed for these conditions when compared to the CL condition (See Chapter 5). Greater hip flexion angles in these postures decrease the magnitude of the moment arm for the gluteus maximus. This may partly explain why the muscle force production of the gluteus maximus was greater in the CLFT and IMIT conditions than the CL condition. The difference in moment arm magnitudes will also impact the differences found between the CL and CLFT in accelerations induced by the gluteus maximus muscle in the vertical and AP directions.

These induced acceleration results among the different human postures can be compared with previous work performed to evaluate the function of muscles in various crouched postures. Most previous studies focused on muscle function during crouched posture walking as it applies to children with cerebral palsy, however some similarities between our results and this prior work exist. The heavy reliance on vastus group muscles to contribute to anterior and posterior accelerations in crouched posture walking agrees with data reported by Steele et al. (Steele et al., 2013) and we found the soleus muscle to have a reduced ability to accelerate the center of mass vertically (Correa et al., 2012). However, unlike this prior work we found the anterior accelerations induced by the gastrocnemius and the posterior accelerations induced by the rectus femoris were both greater in the normal posture than the human crouched postures (Steele et al., 2013). Some of the discrepancies between our study and these others are likely due to the subject population: we instructed healthy adult subjects to perform crouched walking, while the past research studies analyzed the typical crouched gait mechanics of children with cerebral palsy.

6.4.2 The Effect of Morphology on Muscle Function During Gait

We sought to better understand the unique effects of morphology on muscle function during gait by comparing the results of an induced acceleration analysis on chimpanzee bipedal gait with the results on humans walking with gait mechanics that best imitate chimpanzees. There were several differences in muscle function between these two species, suggesting that muscle function in humans walking with crouched postures is distinct from the muscle function in chimpanzees. There were differences between species in both anterior-posterior and vertical accelerations induced by the gluteus maximus and vastus groups. The gluteus maximus and vastus group muscles are important muscles in crouched posture walking, as they produce hip and knee extensor torque and help to counteract the acceleration due to gravity in this posture. In the crouched posture, the gluteus maximus and vastus muscles must compensate for reduced ability of the skeletal system to support the weight of the body (Foster et al., 2013). Previous research has linked an increase in activation of these muscle groups to a greater metabolic cost of walking with a crouched posture, based on having humans walk with a crouched posture (Foster et al., 2013). However, the results from this study suggest roles the gluteus maximus and vastus groups (muscles that are primarily active during the first half of stance) play in accelerating the body upwards (supporting body weight) and anterior-posterior are different between humans and chimpanzees.

Chimpanzees seem to rely far less on their vastus group during bipedal walking than humans walking with a crouched posture, both for relative force production (Figure 6.3D) and vertical accelerations induced on the whole-body center of mass (Figure 6.10D). Instead, chimpanzees rely more heavily on the gluteus maximus muscle to produce vertical accelerations on the center of mass (Figure 6.10A). The substantial demand placed on the vastus group in human crouched posture walking is evidence of the different strategy used by humans to perform crouched posture gait. Therefore, previous attempts to make inferences about the evolution of hominin bipedalism based on having modern humans walk with crouched postures may be seriously confounded.

Previous researchers have suggested that the hamstrings muscle group plays a significant role in determining whether a species will walk with an upright or crouched posture (Aiello & Dean, 2002; Fleagle & Anapol, 1992; Kozma et al., 2018; Lovejoy, 2005). A short hamstring muscle moment arm when the hip of a chimpanzee is extended has been hypothesized as one potential explanation for why chimpanzees flex their hips when walking (Fleagle & Anapol, 1992). However, in this study the hamstrings muscle played only a small role (when compared to gluteus maximus, vastus group, and the plantar flexors) in accelerating the whole-body center of mass in both chimpanzees and humans. In addition, even though there are big differences between species in hip joint morphology, the average acceleration induced by the hamstrings was similar between humans and chimpanzees in the vertical (Figure 6.10E) and medial-lateral directions (Figure 6.12E). There was a significant difference in anterior-posterior acceleration induced by the hamstrings between species (Figure 6.11E), but this magnitude was small. These findings are in conflict with previous hypotheses that the hamstrings muscle, specifically the moment arm of the hamstrings to the hip joint, plays a key role in determining whether a species will walk with an upright posture or a crouched posture (Kozma et al., 2018). Our results suggest that the hamstrings muscle does not play as important of a role in determining whether a species walks with an upright or crouched posture, and may instead be more important for other tasks such as running or climbing. Instead, the gluteus maximus muscle group seems to play a key role as a hip extensor, and accelerating the center of mass upwards, during the early part of stance phase for both humans and chimpanzees. Like the hamstrings muscle, the size and orientation of the gluteus maximus has also been hypothesized to be important in determining whether a species will walk with an upright or crouched posture (Greiner, 2002; Stern Jr, 1972). It is important to note that for this study, the gluteus maximus muscle group included the ischiofemoral part of the gluteus maximus, which tends to operate more like a uniarticular hamstrings muscle (crossing the hip) than the rest of the gluteus maximus. Future work should look at how these muscle groupings affect the overall results and conclusions in this study.

The action of the gluteus maximus and gluteus medius were different between humans and chimpanzees. There was an average anterior acceleration induced by the gluteus maximus in the human crouched posture conditions, but an average posterior acceleration by this same muscle group in the chimpanzee. In the normal human conditions, there was an average upward acceleration induced by the gluteus medius. Then, in the human crouched posture conditions, the upward acceleration induced by the gluteus medius was less than the normal human conditions. In the chimpanzees however, there was an average downward acceleration induced by the gluteus medius. This progression from a greater upward acceleration in the normal human condition, to a slight positive upward acceleration in the human crouched postures, to a downward acceleration in the chimpanzees, demonstrates the interaction of both posture and morphology on muscle function. One potential explanation for the distinct functions of the gluteus maximus and gluteus medius between humans and chimpanzees are the shape of the iliac blades. In chimpanzees, the iliac blades are oriented in the frontal plane, as opposed to humans who have a more frontal plane orientation of their iliac blades. This affects the way these muscles act around the hip, with the flatter shape of the chimpanzee iliac blades affecting where this muscle group originates from relative to the pelvis (Aiello & Dean, 2002; Stern Jr. & Susman, 1981a). Stern and Susman (Stern Jr. & Susman, 1981b) have previously written about the distinct actions of the gluteus medius muscle group between humans and chimpanzees, which agrees with the findings from this study. Stern and Susman concluded that the gluteus medius muscle group functions primarily as a way to maintain balance in both humans and chimpanzees, but that the action it performs to maintain balance is different between species (in humans: prevent collapse into adduction, in chimpanzees: prevent collapse into lateral rotation). Our results compare favorably to their discussion, as the gluteus medius muscle group accelerates the center of mass in different directions in the vertical direction between species. Taken together, these results are evidence that the function of muscles (especially gluteus maximus, gluteus medius, and vastus group) in the human crouched posture conditions are not equivalent to the role that these muscles play in chimpanzee bipedal gait.

6.4.3 Limitations

The induced acceleration results in this study depend, in part, on the predictions of muscle forces obtained with static optimization. In this study, static optimization was implemented without accounting for the force-length-velocity relationship in muscles, which could have affected our predictions of muscle forces. With static optimization, the muscle redundancy problem is solved by predicting muscle forces based on minimizing the sum of the squared muscle activations at each point in the gait cycle. Including the force-length-velocity relationship would have likely altered the predicted activation of a muscle at a given force, and thus could have affected how the force was disturbed among the many muscles that cross any particular joint. However, Lin et al. (Lin et al., 2012) found that static optimization, computed muscle control, and neuromusculoskeletal tracking, the latter two of which include a force-length-velocity relationship, give similar predictions of muscle forces in both walking and running. This, along with a general agreement in the timing of muscle force production with electromyography data (Grasso et al., 2000), lends confidence to the predictions of muscle forces in this study.

Another potential limitation of this study was the degree to which the human subjects were able to imitate the chimpanzee bipedal gait mechanics. Although a strong attempt was made to instruct humans to walk like chimpanzees, there remained differences between species in gait kinematics and ground reaction forces. The instructions given in this study, specifically the IMIT condition which included both sagittal and frontal plane instructions, went beyond what previous studies had done in attempting to collect “chimpanzee-like” gait mechanics with human subjects. However, even though there remained some difference in gait mechanics, the function of some muscles were distinct between species (see the magnitude differences in the vastus group or the anterior versus posterior induced acceleration induced by the gluteus maximus). The function of muscles during gait will be dependent, in part, on the muscle moment arms relative to the joint centers in the lower limbs. The differences in musculoskeletal morphology between humans and chimpanzees, and the corresponding differences in muscle moment arms of analogous muscles in the lower limbs, mean that even if we were able to have humans walk with the same kinematics and ground reaction forces as the chimpanzees, differences in muscle function would persist. Therefore, we think many of the differences in muscle function between these species would hold even if the differences in gait mechanics were further reduced.

Another potential limitation was that we did not have experimental data on the motion of the upper body in the chimpanzee trials. We were able to implement trunk data collected on the same chimpanzees (Thompson et al., 2015), in combination with data from other highly trained chimpanzees walking bipedally (Pontzer et al., 2014), to give a reasonable estimate as to the orientation of the chimpanzee trunk during gait (approximately 25 degrees). RRA further modified the orientation of the trunk throughout the gait cycle to reduce the residual forces, but only ± 0.5 degrees for each degree-of-freedom. The sensitivity of the estimated trunk orientation and motion was tested by assigning other trunk angles and re-running the analysis. Different trunk orientations (0, 15, and 35 degrees) did not affect the general pattern or magnitude of the induced acceleration results, so this gives us confidence that the conclusions in this study are not very sensitive to the orientation of the trunk segment.

Lastly, the induced acceleration results obtained in this study can be sensitive to how the musculoskeletal system is modeled (Chen, 2006). We tested some of these sensitivities by removing the trunk segment in our models and re-running the induced acceleration analysis. Without the trunk segment, the induced acceleration patterns were generally consistent with the results presented in this study. Future work could be done to test how modeling other segments, such as the foot segment in the human and chimpanzee models, could affect the conclusions in this study.

6.4.4 Implications for Studying the Evolution of Human Bipedalism

The results from this study indicate that crouched posture human walking and the bipedal gait used by chimpanzees are generally not equivalent. Even when instructing humans to walk in a manner similar to chimpanzees there were differences in muscle function, in particular, in muscle groups such as the gluteus maximus and vastus group that are thought to be important to crouched posture gait. In most cases, the significant differences in muscle function reflected differences in magnitude, however the gluteus maximus in the vertical direction and gluteus medius in the anterior-posterior direction had opposite functions between species. The differences in muscle function between these species adds to a growing list of distinctive features when comparing human crouched posture walking with chimpanzee walking, including differences in center of mass motion (Demes et al., 2015) as well as kinematics and ground reaction forces (Study 1). These persistent differences between humans and chimpanzees, and the fact that both morphology and posture play important roles in determining muscle function, makes it difficult to use this crouched posture paradigm when studying the evolution of human bipedalism to determine whether extinct human ancestors would have walked upright or in a crouched posture. However, comparing the gait of these closely-related species may provide a bracket around many possible gait mechanics that could have been used by the last common ancestor of humans and chimpanzees as well as the hominin lineage (Witmer, 1995). This could be used in combination with predictive musculoskeletal modeling studies, where specific morphological features are systematically manipulated to better understand the effects of morphology on gait mechanics.

6.4.5 Conclusion

Both posture and morphology impact the roles that muscles play in inducing accelerations on the whole-body center of mass. When compared to normal human walking, human crouched posture walking results in greater contributions of the gluteus maximus, vastus group, and soleus muscle to the acceleration of the center of mass, while reducing the contribution of the gastrocnemius and rectus femoris. Although we instructed humans to walk with a “chimpanzee-like” gait, the humans seemed to have performed these patterns with distinct muscle function when compared to chimpanzees. It seems likely that differences in the shape of the pelvis between species is an important factor that influences how muscles like the gluteus maximus and gluteus medius perform. In all, the results from this study provide further evidence that conclusions about the evolution of human bipedalism drawn from human crouched posture walking should be viewed with caution.

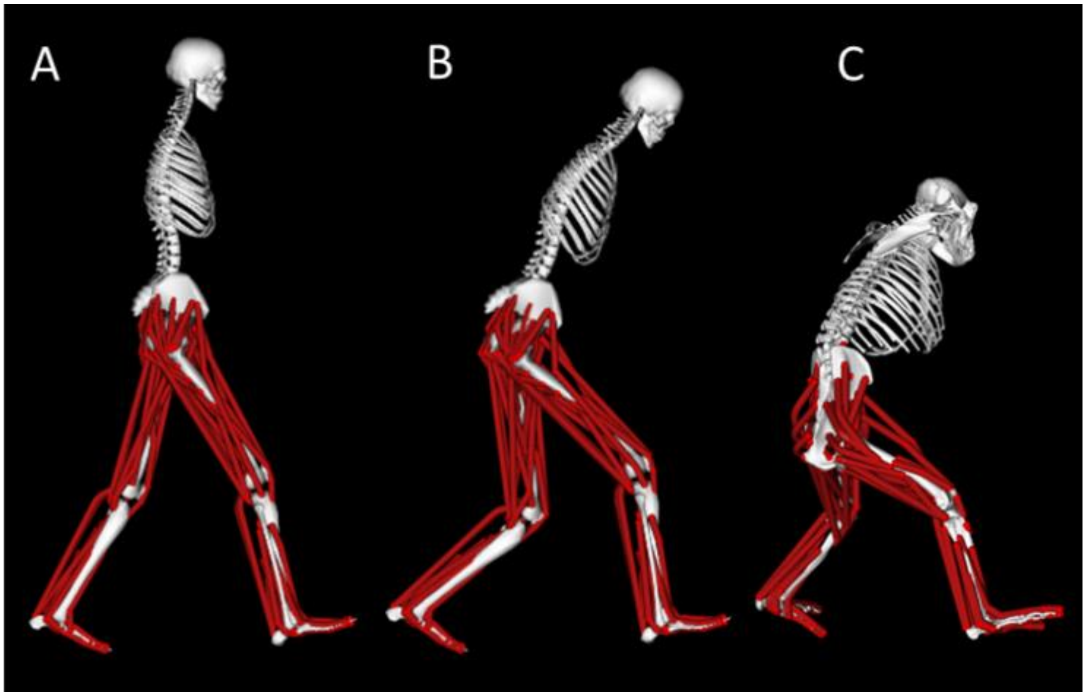


Figure 6.1: Snapshots of (A) normal human walking, (B) IMIT human walking, and (C) bipedal chimpanzee walking.

