MECHANICS OF BIPEDALISM:
AN EXPLORATION OF SKELETAL MORPHOLOGY
AND FORCE PLATE ANAYLSIS

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Abstract

There are several theories on how humans learned to walk, and while these all address the adaptations needed for walking, none adequately describes how our early ancestors developed the mechanism to walk. Our earliest recognizable relatives, the australopithecines, have several variations on a theme: walking upright. There are varied changes as australopithecines approach the genus *Homo*. These changes occurred in the spine, legs, pelvis, and feet, and changes are also in the cranium, arms and hands, but these are features that may have occurred simultaneously with bipedalism. Several analyses of *Australopithecus afarensis*, specifically specimen A.L. 288-1 ("Lucy"), have shown that the skeletal changes are intermediate between apes and humans. Force plate analyses are used to determine if the gait pattern of humans resembles that of apes, and if it is a likely development pattern. The results of both these analyses will give insight into how modern humans developed bipedalism.

Introduction

Bipedalism is classified as movement of the post-cranial body in a vertical position, with the lower limbs shifting as an inverted pendulum, progressing forward. Simply, it is upright walking. Several theories have addressed why bipedalism evolved in hominids, with some unlikely ideas taking hold throughout the history of the issue. Other theories are more likely, but all lack the same characteristic: answering how bipedalism developed. How did bipedalism evolve? How did quadrupedal creatures develop the ability to walk upright? What kinds of adaptations needed to occur in muscle and bone to walk, and how did it happen? Theories that ask why are largely speculative, and the answers to why will be discovered after the mechanics are discovered. Using absolute and relative methods to study bipedalism combines the two systems of studying early hominid (Wood 1978). Absolute studies are concerned with biomechanics and assessments of bones, while relative methods examine fossils. Studying bipedalism from a mechanical point-of-view can answer the how bipedalism developed in different ways. Biomechanics is used to study how muscles and bone work together, and can show the evolutionary relationships from primate to human. In addition to biomechanics, force-plate studies can show the different pressures applied by a body in motion.

Studying bipedal mechanics can open doors as to how *Homo sapiens*, modern humans, learned this very basic, almost inherent skill. From there, research can look at the different physiological problems that affect the human body. Bipedalism studies can be used to develop theories about how hominids evolved into humans from the first ancestors we recognize, as well as theorizing how evolution affects other species.

Four questions, or research topics, are addressed in this paper:

1. How is the body adapted to standing upright versus ape-like squatting?

2. What resemblance do australopithecine skeletons show compared to humans and apes?

3. What are the differences in gait between humans and apes?

4. What do these differences and similarities mean?

In order to fully address these questions, several areas of bipedalism studies should be reviewed for the reader to have an understanding of this paper. To facilitate this, the background portion of this paper concentrates on theories of bipedalism, an explanation of walking, and basic bone morphology and musculature of humans, *Pan troglodytes* (chimpanzee), and *Australopithecus afarensis*.

However, comparisons of skeletons and muscles can only go so far. Jack Prost (1985) writes, "If chimpanzee bipedalism is a good model for prehuman bipedalism, it must be shown that human motion patterns have evolved from the chimpanzee motor patterns." Answering the questions proposed involves looking at musculature, skeletons and force plate data attempting just such a model. Examining force plate data with the famed Laetoli footprints can give evidence to such models of chimpanzee, human and australopithecine motor patterns.

Methods

Investigating the several bipedalism strategies that have been proposed for the development of upright walking will illustrate the need for research in mechanical studies. To sufficiently understand the morphology of *Australopithecus afarensis*, research on several different reports and analyses of specimen A.L. 288-1, "Lucy", was conducted. The morphology was compared with that of anatomical discussions of humans and apes. Analysis of force-plate data using Microsoft Excel, as well as

researching how force-plate data applies to bipedalism studies will show how gait is important in determining how bipedalism developed.

- *Bipedalism Strategies*

Bipedalism strategies have been proposed since the time of Darwin. To comprehensively research and discuss all theories would entail a thesis unto itself. Therefore, only major ideas are discussed.

- *Anatomy*

Research using data from reports of specimen A.L. 288-1 was compared to data compiled from several sources on the human skeleton. The morphology describes the specific bones needed for bipedalism. The bones that are discussed are from the lower post-cranial region: the pelvis, sacrum, femur, tibia, fibula and calcaneous. The musculature examined looks at the muscles responsible for movement at the hip, knee and foot.