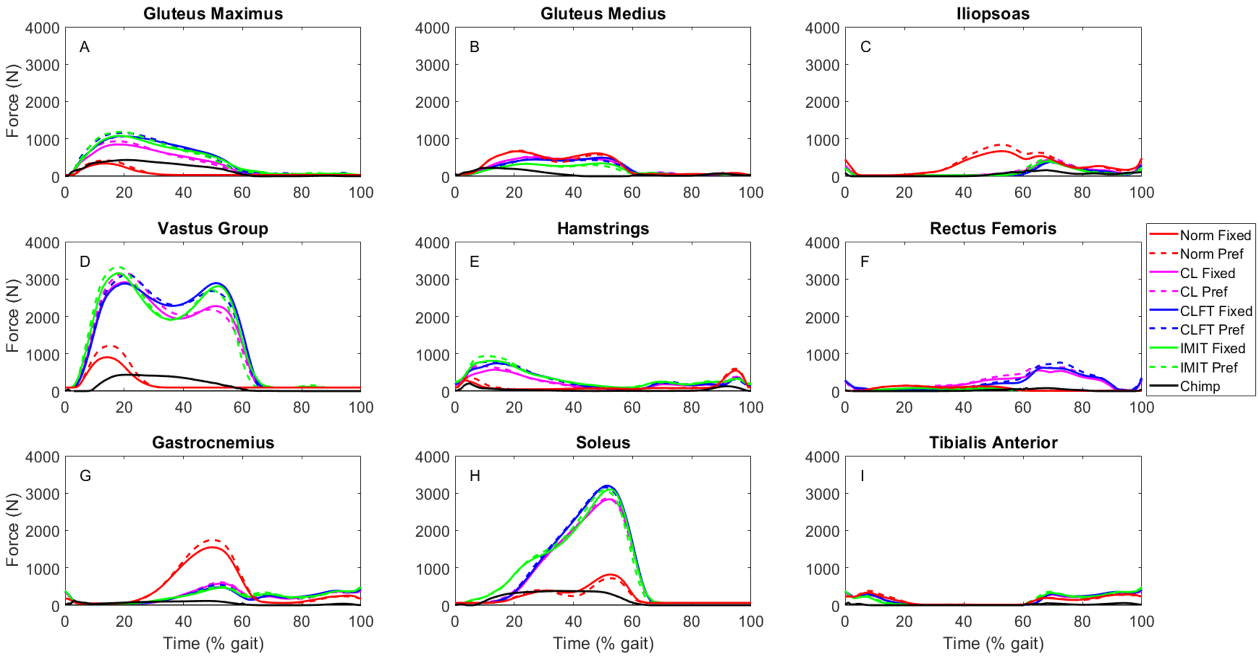


Figure 6.2: Estimated muscles forces from static optimization for each of the nine major muscle groups for each of the eight human posture conditions and the chimpanzee condition.

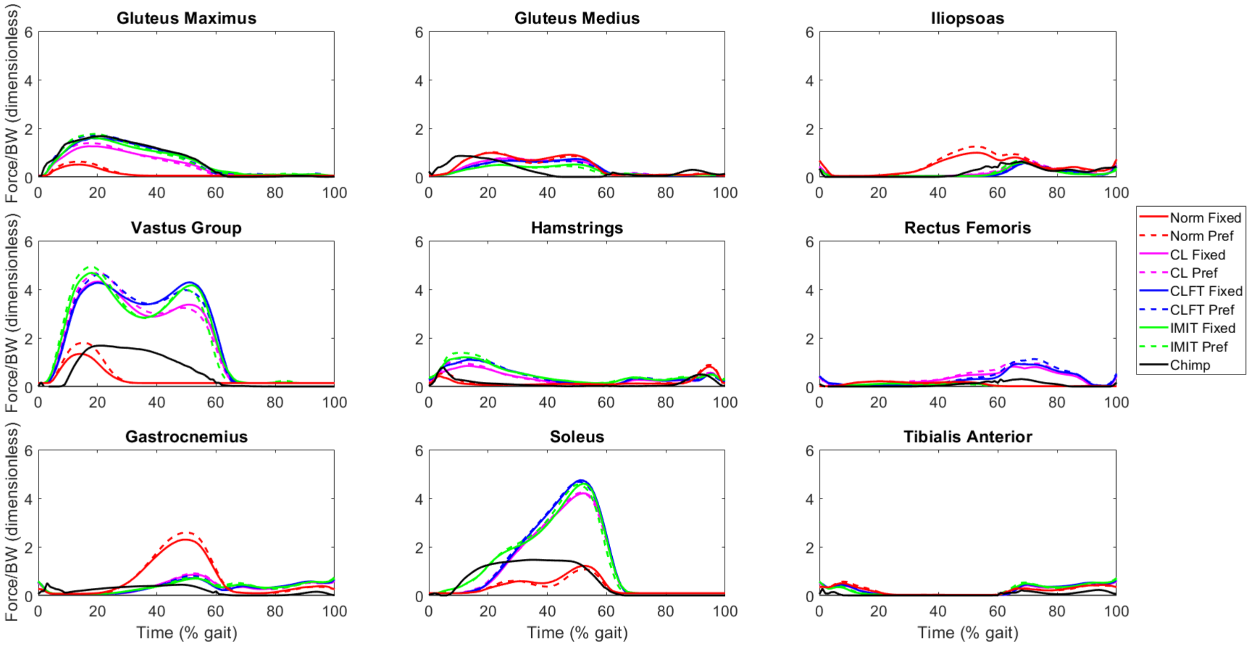


Figure 6.3: Estimated muscles forces from static optimization for each of the nine major muscle groups for each of the eight human posture conditions and the chimpanzee condition normalized to body weight, units are dimensionless.

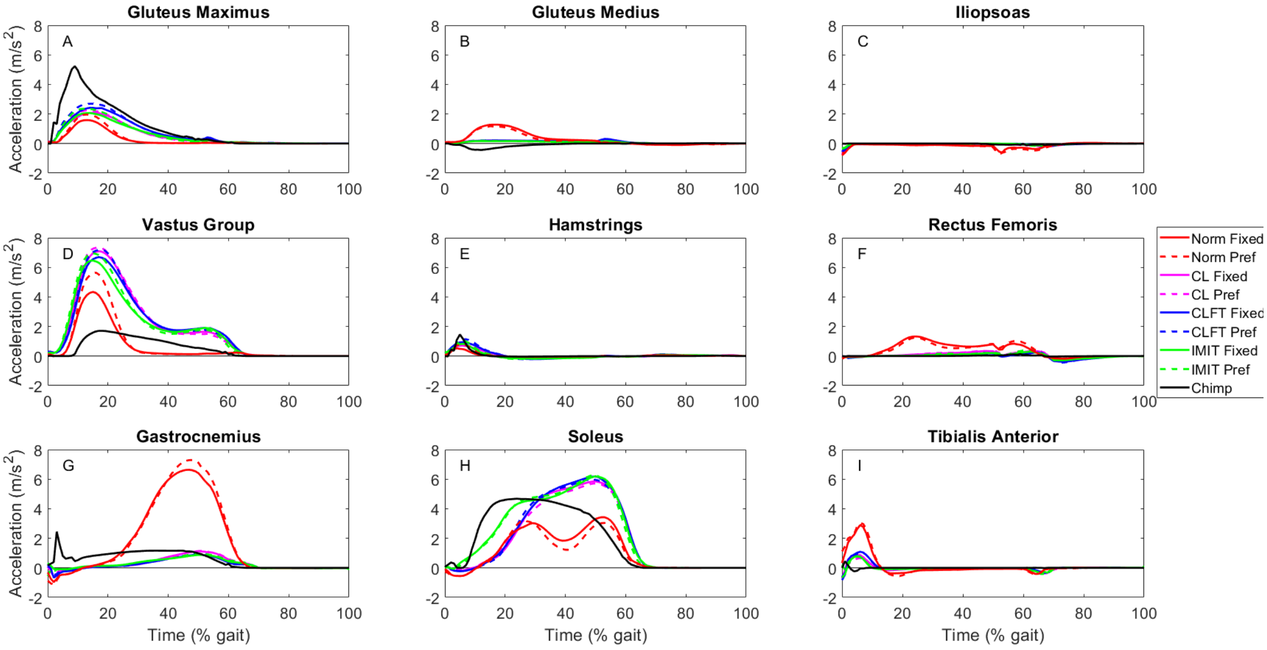


Figure 6.4: Induced accelerations for the vertical direction for each muscle for each human condition and the chimpanzees

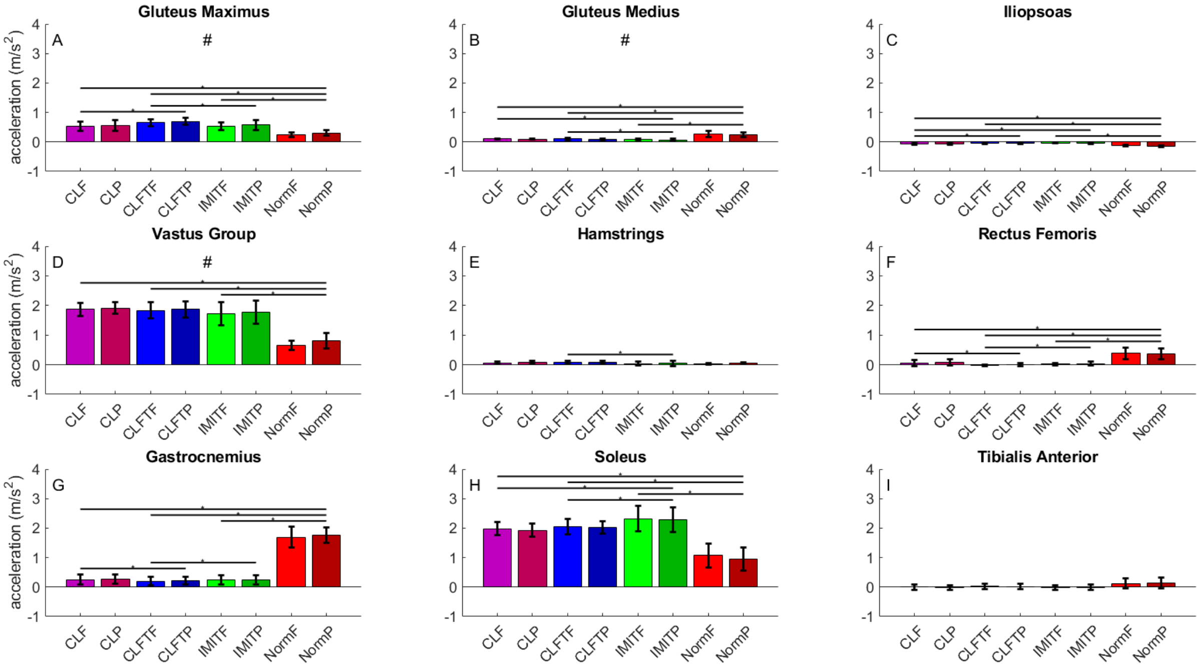


Figure 6.5: Average vertical accelerations calculated across the gait cycle. Number symbols (#) indicate that speed had a significant effect on the vertical accelerations. Horizontal bars with asterisks indicate there was a significant effect of posture on vertical accelerations.

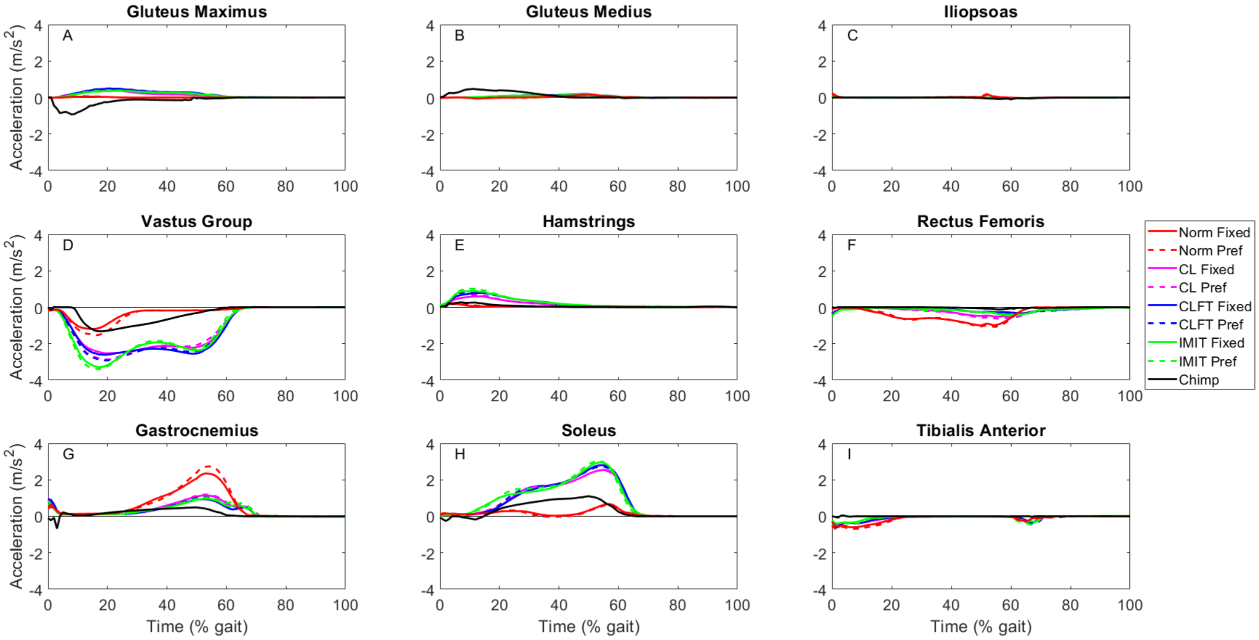


Figure 6.6: Induced acceleration results for the anterior-posterior direction for each muscle for each human condition and the chimpanzees

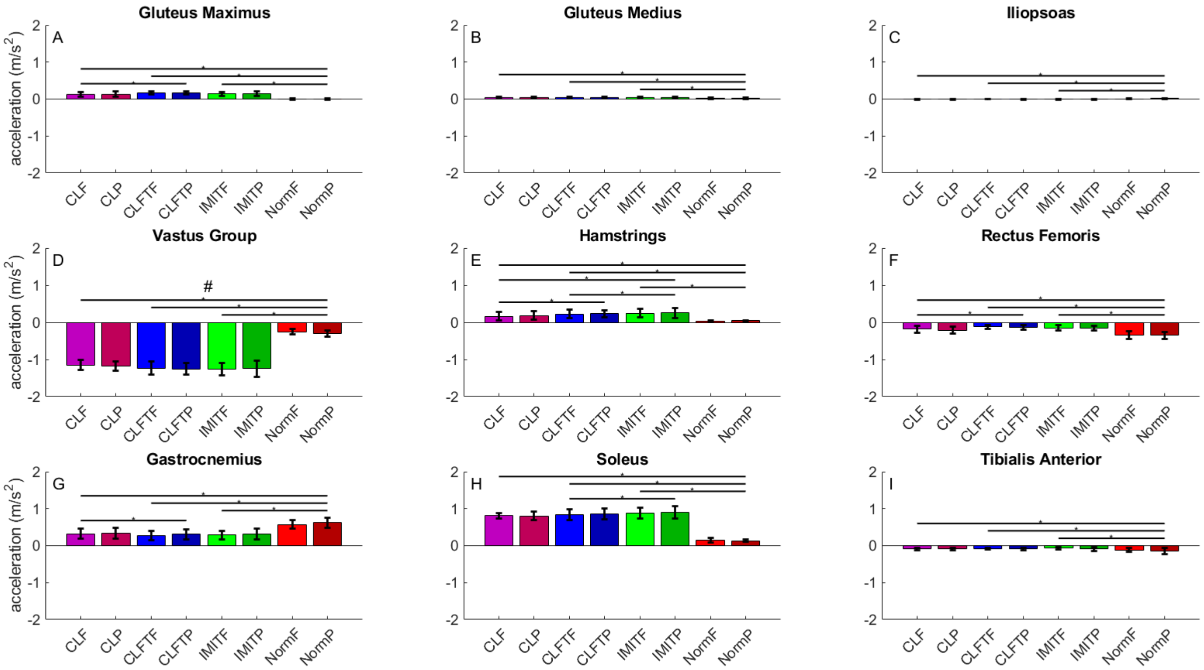


Figure 6.7: Average AP accelerations calculated across the gait cycle. Number symbols (#) indicate that speed had a significant effect on the AP accelerations. Horizontal bars with asterisks indicate there was a significant effect of posture on AP accelerations.

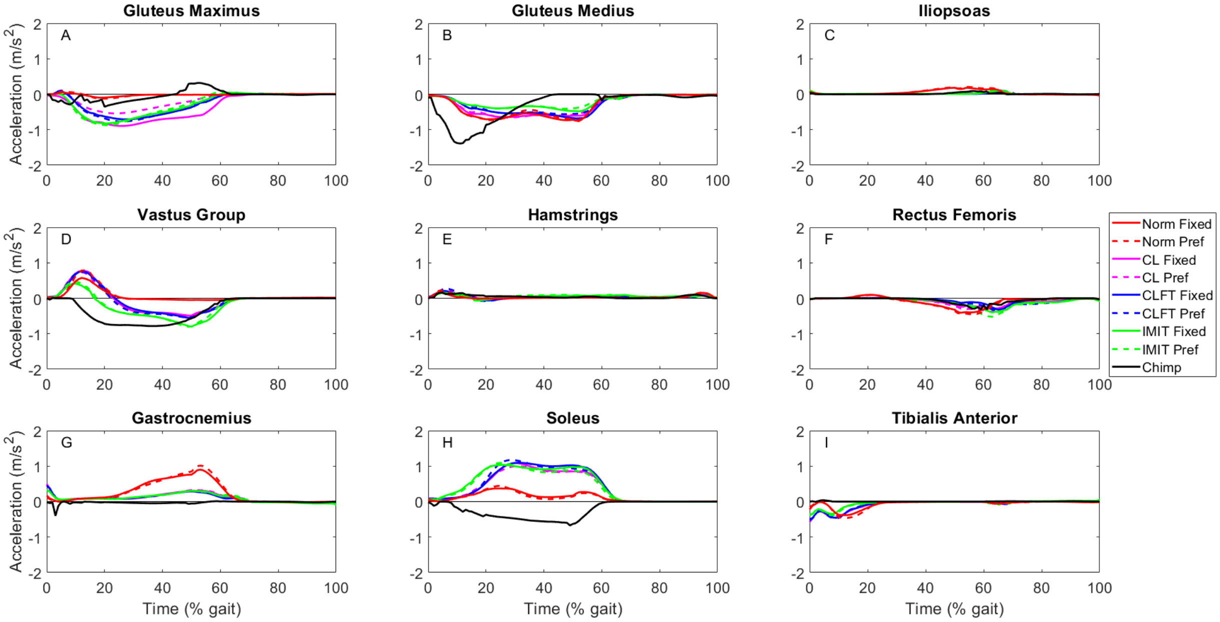


Figure 6.8: Induced acceleration results for the medial-lateral direction for each muscle for each human condition and the chimpanzees

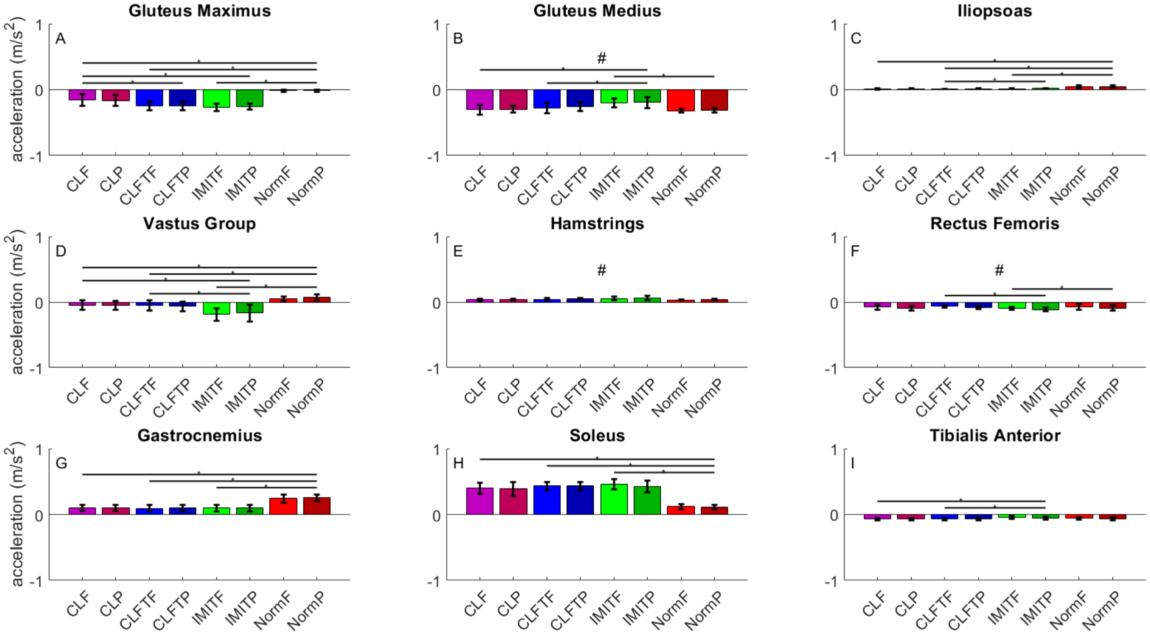


Figure 6.9: Average ML accelerations calculated across the gait cycle. Number symbols (#) indicate that speed had a significant effect on the ML accelerations. Horizontal bars with asterisks indicate there was a significant effect of posture on ML accelerations.

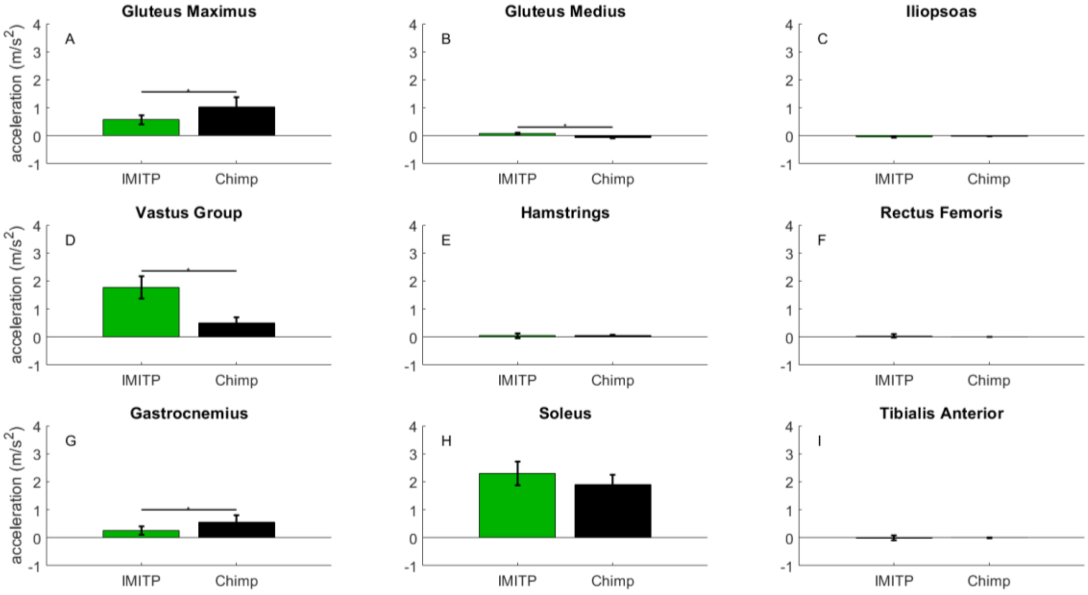


Figure 6.10: Average vertical accelerations calculated across the gait cycle for the human IMIT preferred condition compared with the chimpanzee results. Horizontal bars with asterisks indicate there was a significant effect of species on anterior-posterior accelerations.

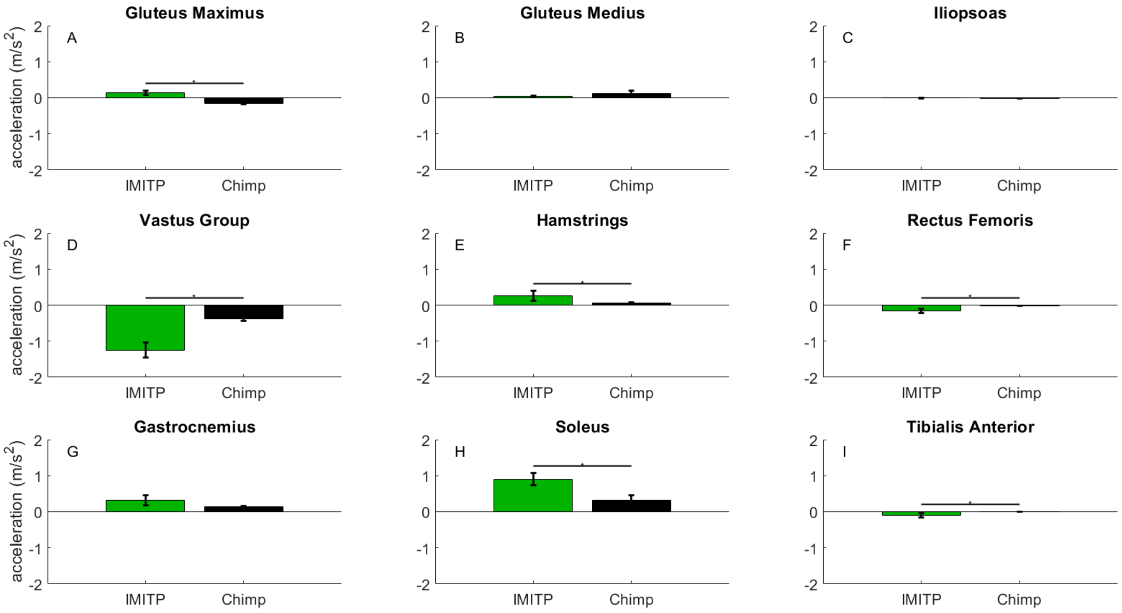


Figure 6.11: Average anterior-posterior accelerations calculated across the gait cycle for the human IMIT preferred condition compared with the chimpanzee results. Horizontal bars with asterisks indicate there was a significant effect of species on anterior-posterior accelerations.