- *Force Plate Data*

The force plate data came from experiments performed in April and May 2006 at the University of Wisconsin- La Crosse GAIT Lab in the Health Sciences Center. The Kistler® force plates are 1.5m x1m in size, and are arranged in an "L" shape. Only one plate was actively receiving data at the time of the experiment. Reflective markers were attached to the subject in 24 points, and most relevant to the data collected are the calcaneal tuberosity, navicular tuberosity, head of the first metatarsal and tuberosity of the fifth metatarsal (Figures 1, 2). Subjects were instructed to walk at a normal pace across the force plate and then to mimic an ape-like movement pattern. This is the classic "bent-knee, bent-hip" stance seen when chimpanzees are walking upright. The data received from the experiments was compiled into Microsoft Excel. Graphs were created

to show force and foot angle normalized to body weight. The graphs were further compared to accepted graphs of similar biomechanics studies. Evaluating the graphs with other biomechanics studies determines whether humans are able to emulate other methods of bipedal movement. Comparing these graphs to established graphs of gait pressure (Kimura 1985) for different hominoids will be used to determine whether it is possible to walk in either manner and therefore it can be extrapolated whether australopithecines walked in a similar method.

Background

Theories of Bipedalism

Anthropologists have been devising ideas about the development of upright walking for years, building upon each other's work or conceiving new ideas. Not only does debate rage on whether hominids could walk upright, but on whether they were exclusively upright, the degree of uprightness, and even if under certain conditions moved quadrupedally (Lovejoy 1978). Many of these bipedalism theories are now outdated, and if not disproved, are highly unlikely based on new research. However, looking at the basic ideas of the different hypotheses illustrates how little consideration was given to hominids having the ability to walk. These earlier theories are also hard to test scientifically, leading to a revolution of sorts in bipedalism theories. Although more recent theories do have a mechanical-base, it is much easier to speculate on why bipedalism developed without giving thought to the idea being probable. It is important to discover how bipedalism developed, as from there, evaluating the theories will become much easier (Sellers et al. 2002). Theories concerning how hominids developed walking behavior can be divided into two categories: cultural behaviors or physiological

advantages. In addition, bipedal theories can be grouped into both categories, depending on the point of view taken.

- *Cultural Behaviors*

These ideas all involve hominids becoming bipedal in order to carry an item, whether it is a tool, an infant or food. Most research based on the carrying theories state that carrying freed the hands, and allowed the body to balance on two legs, rather than four. A different cultural behavior that is not necessarily related to carrying is the development of bipedalism from climbing. While this theory can also be categorized as a physiological advantage, categorizing climbing as a behavior is more accurate, as it involves planning and an ability to recognize cause-and-effect.

o Carrying Tools or Weapons

In 1871, Charles Darwin (Langdon 2005, McHenry 1980) proposed that hominids who carried tools would have an advantage over those who did not. Among other anthropologists, Sherwood Washburn (Langdon 2005) agreed with this theory. Raymond Dart (ibid.) also proposed a similar carrying theory, stating that hominids carried weapons, which allowed them to walk upright. This is commonly referred to as the "Killer Ape" theory. However, these theories are largely defunct, as tools have been found well after bipedalism developed (Klein 1999). Evidence places bipedalism developing, at the very latest, by three million years ago. The first recognizable, transported stone tools appear about two million years ago, placing tool carrying much later in hominid history.

o Caring for Infants

C. O. Lovejoy (Lovejoy et al. 1973, Lovejoy 2005) is generally the impetus behind this theory. It follows the same basis as tool carrying, but goes farther and suggests that in addition to carrying an infant, that a male is supplying the mother with food, who cannot leave the infant and is unable to find her own food. This theory follows the classic "Man the Hunter" scenario, and suggests that males of the species were mostly responsible for bipedalism. Feminist issues aside, the theory that carrying an infant required a bipedal stance is made invalid by studies of apes: chimpanzees are able to carry an infant while quadrupedal (Kingdon 2005). However, some Japanese monkeys have been observed walking upright while carrying food and other objects, a behavior that has been suggested as a proto-typical example for development of bipedalism (Iwamoto 1985).

○ Food Acquisition

This hypothesis suggests that hominids became bipedal in order to reach a greater supply of food hanging from trees (Stanford 2003); seeds that were out of reach when quadrupedal (Kingdon 2003); that foraging is more efficient when bipedal (Iwamoto 1985, Langdon 2005); or that food was carried back to a home base (Hewes 1965). These ideas have been proposed by several authorities who study chimpanzee or hunter-gatherer groups, and while there is no way to test these hypotheses, there is no way to prove them either. However, some anthropologists have suggested the converse: if bipedalism helps in food acquisition, why haven't more apes become bipedal? This is a circular argument, and more research or new discoveries appear to be the only way to shed light on these hypotheses. The seed-eating hypothesis however, has been invalidated based on

microwear samples of teeth, which show that marks on teeth was caused by foods or wear other than seeds (Langdon 2005).

o Climbing

This has become one of the most popular and widely debated theories. The climbing hypothesis stems mostly from the idea that the body is already vertical when climbing a tree, and as such, is already adapted to a vertical posture and to carrying weight in an upright manner (Preuschoft and Witte 1991, Prost 1980, Stern and Susman 1983). Climbing also allows for the hominid to assist its body in being upright by grasping branches above its head. This theory is based on studies from biomechanics, and as such, has a more scientific background. However, bipedalism stemming from a climbing environment necessitates a reason for the hominid to leave the trees. Chimpanzee studies have shown that the animals will go to ground to find food, but they generally stay in the trees. Evidence of skeletal morphology supports a non-habitual arboreal pattern in the size comparisons of *A. afarensis* limbs, especially evidenced by physiological changes in the upper limbs. (Jungers 1982, Latimer 1991, McHenry 1982, Rose 1991).