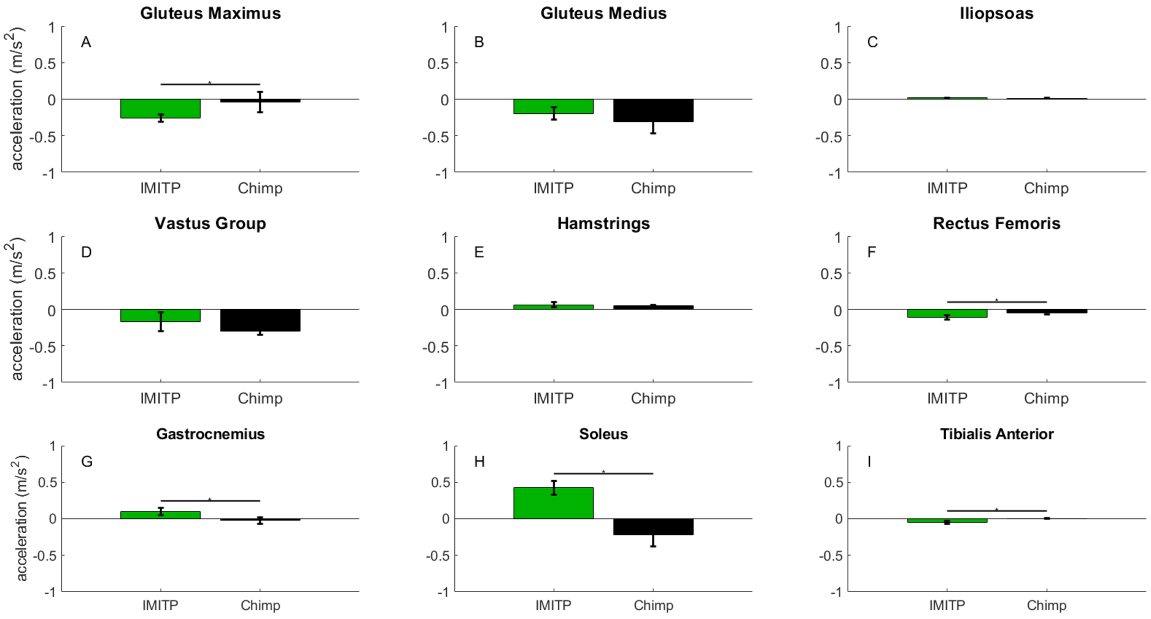


Figure 6.12: Average medial-lateral accelerations calculated across the gait cycle for the human IMIT preferred condition compared with the chimpanzee results. Horizontal bars with asterisks indicate there was a significant effect of species on vertical accelerations.

CHAPTER 7

SUMMARY

7.1 Introduction

Upright, habitual bipedal walking is considered a hallmark of human evolution. Normal human walking is characterized by extended legs during stance and a two-peaked ground reaction force. Our closest living relatives, chimpanzees, are facultative bipeds but walk with a flexed, abducted hind-limb posture and a monophasic ground reaction force. The distinct morphology between humans and chimpanzees, such as differential pelvis and lumbar spine shapes, likely play an important role in influencing the different gait kinematics between species. However, the differences in habitual posture used by these species could also impact the observed gait mechanics, as body segments are dynamically coupled such that the movement of one segment or joint will influence the movement of other, linked segments or joints.

An important question in human evolution is when our ancestors began walking with an upright posture, rather than with a flexed limb posture like modern chimpanzees. In order to better understand how upright bipedalism evolved, researchers have compared human gait and chimpanzee gait. Some researchers have used humans walking with a crouched, chimpanzee-like posture to draw conclusions about how extinct species, like *Au. afarensis*, would have walked (Carey & Crompton, 2005; Foster et al., 2013). However, it remains unclear how well human crouched posture walking approximates the gait mechanics of an animal such as the chimpanzee that is primarily adapted for arboreal locomotion. In addition, it is important to better understand how the muscles in these species function during gait in order to understand why chimpanzees walk with a flexed hind-limb posture even though it is considered to less economical than using an upright posture. The aim of this dissertation was to better understand the roles that morphology and posture play in determining gait mechanics in humans and chimpanzees.

7.2 The Roles of Morphology and Posture on Kinematics and Ground Reaction Forces

The aim of study 1 (Chapter 5) was to determine the degree to which human kinematics and GRFs converge to those of chimpanzees as humans walk with different crouched postures meant to mimic chimpanzee walking. We recruited ten healthy adult subjects and instructed them to walk with a normal gait, as well as with three crouched limb postures: crouched-limb (CL; bend at the hips and knees while walking), crouched-limb flexed-trunk (CLFT; same as CL plus a forward leaning trunk), and an imitation condition (IMIT; same as CLFT plus focus on elevating the pelvis on the swing side). The human subjects walked overground at their preferred speed (1.30 ± 0.15 m s^{-1}) and at a speed matched to the average, absolute speed of the chimpanzees (1.09 m s^{-1}) while kinematic and ground reaction forces were collected for each of the four posture conditions. We compared each of the eight (two speeds times four postures) human conditions to the chimpanzee bipedal gait from previously published data using zero-lag cross correlation coefficients and root-mean-square differences. We found that the crouched human postures resulted in more chimpanzee-like gait mechanics compared to a normal human posture, with the IMIT condition resulting in the most chimpanzee-like gait. Compared with the CLFT condition, the additional frontal plane instruction given in the IMIT condition resulted in a more chimpanzee-like pelvis list pattern. However, some substantial differences between the humans and chimpanzees remained, as, for example, none of the human postures produced as much hip abduction during stance or a monophasic vertical ground reaction force as observed for chimpanzees. There were only small effects of the two speeds performed by the human subjects on how well the gait mechanics matched the chimpanzee gait. Posture alone also played a role in impacting gait mechanics, as the CL and CLFT conditions resulted in greater hip abduction and an out-of-phase pelvis list pattern when compared with the normal human gait mechanics. The differences that remain between the human crouched posture conditions and the chimpanzees likely reflect the stark differences in morphology between the two species, including differences in pelvis shape and lumbar lordosis; however, we cannot rule out other possible factors that may influence gait mechanics like metabolic energy expenditure and stability. These results indicate that both posture and morphology play important roles in influencing gait mechanics. In addition, these results suggest that researchers should be cautious when using human crouched posture gait to interpret how extinct human ancestors walked, as modern humans walk with a crouched posture that differs from chimpanzees in important ways, even when an effort is made to mimic chimpanzee walking. As such, modern human couched walking is likely also different from walking in the last common ancestor of humans and chimpanzees (O'Neill et al., 2018).

7.3 The Roles of Morphology and Posture on Muscle Function in Bipedal Gait

The first aim of the study 2 (Chapter 6) was to determine how changes in posture affect muscle function during walking in humans, and the second aim was to determine how differences in morphology between chimpanzees and humans affect muscle function. We defined muscle function as the contribution of individual muscles to the acceleration of the whole-body center of mass. We used an induced acceleration analysis to determine how each muscle accelerates the whole-body center of mass throughout the gait cycle for each of the human conditions from Study 1, as well as for chimpanzees walking bipedally. We compared the results of the induced acceleration analysis among the different human postures to better understand how posture impacts muscle function when morphology is constant. We then compared the induced acceleration results from the human condition that best matched the chimpanzee gait data (IMIT, preferred speed) with the chimpanzee induced acceleration results, to try to isolate the role morphology plays in muscle function when walking patterns are similar. Instructing humans to walk with different crouched postures resulted in differences in muscle functions for almost every muscle group when compared to normal human walking. While most of the changes were in magnitude, in some cases, the crouched posture resulted in muscles reversing the way they accelerated the center of mass across the gait cycle (See Figure 6.9D). Human crouched posture walking resulted in greater contributions of the gluteus maximus, vastus group, and soleus muscle to the acceleration of the center of mass, while reducing the contributions of the gastrocnemius and rectus femoris.

When comparing between species, even though the postures were broadly similar, there were substantial differences in how the major muscle groups accelerated the center of mass. The function of the gluteus maximus and vastus group were significantly different, with a greater reliance on the vastus group while relying less on the gluteus maximus muscle for the human crouched posture gait when compared to chimpanzees. It seems likely that the differences in pelvis shape, which influence the origin of the gluteus maximus and gluteus medius muscle groups, play a significant role in determining the action of these muscles throughout the gait cycle. These differences in the role of these hip muscles could also affect how the other muscles in the hind limb function. It is also possible that since the gluteus maximus muscle is responsible for inducing greater vertical accelerations on the center of mass than the human conditions, that the chimpanzees therefore do not need to utilize their vastus muscle group to the same extent that humans do when walking with crouched postures.

Although our ability to isolate morphology alone was limited because there were remaining differences in gait mechanics, these between-species results suggest that it is difficult to use this human crouched posture paradigm when studying the evolution of human bipedalism. In particular, the muscle strategy used to induce vertical accelerations when the humans walked with crouched postures (relying on the vastus group) was different from how the chimpanzees induced vertical accelerations (relying on the gluteus maximus group). These differences in muscle function in among postures and between species, along with the fact that the morphology of humans and chimpanzees are both distinct from the morphology of our human ancestors as seen in the fossil record, confound any conclusions made about the evolution of human bipedalism based on humans walking with a crouched posture.

7.4 Summary

Taken together, these results show how morphology and posture are important, and sometimes independent, factors impacting the gait mechanics and muscle function of humans and chimpanzees. We were able to give instructions to our human subjects that allowed them to walk with a more chimpanzee-like gait, however some important differences in kinematics, ground reaction forces, and muscle function still remained. It is likely that the distinct shape of the human and chimpanzee pelvis, affecting the function of the gluteus maximus and gluteus medius muscle groups, is an important factor influencing how each species walks. In addition to morphology and posture, other factors like metabolic energy expenditure and balance will influence how each of these species walks. The remaining differences in gait between crouched posture humans and chimpanzees demonstrate some of the limitations of using humans walking with a crouched posture to investigate whether human ancestors would have walked with an upright, extended limb posture (like modern humans) or with more of a crouched posture (like modern chimpanzees).

7.5 Future Directions

Future research may focus on the instructions, feedback, and familiarization protocol given to humans when using the human crouched posture paradigm. It may be possible to further reduce the kinematic and ground reaction force differences with other instructions or more feedback. The use of real-time visual feedback of joint angles or ground reaction forces could be one way to guide human subjects towards a more chimpanzee-like gait. However, it is likely that even with a more chimpanzee-like gait, the muscle function between humans and chimpanzees would remain different in many ways, due to the differences in muscle moment arms based on the distinct musculoskeletal structure between species.

Future research could also utilize predictive musculoskeletal modeling techniques to investigate how specific morphological features impact gait mechanics. Musculoskeletal modeling allows for the systematic manipulation of a specific morphological trait, while holding all others constant, and then predict how the gait mechanics would be different based on the change to the musculoskeletal system. Based on the results of this study, one musculoskeletal feature to target for manipulation could be the shape of the pelvis, specifically the iliac blades, and the resulting differences in muscle attachment points when the pelvis shape is modified. Further evidence of how specific musculoskeletal structure impacts gait mechanics would allow anthropologists to make informed decisions on how extinct human ancestors walked.

APPENDIX

ADDITIONAL TABLES AND FIGURES

The following tables present the results of the zero-lag cross correlations and root-mean-square differences for the kinematics and ground reaction forces when compared between three male human subjects and the three male chimpanzee subjects.

Table A.1: Zero-lag cross-correlation coefficients for each human posture versus chimpanzee for each kinematic variable. Greater, positive values indicate more similar, in-phase kinematic patterns. Asterisks note the variable that matches best with the chimpanzee data.

	Pelvis Tilt	Pelvis List	Pelvis Rot	Hip Flex	Hip Add	Hip Rot	Knee Flex	Ankle Flex	Average
Norm F	-0.27	-0.84	0.99	0.72	-0.38	0.72	0.83	0.61	0.29
Norm P	-0.24	-0.84	0.97	0.74	-0.41	0.73	0.81	0.57	0.29
CL F	-0.67	0.15	0.83	0.86	-0.42	0.52	0.95	0.68	0.36
CL P	-0.51	-0.44	0.82	0.84	-0.34	0.42	0.91	0.67	0.30
CLFT F	0.02	0.00	0.76	0.86	-0.46	0.31	0.91	0.65	0.38
CLFT P	-0.07	-0.13	0.85	0.85	-0.40	0.21	0.90	0.64	0.36
IMIT F	-0.54	0.85	0.95	0.89	-0.26	0.88	0.94	0.65	0.54
IMIT P	-0.36	0.88	0.97	0.89	-0.22	0.89	0.93	0.69	0.58

Table A.2: Root-mean-square-differences for each human posture versus chimpanzee for each kinematic variable. The minimum value for the RMSD measurement is 0, which would indicate the two variables perfectly overlap with each other, while greater RMSD values give an indication of the amount of difference in magnitude that exists between the two variables. Asterisks note the variable that matches best with the chimpanzee data.

	Pelvis Tilt (°)	Pelvis List (°)	Pelvis Rot (°)	Hip Flex (°)	Hip Add (°)	Hip Rot (°)	Knee Flex (°)	Ankle Flex (°)	Avg. (°)
Norm F	4.7	6.8	12.4	29.6	21.3	9.0	30.9	7.1	15.2
Norm P	4.8	6.6	13.2	29.2	21.6	9.2	30.1	7.7	15.3
CL F	10.9	3.5	13.6	9.3	16.3	10.0	11.6	13.8	11.1
CL P	10.7	3.6	12.7	9.4	16.3	10.1	13.0	14.6	11.3
CLFT F	14.3	3.5	13.6	12.4	16.6	10.7	13.1	13.3	12.2
CLFT P	13.5	3.2	13.0	11.2	17.1	10.6	12.4	13.3	11.8
IMIT F	17.1	2.7	12.1	12.5	11.9	8.4	10.6	10.8	10.8
IMIT P	15.8	2.9	10.8	12.2	12.1	8.4	11.5	10.9	10.6

Table A.3: Zero-lag cross-correlation coefficients for each human posture versus chimpanzee for each ground reaction force variable. Greater, positive values indicate more similar, in-phase GRF patterns. Asterisks note the variable that matches best with the chimpanzee data.

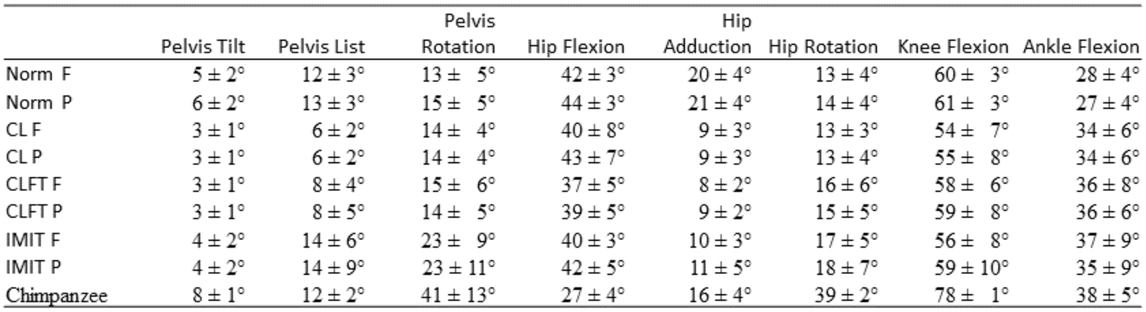
	AP GRF	Vertical GRF	ML GRF	Average
Norm F	0.86	0.83	0.71	0.80
Norm P	0.87	0.84	0.80	0.83
CL F	0.87	0.95	0.94	0.92
CL P	0.90	0.95	0.94	0.93
CLFT F	0.88	0.94	0.90	0.91
CLFT P	0.89	0.95	0.94	0.93
IMIT F	0.92	0.91	0.88	0.90
IMIT P	0.90	0.88	0.81	0.86

Table A.4: Root-mean-square-differences for each human posture versus chimpanzee for each ground reaction force variable. The minimum value for the RMSD measurement is 0, which would indicate the two variables perfectly overlap with each other, while greater RMSD values give an indication of the amount of difference in magnitude that exists between the two variables. Asterisks note the variable that matches best with the chimpanzee data.

	AP GRF (BW)	Vert GRF (BW)	ML GRF (BW)	Average (BW)
Norm F	0.05	0.20	0.02	0.09
Norm P	0.06	0.20	0.02	0.09
CL F	0.04	0.13	0.02	0.06
CL P	0.04	0.12	0.02	0.06
CLFT F	0.04	0.13	0.02	0.06
CLFT P	0.04	0.12	0.02	0.06
IMIT F	0.05	0.17	0.02	0.08
IMIT P	0.07	0.19	0.03	0.09

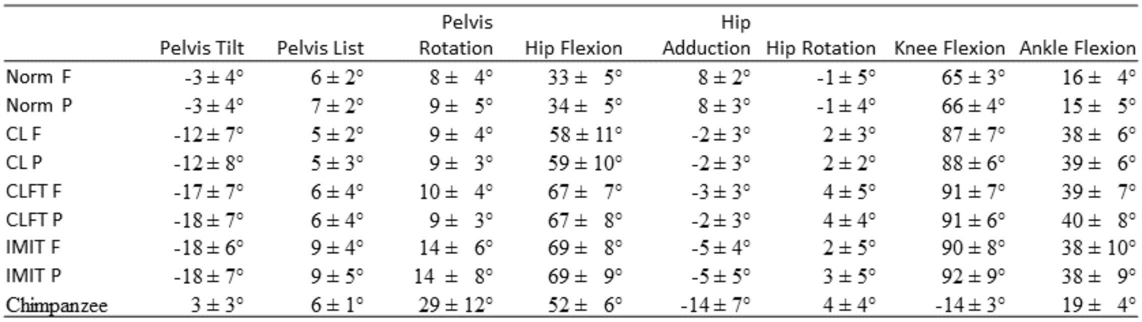
The following tables present the human subject joint range of motion, maximum, and minimum angles for each of the human posture conditions.

Table A.5: The range of motion values for each joint angle evaluated in the eight human conditions.



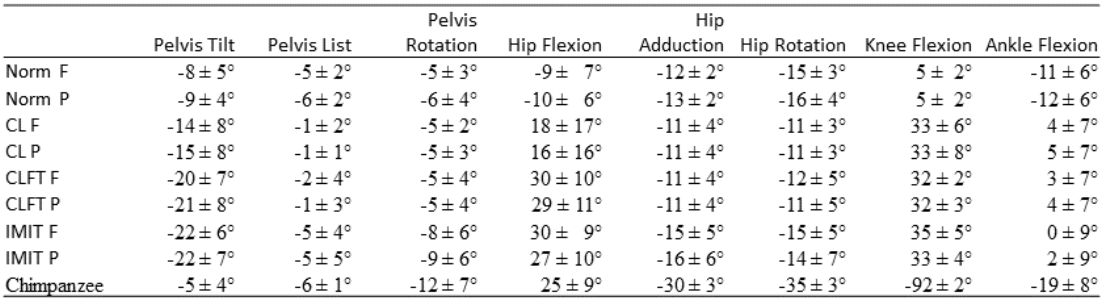
	Pelvis Tilt	Pelvis List	Pelvis Rotation	Hip Flexion	Hip Adduction	Hip Rotation	Knee Flexion	Ankle Flexion
Norm F	5 ± 2°	12 ± 3°	13 ± 5°	42 ± 3°	20 ± 4°	13 ± 4°	60 ± 3°	28 ± 4°
Norm P	6 ± 2°	13 ± 3°	15 ± 5°	44 ± 3°	21 ± 4°	14 ± 4°	61 ± 3°	27 ± 4°
CL F	3 ± 1°	6 ± 2°	14 ± 4°	40 ± 8°	9 ± 3°	13 ± 3°	54 ± 7°	34 ± 6°
CL P	3 ± 1°	6 ± 2°	14 ± 4°	43 ± 7°	9 ± 3°	13 ± 4°	55 ± 8°	34 ± 6°
CLFT F	3 ± 1°	8 ± 4°	15 ± 6°	37 ± 5°	8 ± 2°	16 ± 6°	58 ± 6°	36 ± 8°
CLFT P	3 ± 1°	8 ± 5°	14 ± 5°	39 ± 5°	9 ± 2°	15 ± 5°	59 ± 8°	36 ± 6°
IMIT F	4 ± 2°	14 ± 6°	23 ± 9°	40 ± 3°	10 ± 3°	17 ± 5°	56 ± 8°	37 ± 9°
IMIT P	4 ± 2°	14 ± 9°	23 ± 11°	42 ± 5°	11 ± 5°	18 ± 7°	59 ± 10°	35 ± 9°
Chimpanzee	8 ± 1°	12 ± 2°	41 ± 13°	27 ± 4°	16 ± 4°	39 ± 2°	78 ± 1°	38 ± 5°

Table A.6: The maximum values for each joint angle evaluated in the eight human conditions.



	Pelvis Tilt	Pelvis List	Pelvis Rotation	Hip Flexion	Hip Adduction	Hip Rotation	Knee Flexion	Ankle Flexion
Norm F	-3 ± 4°	6 ± 2°	8 ± 4°	33 ± 5°	8 ± 2°	-1 ± 5°	65 ± 3°	16 ± 4°
Norm P	-3 ± 4°	7 ± 2°	9 ± 5°	34 ± 5°	8 ± 3°	-1 ± 4°	66 ± 4°	15 ± 5°
CL F	-12 ± 7°	5 ± 2°	9 ± 4°	58 ± 11°	-2 ± 3°	2 ± 3°	87 ± 7°	38 ± 6°
CL P	-12 ± 8°	5 ± 3°	9 ± 3°	59 ± 10°	-2 ± 3°	2 ± 2°	88 ± 6°	39 ± 6°
CLFT F	-17 ± 7°	6 ± 4°	10 ± 4°	67 ± 7°	-3 ± 3°	4 ± 5°	91 ± 7°	39 ± 7°
CLFT P	-18 ± 7°	6 ± 4°	9 ± 3°	67 ± 8°	-2 ± 3°	4 ± 4°	91 ± 6°	40 ± 8°
IMIT F	-18 ± 6°	9 ± 4°	14 ± 6°	69 ± 8°	-5 ± 4°	2 ± 5°	90 ± 8°	38 ± 10°
IMIT P	-18 ± 7°	9 ± 5°	14 ± 8°	69 ± 9°	-5 ± 5°	3 ± 5°	92 ± 9°	38 ± 9°
Chimpanzee	3 ± 3°	6 ± 1°	29 ± 12°	52 ± 6°	-14 ± 7°	4 ± 4°	-14 ± 3°	19 ± 4°

Table A.7: The minimum values for each joint angle evaluated in the eight human conditions.



	Pelvis Tilt	Pelvis List	Pelvis Rotation	Hip Flexion	Hip Adduction	Hip Rotation	Knee Flexion	Ankle Flexion
Norm F	-8 ± 5°	-5 ± 2°	-5 ± 3°	-9 ± 7°	-12 ± 2°	-15 ± 3°	5 ± 2°	-11 ± 6°
Norm P	-9 ± 4°	-6 ± 2°	-6 ± 4°	-10 ± 6°	-13 ± 2°	-16 ± 4°	5 ± 2°	-12 ± 6°
CL F	-14 ± 8°	-1 ± 2°	-5 ± 2°	18 ± 17°	-11 ± 4°	-11 ± 3°	33 ± 6°	4 ± 7°
CL P	-15 ± 8°	-1 ± 1°	-5 ± 3°	16 ± 16°	-11 ± 4°	-11 ± 3°	33 ± 8°	5 ± 7°
CLFT F	-20 ± 7°	-2 ± 4°	-5 ± 4°	30 ± 10°	-11 ± 4°	-12 ± 5°	32 ± 2°	3 ± 7°
CLFT P	-21 ± 8°	-1 ± 3°	-5 ± 4°	29 ± 11°	-11 ± 4°	-11 ± 5°	32 ± 3°	4 ± 7°
IMIT F	-22 ± 6°	-5 ± 4°	-8 ± 6°	30 ± 9°	-15 ± 5°	-15 ± 5°	35 ± 5°	0 ± 9°
IMIT P	-22 ± 7°	-5 ± 5°	-9 ± 6°	27 ± 10°	-16 ± 6°	-14 ± 7°	33 ± 4°	2 ± 9°
Chimpanzee	-5 ± 4°	-6 ± 1°	-12 ± 7°	25 ± 9°	-30 ± 3°	-35 ± 3°	-92 ± 2°	-19 ± 8°

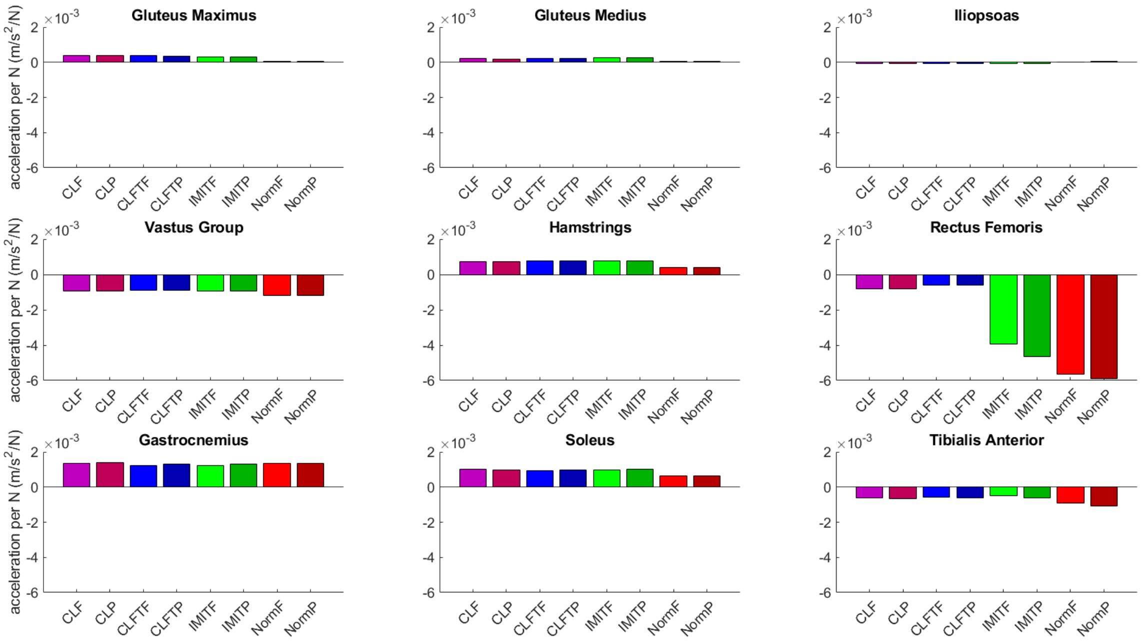


Figure A.1: Accelerations induced in the anterior-posterior direction by each of the nine major muscle groups normalized to muscle force.

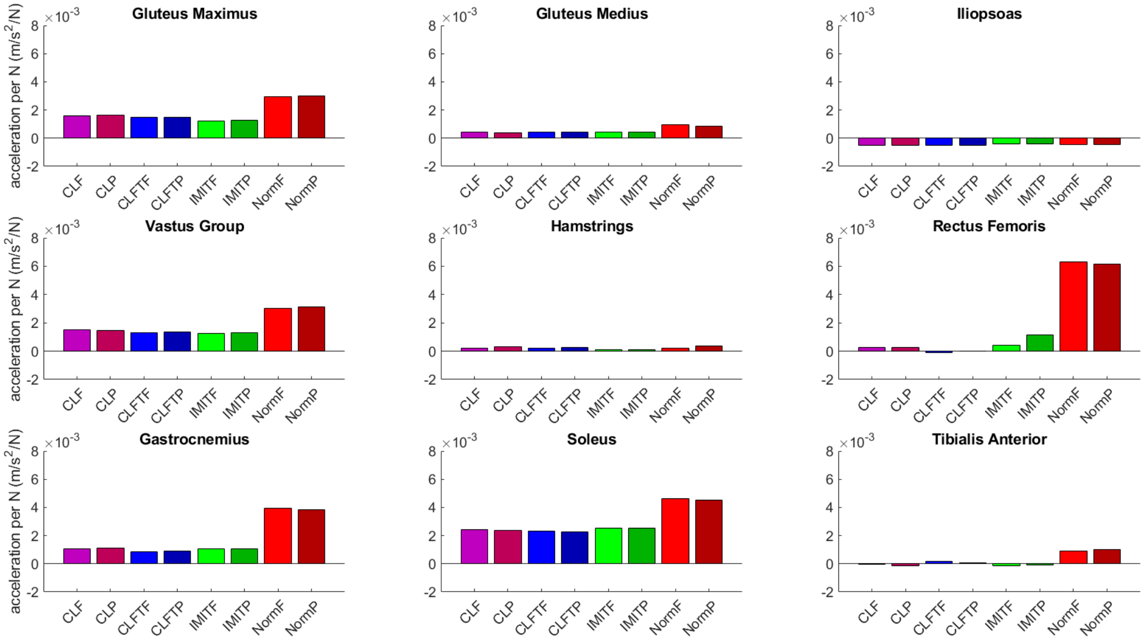


Figure A.2: Accelerations induced in the vertical direction by each of the nine major muscle groups normalized to muscle force.

REFERENCES

Ackermann, M., & van den Bogert, A. J. (2010). Optimality principles for model-based prediction of human gait. *Journal of Biomechanics, 43*(6), 1055-1060. doi:10.1016/j.jbiomech.2009.12.012 [doi]

Aiello, L., & Dean, C. (2002). *An introduction to human evolutionary anatomy* (1st Edition ed.) Academic Press.

Alexander, R. M. N. (2004). Bipedal animals, and their differences from humans. *Journal of Anatomy, 204*(5), 321-330. doi:10.1111/j.0021-8782.2004.00289.x [doi]

Aminiaghdam, S., Rode, C., Muller, R., & Blickhan, R. (2017). Increasing trunk flexion transforms human leg function into that of birds despite different leg morphology. *The Journal of Experimental Biology, 220*(Pt 3), 478-486. doi:10.1242/jeb.148312 [doi]

Anderson, F. C., & Pandy, M. G. (1999). A dynamic optimization solution for vertical jumping in three dimensions. *Computer Methods in Biomechanics and Biomedical Engineering, 2*(3), 201-231. doi:10.1080/10255849908907988

Anderson, F. C., & Pandy, M. G. (2001). Dynamic optimization of human walking. *Journal of Biomechanical Engineering, 123*(5), 381-390.

Anderson, F. C., & Pandy, M. G. (2003). Individual muscle contributions to support in normal walking. *Gait & Posture, 17*(2), 159-169.

Andriacchi, T. P., Ogle, J. A., & Galante, J. O. (1977). Walking speed as a basis for normal and abnormal gait measurements. *Journal of Biomechanics, 10*(4), 261-268. doi:10.1016/0021-9290(77)90049-5

Barak, M. M., Lieberman, D. E., Raichlen, D., Pontzer, H., Warrener, A. G., & Hublin, J. J. (2013). Trabecular evidence for a human-like gait in australopithecus africanus. *PloS One, 8*(11), e77687. doi:10.1371/journal.pone.0077687 [doi]

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society.Series B (Methodological), 57*(1), 289-300.

Blickhan, R., Andrada, E., Muller, R., Rode, C., & Ogihara, N. (2015). Positioning the hip with respect to the COM: Consequences for leg operation. *Journal of Theoretical Biology, 382*, 187-197. doi:10.1016/j.jtbi.2015.06.036 [doi]

Bojsen-MÃ¸ller, F. (1979). Calcaneocuboid joint and stability of the longitudinal arch of the foot at high and low gear push off. *Journal of Anatomy, 129*(Pt 1), 165-176.

Caravaggi, P., Pataky, T., Gunther, M., Savage, R., & Crompton, R. (2010). Dynamics of longitudinal arch support in relation to walking speed: Contribution of the plantar aponeurosis. *Journal of Anatomy, 217*(3), 254-261. doi:10.1111/j.1469-7580.2010.01261.x [doi]

Carey, T. S., & Crompton, R. H. (2005). The metabolic costs of 'bent-hip, bent-knee' walking in humans. *Journal of Human Evolution, 48*(1), 25-44. doi:S0047-2484(04)00142-3 [pii]

Cavagna, G. A., Heglund, N. C., & Taylor, C. R. (1977). Mechanical work in terrestrial locomotion: Two basic mechanisms for minimizing energy expenditure. *The American Journal of Physiology, 233*(5), R243-61.

Cavagna, G. A., & Kaneko, M. (1977). Mechanical work and efficiency in level walking and running. *The Journal of Physiology, 268*(2), 467--81.

Cavagna, G. A., Thys, H., & Zamboni, A. (1976). The sources of external work in level walking and running. *The Journal of Physiology, 262*(3), 639-657.

Charles, J. P., Cappellari, O., Spence, A. J., Wells, D. J., & Hutchinson, J. R. (2016). Muscle moment arms and sensitivity analysis of a mouse hindlimb musculoskeletal model. *Journal of Anatomy, 229*(4), 514-535. doi:10.1111/joa.12461 [doi]

Chen, G. (2006). Induced acceleration contributions to locomotion dynamics are not physically well defined. *Gait & Posture, 23*(1), 37-44. doi:S0966-6362(04)00264-4 [pii]

Chow, C. K., & Jacobson, D. H. (1971). Studies of human locomotion via optimal programming. *Mathematical Biosciences, 10*(3-4), 239-306.

Correa, T. A., Schache, A. G., Graham, H. K., Baker, R., Thomason, P., & Pandy, M. G. (2012). Potential of lower-limb muscles to accelerate the body during cerebral palsy gait. *Gait & Posture, 36*(2), 194-200. doi:10.1016/j.gaitpost.2012.02.014 [doi]

Crompton, R. H., Yu, L., Weijie, W., Gunther, M., & Savage, R. (1998). The mechanical effectiveness of erect and "bent-hip, bent-knee" bipedal walking in australopithecus afarensis. *Journal of Human Evolution, 35*(1), 55-74. doi:S0047248498902226 [pii]

Delp, S. L., Anderson, F. C., Arnold, A. S., Loan, P., Habib, A., John, C. T., . . . Thelen, D. G. (2007). OpenSim: Open-source software to create and analyze dynamic simulations of movement. *IEEE Transactions on Bio-Medical Engineering, 54*(11), 1940-1950. doi:10.1109/TBME.2007.901024

Delp, S. L., & Loan, J. P. (1995). A graphics-based software system to develop and analyze models of musculoskeletal structures. *Computers in Biology and Medicine, 25*(1), 21-34. doi:001048259598882E [pii]

Delp, S. L., Loan, J. P., Hoy, M. G., Zajac, F. E., Topp, E. L., & Rosen, J. M. (1990). An interactive graphics-based model of the lower extremity to study orthopaedic surgical procedures. *IEEE Transactions on Bio-Medical Engineering, 37*(8), 757-767. doi:10.1109/10.102791

Delp, S. L., & Zajac, F. E. (1992). Force- and moment-generating capacity of lower-extremity muscles before and after tendon lengthening. *Clinical Orthopaedics and Related Research, (284)*(284), 247-259.

Demes, B., Thompson, N. E., O'Neill, M. C., & Umberger, B. R. (2015). Center of mass mechanics of chimpanzee bipedal walking. *American Journal of Physical Anthropology, 156*(3), 422-433. doi:10.1002/ajpa.22667 [doi]

den Otter, A. R., Geurts, A. C., Mulder, T., & Duysens, J. (2004). Speed related changes in muscle activity from normal to very slow walking speeds. *Gait & Posture, 19*(3), 270-278. doi:10.1016/S0966-6362(03)00071-7 [doi]

Donelan, J. M., Kram, R., & Kuo, A. D. (2002). Mechanical work for step-to-step transitions is a major determinant of the metabolic cost of human walking. *The Journal of Experimental Biology, 205*(Pt 23), 3717-3727.

Elftman, H. (1944). The bipedal walking of the chimpanzee. *Journal of Mammalogy, 25*(1), 67-71.

Erdemir, A., McLean, S., Herzog, W., & van den Bogert, A. J. (2007). Model-based estimation of muscle forces exerted during movements. *Clinical Biomechanics (Bristol, Avon), 22*(2), 131-154. doi:10.1016/j.clinbiomech.2006.09.005

Fernandez, P. J., Holowka, N. B., Demes, B., & Jungers, W. L. (2016). Form and function of the human and chimpanzee forefoot: Implications for early hominin bipedalism. *Scientific Reports, 6*, 30532. doi:10.1038/srep30532 [doi]

Finley, F. R., & Cody, K. A. (1970). Locomotive characteristics of urban pedestrians. *Archives of Physical Medicine and Rehabilitation, 51*(7), 423-426.

Fleagle, J. G., & Anapol, F. C. (1992). The indriid ischium and hominid hip. *Journal of Human Evolution, 22*(4-5), 285-305.

Foster, A. D., Raichlen, D. A., & Pontzer, H. (2013). Muscle force production during bent-knee, bent-hip walking in humans. *Journal of Human Evolution, 65*(3), 294-302. doi:10.1016/j.jhevol.2013.06.012 [doi]

Gage, J. R. (1990). An overview of normal walking. *Instructional Course Lectures, 39*, 291-303.

Garber, C. E., Blissmer, B., Deschenes, M. R., Franklin, B. A., Lamonte, M. J., Lee, I. M., . . . American College of Sports Medicine. (2011). American college of sports medicine position stand. quantity and quality of exercise for developing and maintaining cardiorespiratory, musculoskeletal, and neuromotor fitness in apparently healthy adults: Guidance for prescribing exercise. *Medicine and Science in Sports and Exercise, 43*(7), 1334-1359. doi:10.1249/MSS.0b013e318213fefb [doi]

Gatesy, S. M., & Biewener, A. A. (1991). Bipedal locomotion: Effects of speed, size and limb posture in birds and humans. *Journal of Zoology, 224*(1), 127-147.

Gordon, K. E., Ferris, D. P., & Kuo, A. D. (2009). Metabolic and mechanical energy costs of reducing vertical center of mass movement during gait. *Archives of Physical Medicine and Rehabilitation, 90*(1), 136-144. doi:10.1016/j.apmr.2008.07.014; 10.1016/j.apmr.2008.07.014

Grasso, R., Zago, M., & Lacquaniti, F. (2000). Interactions between posture and locomotion: Motor patterns in humans walking with bent posture versus erect posture. *Journal of Neurophysiology, 83*(1), 288-300.

Greiner, T. M. (2002). The morphology of the gluteus maximus during human evolution: Prerequisite or consequence of the upright bipedal posture? *Human Evolution, 17*(1), 79-94. doi:10.1007/BF02436430

Grieve, D. W., & Gear, R. J. (1966). The relationships between length of stride, step frequency, time of swing and speed of walking for children and adults. *Ergonomics, 9*(5), 379-399. doi:10.1080/00140136608964399

Griffin, T. M., Roberts, T. J., & Kram, R. (2003). Metabolic cost of generating muscular force in human walking: Insights from load-carrying and speed experiments. *Journal of Applied Physiology (Bethesda, Md.: 1985), 95*(1), 172-183. doi:10.1152/japplphysiol.00944.2002

Hamner, S. R., Seth, A., & Delp, S. L. (2010). Muscle contributions to propulsion and support during running. *Journal of Biomechanics, 43*(14), 2709-2716. doi:10.1016/j.jbiomech.2010.06.025 [doi]

Hamner, S. R., Seth, A., Steele, K. M., & Delp, S. L. (2013). A rolling constraint reproduces ground reaction forces and moments in dynamic simulations of walking, running, and crouch gait. *Journal of Biomechanics, 46*(10), 1772-1776. doi:10.1016/j.jbiomech.2013.03.030 [doi]

Hatze, H. (1976). The complete optimization of a human motion. *Mathematical Biosciences, 28*(1-2), 99-135.

Hicks, J. H. (1954). The mechanics of the foot: II. the plantar aponeurosis and the arch. *Journal of Anatomy, 88,* 25-30.1.

Hicks, J. L., Schwartz, M. H., Arnold, A. S., & Delp, S. L. (2008). Crouched postures reduce the capacity of muscles to extend the hip and knee during the single-limb stance phase of gait. *Journal of Biomechanics, 41*(5), 960-967. doi:10.1016/j.jbiomech.2008.01.002 [doi]

Hill, A. V. (1938). The heat of shortening and the dynamic constants of muscle. *Proceedings of the Royal Society of London.Series B - Biological Sciences, 126*(843), 136-195. doi:10.1098/rspb.1938.0050

Hof, A. L., Elzinga, H., Grimmius, W., & Halbertsma, J. P. (2002). Speed dependence of averaged EMG profiles in walking. *Gait & Posture, 16*(1), 78-86. doi:S0966636201002065 [pii]

Holowka, N. B., O'Neill, M. C., Thompson, N. E., & Demes, B. (2017). Chimpanzee and human midfoot motion during bipedal walking and the evolution of the longitudinal arch of the foot. *Journal of Human Evolution, 104,* 23-31. doi:S0047-2484(16)30238-X [pii]

Holt, K. G., Hamill, J., & Andres, R. O. (1991). Predicting the minimal energy costs of human walking. *Medicine and Science in Sports and Exercise, 23*(4), 491-498.

Hunt, K. D. (1992). Positional behavior of pan troglodytes in the mahale mountains and gombe stream national parks, tanzania. *American Journal of Physical Anthropology, 87*(1), 83-105. doi:10.1002/ajpa.1330870108 [doi]

Hutchinson, J. R., Anderson, F. C., Blemker, S. S., & Delp, S. L. (2005). Analysis of hindlimb muscle moment arms in tyrannosaurus rex using a three-dimensional musculoskeletal computer model: Implications for stance, gait, and speed. *Paleobiology, 31*(4), 676-701.

Jahnsen, R., Villien, L., Aamodt, G., Stanghelle, J. K., & Holm, I. (2004). Musculoskeletal pain in adults with cerebral palsy compared with the general population. *Journal of Rehabilitation Medicine, 36*(2), 78-84.

Jenkins, F. A.,Jr. (1972). Chimpanzee bipedalism: Cineradiographic analysis and implications for the evolution of gait. *Science (New York, N.Y.), 178*(4063), 877-879.

Johanson, D. C., Lovejoy, C. O., Kimbel, W. H., White, T. D., Ward, S. C., Bush, W. E., . . . Coppens, Y. (1982). Morphology of the pliocene partial hominid skeleton (A.L. 288-1) from the hadar formation, ethiopia. *Am J Phys Anthropol, 57*(4), 403-451.

Johanson, D. C., & Taieb, M. (1976). Plio-pleistocene hominid discoveries in hadar, ethiopia. *Nature, 260*, 293-297.

John, C. T., Seth, A., Schwartz, M. H., & Delp, S. L. (2012a). Contributions of muscles to mediolateral ground reaction force over a range of walking speeds. *Journal of Biomechanics, 45*(14), 2438-2443. doi:10.1016/j.jbiomech.2012.06.037 [doi]

John, C. T., Seth, A., Schwartz, M. H., & Delp, S. L. (2012b). Contributions of muscles to mediolateral ground reaction force over a range of walking speeds. *Journal of Biomechanics, 45*(14), 2438-2443. doi:10.1016/j.jbiomech.2012.06.037 [doi]

Johnson, W. L., Jindrich, D. L., Roy, R. R., & Edgerton, V. R. (2008). A three-dimensional model of the rat hindlimb: Musculoskeletal geometry and muscle moment arms. *Journal of Biomechanics, 41*(3), 610-619. doi:10.1016/j.jbiomech.2007.10.004 [doi]

Kerr Graham, H., & Selber, P. (2003). Musculoskeletal aspects of cerebral palsy. *The Journal of Bone and Joint Surgery.British Volume, 85*(2), 157-166.

Kozma, E. E., Webb, N. M., Harcourt-Smith, W. E. H., Raichlen, D. A., D'Aout, K., Brown, M. H., . . . Pontzer, H. (2018). Hip extensor mechanics and the evolution of walking and climbing capabilities in humans, apes, and fossil hominins. *Proceedings of the National Academy of Sciences of the United States of America, 115*(16), 4134-4139. doi:10.1073/pnas.1715120115 [doi]

Kram, R., & Taylor, C. R. (1990). Energetics of running: A new perspective. *Nature, 346*(6281), 265-267. doi:10.1038/346265a0

Kuo, A. D. (1998). A least-squares estimation approach to improving the precision of inverse dynamics computations. *Journal of Biomechanical Engineering, 120*(1), 148-159.

Kuo, A. D. (2001). A simple model of bipedal walking predicts the preferred speed-step length relationship. *Journal of Biomechanical Engineering, 123*(3), 264-269.

Kuo, A. D., Donelan, J. M., & Ruina, A. (2005). Energetic consequences of walking like an inverted pendulum: Step-to-step transitions. *Exercise and Sport Sciences Reviews, 33*(2), 88-97.

Kwon, J. W., Son, S. M., & Lee, N. K. (2015). Changes of kinematic parameters of lower extremities with gait speed: A 3D motion analysis study. *Journal of Physical Therapy Science, 27*(2), 477-479. doi:jpts-2014-485 [pii]

Lai, A. K. M., Arnold, A. S., & Wakeling, J. M. (2017). Why are antagonist muscles co-activated in my simulation? A musculoskeletal model for analysing human locomotor tasks. *Annals of Biomedical Engineering,* doi:10.1007/s10439-017-1920-7 [doi]

Larsson, L. E., Odenrick, P., Sandlund, B., Weitz, P., & Oberg, P. A. (1980). The phases of the stride and their interaction in human gait. *Scandinavian Journal of Rehabilitation Medicine, 12*(3), 107-112.

Lee, L. F., & Umberger, B. R. (2016). Generating optimal control simulations of musculoskeletal movement using OpenSim and MATLAB. *PeerJ, 4,* e1638. doi:10.7717/peerj.1638 [doi]

Li, Y., Crompton, R. H., Alexander, R. M., Gunther, M. M., & Wang, W. J. (1996). Characteristics of ground reaction forces in normal and chimpanzee-like bipedal walking by humans. *Folia Primatologica; International Journal of Primatology, 66*(1-4), 137-159.

Lim, Y. P., Lin, Y. C., & Pandy, M. G. (2017). Effects of step length and step frequency on lower-limb muscle function in human gait. *Journal of Biomechanics, 57*, 1-7. doi:S0021-9290(17)30146-X [pii]

Lin, Y. C., Dorn, T. W., Schache, A. G., & Pandy, M. G. (2012). Comparison of different methods for estimating muscle forces in human movement. *Proceedings of the Institution of Mechanical Engineers.Part H, Journal of Engineering in Medicine, 226*(2), 103-112.

Liu, M. Q., Anderson, F. C., Pandy, M. G., & Delp, S. L. (2006). Muscles that support the body also modulate forward progression during walking. *Journal of Biomechanics, 39*(14), 2623-2630. doi:S0021-9290(05)00397-0 [pii]

Liu, M. Q., Anderson, F. C., Schwartz, M. H., & Delp, S. L. (2008a). Muscle contributions to support and progression over a range of walking speeds. *Journal of Biomechanics, 41*(15), 3243-3252. doi:10.1016/j.jbiomech.2008.07.031 [doi]

Liu, M. Q., Anderson, F. C., Schwartz, M. H., & Delp, S. L. (2008b). Muscle contributions to support and progression over a range of walking speeds. *Journal of Biomechanics, 41*(15), 3243-3252. doi:10.1016/j.jbiomech.2008.07.031 [doi]

Lovejoy, C. O. (1988). Evolution of human walking. *Scientific American, 259*(5), 118-125.

Lovejoy, C. O. (2005). The natural history of human gait and posture. part 1. spine and pelvis. *Gait & Posture, 21*(1), 95-112. doi:S0966636204000141 [pii]

Lovejoy, C. O. (2007). The natural history of human gait and posture. part 3. the knee. *Gait & Posture, 25*(3), 325-341. doi:S0966-6362(06)00091-9 [pii]

Lovejoy, C. O., & McCollum, M. A. (2010). Spinopelvic pathways to bipedality: Why no hominids ever relied on a bent-hip-bent-knee gait. *Philosophical Transactions of the Royal Society of London.Series B, Biological Sciences, 365*(1556), 3289-3299. doi:10.1098/rstb.2010.0112 [doi]

Lovejoy, C. O. (2009). Reexamining human origins in light of *ardipithecus ramidus*. *Science, 326*(5949), 74-74e8. doi:10.1126/science.1175834

Lu, T. W., & O'Connor, J. J. (1999). Bone position estimation from skin marker co-ordinates using global optimisation with joint constraints. *Journal of Biomechanics, 32*(2), 129-134.

McCollum, M. A., Rosenman, B. A., Suwa, G., Meindl, R. S., & Lovejoy, C. O. (2010). The vertebral formula of the last common ancestor of african apes and humans. *Journal of Experimental Zoology.Part B, Molecular and Developmental Evolution, 314*(2), 123-134. doi:10.1002/jez.b.21316 [doi]

McCrory, J. L., Chambers, A. J., Daftary, A., & Redfern, M. S. (2014). The pregnant "waddle": An evaluation of torso kinematics in pregnancy. *Journal of Biomechanics, 47*(12), 2964-2968. doi:https://doi.org/10.1016/j.jbiomech.2014.07.009

McGeer, T. (1990). Passive dynamic walking. *The International Journal of Robotics Research, 9*(2), 62-82.

McHenry, H. M. (1975). The ischium and hip extensor mechanism in human evolution. *American Journal of Physical Anthropology, 43*(1), 39-46. doi:10.1002/ajpa.1330430107 [doi]

Miller, R. H. (2014). A comparison of muscle energy models for simulating human walking in three dimensions. *Journal of Biomechanics*, *47*(6), 1373-1381. doi:10.1016/j.jbiomech.2014.01.049 [doi]

Mochon, S., & McMahon, T. A. (1980). Ballistic walking. *Journal of Biomechanics, 13*(1), 49-57.

Molen, N. H., Rozendal, R. H., & Boon, W. (1972). Fundamental characteristics of human gait in relation to sex and location. *Proceedings of the Koninklijke Nederlandse Akademie Van Wetenschappen.Series C.Biological and Medical Sciences*, *45*(3), 215-223.

Montgomery, J., Balasubramanian, R., Mardula, K., & Allan, C. (2013). New tendon-transfer surgery for ulnar-median nerve palsy using embedded adaptive engineering mechanisms. *Computer Methods in Biomechanics and Biomedical Engineering, 11*, 1-2.

Murray, M. P. (1967). Gait as a total pattern of movement. *American Journal of Physical Medicine, 46*(1), 290-333.

Murray, M. P., Mollinger, L. A., Gardner, G. M., & Sepic, S. B. (1984). Kinematic and EMG patterns during slow, free, and fast walking. *Journal of Orthopaedic Research : Official Publication of the Orthopaedic Research Society, 2*(3), 272-280. doi:10.1002/jor.1100020309 [doi]

Nagano, A., Umberger, B. R., Marzke, M. W., & Gerritsen, K. G. (2005). Neuromusculoskeletal computer modeling and simulation of upright, straight-legged, bipedal locomotion of australopithecus afarensis (A.L. 288-1). *American Journal of Physical Anthropology, 126*(1), 2-13. doi:10.1002/ajpa.10408 [doi]

Neptune, R. R., Kautz, S. A., & Zajac, F. E. (2001). Contributions of the individual ankle plantar flexors to support, forward progression and swing initiation during walking. *Journal of Biomechanics, 34*(11), 1387-1398. doi:http://dx.doi.org/10.1016/S0021-9290(01)00105-1

Neptune, R. R., Sasaki, K., & Kautz, S. A. (2008). The effect of walking speed on muscle function and mechanical energetics. *Gait & Posture, 28*(1), 135-143. doi:10.1016/j.gaitpost.2007.11.004

Nilsson, J., & Thorstensson, A. (1987). Adaptability in frequency and amplitude of leg movements during human locomotion at different speeds. *Acta Physiologica Scandinavica, 129*(1), 107-114. doi:10.1111/j.1748-1716.1987.tb08045.x

Ogihara, N., Makishima, H., & Nakatsukasa, M. (2010). Three-dimensional musculoskeletal kinematics during bipedal locomotion in the japanese macaque, reconstructed based on an anatomical model-matching method. *Journal of Human Evolution, 58*(3), 252-261. doi:10.1016/j.jhevol.2009.11.009 [doi]

O'Neill, M. C., Demes, B., Larson, S. G., & Umberger, B. R. (2016). Pelvis shape and hominin walking: Insights from the three-dimensional mechanics of the lesser gluteals and hamstrings in human and chimpanzee bipedalism
. *Conference: American Association of Physical Anthropologists,* , 1.

O'Neill, M. C., Demes, B., Thompson, N. E., & Umberger, B. R. (2018). Three-dimensional kinematics and the origin of the hominin walking stride. *Journal of the Royal Society, Interface, 15*(145), 10.1098/rsif.2018.0205. doi:20180205 [pii]

O'Neill, M. C., Lee, L. F., Demes, B., Thompson, N. E., Larson, S. G., Stern Jr., J. T., & Umberger, B. R. (2015). Three-dimensional kinematics of the pelvis and hind limbs in chimpanzee (pan troglodytes) and human bipedal walking. *Journal of Human Evolution, 86*, 32-42. doi:10.1016/j.jhevol.2015.05.012 [doi]

O'Neill, M. C., Lee, L. F., Larson, S. G., Demes, B., Stern Jr., J. T., & Umberger, B. R. (2013). A three-dimensional musculoskeletal model of the chimpanzee (pan troglodytes) pelvis and hind limb. *The Journal of Experimental Biology, 216*(Pt 19), 3709-3723. doi:10.1242/jeb.079665 [doi]

O'Neill, M. C., Ogihara, N., Nakatsukasa, M., Demes, B., Thompson, N. E., & Umberger, B. R. (2018). Three-dimensional kinematics and the origin of the human walking stride. *Journal of the Royal Society, Interface, Submitted*

O'Neill, M. C., Umberger, B. R., Holowka, N. B., Larson, S. G., & Reiser, P. J. (2017). Chimpanzee super strength and human skeletal muscle evolution. *Proceedings of the National Academy of Sciences of the United States of America, 114*(28), 7343-7348. doi:10.1073/pnas.1619071114 [doi]

Ounpuu, S., & Winter, D. A. (1989). Bilateral electromyographical analysis of the lower limbs during walking in normal adults. *Electroencephalography and Clinical Neurophysiology, 72*(5), 429-438.

Plotnik, M., Azrad, T., Bondi, M., Bahat, Y., Gimmon, Y., Zeilig, G., . . . Siev-Ner, I. (2015). Self-selected gait speed--over ground versus self-paced treadmill walking, a solution for a paradox. *Journal of Neuroengineering and Rehabilitation, 12,* 20-015-0002-z. doi:10.1186/s12984-015-0002-z [doi]

Pontzer, H., Raichlen, D. A., & Rodman, P. S. (2014). Bipedal and quadrupedal locomotion in chimpanzees. *Journal of Human Evolution, 66,* 64-82. doi:10.1016/j.jhevol.2013.10.002 [doi]

Pontzer, H., Raichlen, D. A., & Sockol, M. D. (2009). The metabolic cost of walking in humans, chimpanzees, and early hominins. *Journal of Human Evolution, 56*(1), 43-54. doi:10.1016/j.jhevol.2008.09.001 [doi]

Ralston, H. J. (1958). Energy-speed relation and optimal speed during level walking. *Internationale Zeitschrift Fur Angewandte Physiologie, Einschliesslich Arbeitsphysiologie, 17*(4), 277-283.

Roberts, T. J., Chen, M. S., & Taylor, C. R. (1998). Energetics of bipedal running. II. limb design and running mechanics. *The Journal of Experimental Biology, 201*(Pt 19), 2753-2762.

Rodman, P. S., & McHenry, H. M. (1980). Bioenergetics and the origin of hominid bipedalism. *American Journal of Physical Anthropology, 52*(1), 103-106. doi:10.1002/ajpa.1330520113 [doi]

Rose, J., & Gamble, J. G. (2005). *Human walking* (Third Edition ed.) LWW.

Rose, M. D. (1991). The process of bipedalization in hominids. *Origine(s) De La Bipedie Chez Les Hominides, ,* 37-48.

Rose, J., Gamble, J. G., Medeiros, J., Burgos, A., & Haskell, W. L. (1989a). Energy cost of walking in normal children and in those with cerebral palsy: Comparison of heart rate and oxygen uptake. *Journal of Pediatric Orthopedics, 9*(3), 276-279.

Rose, J., Gamble, J. G., Medeiros, J., Burgos, A., & Haskell, W. L. (1989b). Energy cost of walking in normal children and in those with cerebral palsy: Comparison of heart rate and oxygen uptake. *Journal of Pediatric Orthopedics, 9*(3), 276-279.

Saha, D., Gard, S., & Fatone, S. (2008). The effect of trunk flexion on able-bodied gait. *Gait & Posture, 27*(4), 653-660. doi:S0966-6362(07)00214-7 [pii]

Sarringhaus, L. A., MacLatchy, L. M., & Mitani, J. C. (2014). Locomotor and postural development of wild chimpanzees. *Journal of Human Evolution, 66*, 29-38. doi:10.1016/j.jhevol.2013.09.006 [doi]

Saunders, J., Inman, V. T., & Eberhart, H. D. (1953). The major determinants in normal and pathological gait. *J Bone Joint Surg Am, 35*, 543-558.

Schwartz, M. H., Rozumalski, A., & Trost, J. P. (2008). The effect of walking speed on the gait of typically developing children. *Journal of Biomechanics, 41*(8), 1639-1650. doi:10.1016/j.jbiomech.2008.03.015 [doi]

Segal, N. A., Boyer, E. R., Teran-Yengle, P., Glass, N. A., Hillstrom, H. J., & Yack, H. J. (2013). Pregnancy leads to lasting changes in foot structure. *American Journal of Physical Medicine & Rehabilitation, 92*(3), 232-240. doi:10.1097/PHM.0b013e31827443a9 [doi]

Selgrade, B. P., Thajchayapong, M., Lee, G. E., Toney, M. E., & Chang, Y. H. (2017). Changes in mechanical work during neural adaptation to asymmetric locomotion. *The Journal of Experimental Biology, 220*(Pt 16), 2993-3000. doi:10.1242/jeb.149450 [doi]

Sellers, W. I., Cain, G. M., Wang, W., & Crompton, R. H. (2005). Stride lengths, speed and energy costs in walking of australopithecus afarensis: Using evolutionary robotics to predict locomotion of early human ancestors. *Journal of the Royal Society, Interface, 2*(5), 431-441. doi:E0LQC88DXV72UAGQ [pii]

Shefelbine, S. J., Tardieu, C., & Carter, D. R. (2002). Development of the femoral bicondylar angle in hominid bipedalism. *Bone, 30*(5), 765-770. doi:S8756328202007007 [pii]

Sherman, M. A., Seth, A., & Delp, S. L. (2011). Simbody: Multibody dynamics for biomedical research. *Procedia IUTAM, 2*, 241-261.

Sockol, M. D., Raichlen, D. A., & Pontzer, H. (2007). Chimpanzee locomotor energetics and the origin of human bipedalism. *Proceedings of the National Academy of Sciences of the United States of America, 104*(30), 12265-12269. doi:0703267104 [pii]

Steele, K. M., Demers, M. S., Schwartz, M. H., & Delp, S. L. (2012). Compressive tibiofemoral force during crouch gait. *Gait & Posture, 35*(4), 556-560. doi:10.1016/j.gaitpost.2011.11.023 [doi]

Steele, K. M., Seth, A., Hicks, J. L., Schwartz, M. H., & Delp, S. L. (2013). Muscle contributions to vertical and fore-aft accelerations are altered in subjects with crouch gait. *Gait & Posture, 38*(1), 86-91. doi:10.1016/j.gaitpost.2012.10.019 [doi]

Steele, K. M., Seth, A., Hicks, J. L., Schwartz, M. S., & Delp, S. L. (2010). Muscle contributions to support and progression during single-limb stance in crouch gait. *Journal of Biomechanics, 43*(11), 2099-2105. doi:10.1016/j.jbiomech.2010.04.003 [doi]

Steele, K. M., van der Krogt, M. M., Schwartz, M. H., & Delp, S. L. (2012). How much muscle strength is required to walk in a crouch gait? *Journal of Biomechanics, 45*(15), 2564-2569. doi:10.1016/j.jbiomech.2012.07.028 [doi]

Stern Jr, J. T. (1972). Anatomical and functional specializations of the human gluteus maximus. *American Journal of Physical Anthropology, 36*(3), 315-339. doi:10.1002/ajpa.1330360303 [doi]

Stern Jr., J. T. (1999). The cost of bent-knee, bent-hip bipedal gait. A reply to crompton et al. *Journal of Human Evolution, 36*(5), 567-570. doi:S0047248499902907 [pii]

Stern Jr., J. T., & Susman, R. L. (1983). The locomotor anatomy of australopithecus afarensis. *American Journal of Physical Anthropology, 60*(3), 279-317. doi:10.1002/ajpa.1330600302 [doi]

Stern Jr., J. T., & Susman, R. L. (1981a). Electromyography of the gluteal muscles in hylobates, pongo, and pan: Implications for the evolution of hominid bipedality. *American Journal of Physical Anthropology, 55*(2), 153-166. doi:10.1002/ajpa.1330550203

Stern Jr., J. T., & Susman, R. L. (1981b). Electromyography of the gluteal muscles in hylobates, pongo, and pan: Implications for the evolution of hominid bipedality. *American Journal of Physical Anthropology, 55*(2), 153-166. doi:10.1002/ajpa.1330550203

Steudel-Numbers, K. L., & Tilkens, M. J. (2004). The effect of lower limb length on the energetic cost of locomotion: Implications for fossil hominins. *Journal of Human Evolution, 47*(1-2), 95-109. doi:10.1016/j.jhevol.2004.06.002 [doi]

Susman, R. L. (1983). Evolution of the human foot: Evidence from plio-pleistocene hominids. *Foot & Ankle, 3*(6), 365-376.

Susman, R. L., Stern Jr., J. T., & Jungers, W. L. (1984). Arboreality and bipedality in the hadar hominids. *Folia Primatologica; International Journal of Primatology, 43*(2-3), 113-156.

Tardieu, C., & Trinkaus, E. (1994). Early ontogeny of the human femoral bicondylar angle. *American Journal of Physical Anthropology, 95*(2), 183-195. doi:10.1002/ajpa.1330950206 [doi]

Taylor, C. R., Heglund, N. C., & Maloiy, G. M. (1982). Energetics and mechanics of terrestrial locomotion. I. metabolic energy consumption as a function of speed and body size in birds and mammals. *The Journal of Experimental Biology, 97*, 1-21.

Taylor, C. R., & Rowntree, V. J. (1973). Running on two or on four legs: Which consumes more energy? *Science (New York, N.Y.), 179*(4069), 186-187.

Thelen, D. G., & Anderson, F. C. (2006). Using computed muscle control to generate forward dynamic simulations of human walking from experimental data. *Journal of Biomechanics, 39*(6), 1107-1115. doi:10.1016/j.jbiomech.2005.02.010

Thompson, N. E., Demes, B., O'Neill, M. C., Holowka, N. B., & Larson, S. G. (2015). Surprising trunk rotational capabilities in chimpanzees and implications for bipedal walking proficiency in early hominins. *Nature Communications, 6*, 8416. doi:10.1038/ncomms9416 [doi]

Thorpe, S. K., Crompton, R. H., Gunther, M. M., Ker, R. F., & McNeill Alexander, R. (1999). Dimensions and moment arms of the hind- and forelimb muscles of common chimpanzees (pan troglodytes). *American Journal of Physical Anthropology, 110*(2), 179-199. doi:10.1002/(SICI)1096-8644(199910)110:23.0.CO;2-Z [pii]

Thorpe, S. K., Crompton, R. H., & Wang, W. J. (2004). Stresses exerted in the hindlimb muscles of common chimpanzees (pan troglodytes) during bipedal locomotion. *Folia Primatologica; International Journal of Primatology, 75*(4), 253-265. doi:10.1159/000078937 [doi]

Umberger, B. R., Gerritsen, K. G., & Martin, P. E. (2003). A model of human muscle energy expenditure. *Computer Methods in Biomechanics and Biomedical Engineering, 6*(2), 99-111. doi:10.1080/1025584031000091678

Wang, W. J., Crompton, R. H., Li, Y., & Gunther, M. M. (2003). Energy transformation during erect and 'bent-hip, bent-knee' walking by humans with implications for the evolution of bipedalism. *Journal of Human Evolution, 44*(5), 563-579. doi:S0047248403000459 [pii]

Ward, C. V. (2002). Interpreting the posture and locomotion of australopithecus afarensis: Where do we stand? *American Journal of Physical Anthropology, Suppl 35*, 185-215.

Whitcome, K. K., Miller, E. E., & Burns, J. L. (2017). Pelvic rotation effect on human stride length: Releasing the constraint of obstetric selection. *Anatomical Record (Hoboken, N.J.: 2007), 300*(4), 752-763. doi:10.1002/ar.23551 [doi]

White, T. D., Asfaw, B., Beyene, Y., Haile-Selassie, Y., Lovejoy, C. O., Suwa, G., & WoldeGabriel, G. (2009). *Ardipithecus ramidus* and the paleobiology of early hominids. *Science, 326*(5949), 64-86. doi:10.1126/science.1175802

Winter, D. A. (1983). Energy generation and absorption at the ankle and knee during fast, natural, and slow cadences. *Clinical Orthopaedics and Related Research, (175)*(175), 147-154.

Winter, D. A. (1990). *Biomechanics and motor control of human movement* (Second Edition ed.). New York: John Wiley & Sons.

Witmer, L. (1995). The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils. In J. Thomson (Ed.), *Functional morphology in vertebrate paleontology* (pp. 19-33). Cambridge: Cambridge University Press.

Wolff, J. (1986). *The law of bone remodelling*. Berlin, Germany: Springer-Verlag.

Wren, T. A., Rethlefsen, S., & Kay, R. M. (2005). Prevalence of specific gait abnormalities in children with cerebral palsy: Influence of cerebral palsy subtype, age, and previous surgery. *Journal of Pediatric Orthopedics, 25*(1), 79-83. doi:00004694-200501000-00018 [pii]

Yaguramaki, N., Nichizawa, S., Adachi, K., & Endo, B. (1995). The relationship between posture and external force in walking. *Journal of Anthropological Sciences, 103*(2), 117-140.

Yamaguchi, G. T., & Zajac, F. E. (1989). A planar model of the knee joint to characterize the knee extensor mechanism. *Journal of Biomechanics, 22*(1), 1-10.

Zajac, F. E. (1989). Muscle and tendon: Properties, models, scaling, and application to biomechanics and motor control. *Critical Reviews in Biomedical Engineering, 17*(4), 359-411.

Zajac, F. E., & Gordon, M. E. (1989). Determining muscle's force and action in multi-articular movement. *Exercise and Sport Sciences Reviews, 17*, 187-230.

Zajac, F. E., Neptune, R. R., & Kautz, S. A. (2002). Biomechanics and muscle coordination of human walking. part I: Introduction to concepts, power transfer, dynamics and simulations. *Gait & Posture, 16*(3), 215-232.

Zarrugh, M. Y., & Radcliffe, C. W. (1978). Predicting metabolic cost of level walking. *European Journal of Applied Physiology and Occupational Physiology, 38*(3), 215-223.

Zarrugh, M. Y., Todd, F. N., & Ralston, H. J. (1974). Optimization of energy expenditure during level walking. *European Journal of Applied Physiology and Occupational Physiology, 33*(4), 293-306.