• *Physiological Advantages*

These theories are based on bipedalism giving the hominid a benefit in a functional manner, either benefiting or changing the body's function. Most of these theories were developed in the latter half of the twentieth century. The theories reveal a wide range of methods for scientific testing, although some have been disproved with the improvements of dating methods and testing. Theories that fall into this category involve reproductive success, thermoregulation and energy use.

o Reproductive Success

This theory is part of the infant carrying idea, but involves the development and reorganization of the pelvis in hominids to account for a larger brained fetus at birth (Lovejoy et al. 1973, Lovejoy 2005). Also part of this theory is that the ability of a female to bear children is limited by how many infants she can carry at a time. The fact that the pelvis has been restructured from ape to human is evident, and features of the australopithecine pelvis corroborate this evidence. In addition, body mass is almost entirely devoted to locomotion, and changes to the pelvis are made to accommodate locomotion, rather than to childbirth (Zihlman 1978).

o Energy Use

Energetics theories are mostly based on the ability of scientists to measure how efficient bipedalism is against quadrupedalism. Studies have shown that some monkeys that are able to move in both manners use the same amount of energy, and only those that are habitually bipedal (humans) or mostly quadrupedal (chimpanzees) have a greater energy use when moving in the opposite habitual pattern (Carrier 1984, Ishida 1991, Leonard and Robertson 1997, Rodman and McHenry 1980, Wang et al. 2003). These studies also show that the muscles used in bipedal walking in apes, monkeys and humans differ in energy use, suggesting that each organism had adapted to efficiently using the muscles needed in walking (Ishida et al. 1985). Other studies have suggested that more important than anatomical arrangements are the muscular costs of body mass (McGowan 1999).

o Thermoregulation

The theory of thermoregulation states that being upright exposes less of the body to sunlight than being on all fours (Langdon 2005). This theory requires that hominids need to have moved out to a reasonably treeless habitat, such as a savanna. However, most finds of early hominids have occurred in the context of a forest environment.

The bipedalism theories outlined illustrate the varied ideas and wide interests of those who developed them. However, almost all of these theories lack a method to test them scientifically, or have been disproved by research. Theories that are based on speculation are easier to believe, but cannot be backed up by science. Studying bipedalism using a skeletal evaluation and mechanics basis allows for a scientific background to look at aspects of the development of walking.

Laetoli Footprints

The Laetoli footprints are located in Laetoli, Tanzania (Figure 3). They were discovered in 1978 and excavated by Mary Leakey. There are three trails that reveal the impressions of three hominids walking near each other. Trail G-1 contains 38 footprints and Trails G-2 and G-3 contain 31 (Day and Wickens 1980, Tuttle et al. 1990). Trail G-3 partially overlays trail G-2. The footprints are in volcanic ash, became wet and consolidated into a tuff; it is dated from 3.6 to 3.75 million years B.P. (Day and Wickens 1980). This date also indicates that a human bipedal gait was definitely around by 3.6 million years ago (McHenry 1986) and at least one million years before the appearance of tools (Tuttle 1990). The age of the footprints coincide with two species of hominid living at that time: *Australopithecus anamensis* and *Australopithecus afarensis* (Klein 1999). The age however, is at the very tail end of existence for *A. anamensis*, and is subsequently the footprints are believed to be from *A. afarensis*. However, skull

fragments belonging to early *Homo* species have been found nearby, leading some to speculate that the footprints belong to *Homo* (Klein 1999). Studies of the Laetoli footprints reveal through photogrammetric processes that the feet are similar in shape to those of unshod humans, and that the contours of the walking gait are also similar (Day 1991). The footprints also have a gap between the first (hallux) and second toes, similar to apes, but much more akin to the footprints that people who have not worn shoes regularly show (Tuttle 1990). The pattern of weight transmission and force distribution make it possible to see the same pattern shown by modern man, as well as determining the speed of gait (Charteris et al. 1982). The Laetoli footprints show that the australopithecines were walking slowly.

Research Subjects and Skeletal Characteristics

By comparing the different skeletal aspects of *Homo sapiens, Pan troglodytes* and *Australopithecus afarensis*, I will be able to show how the hominids are related. Focusing on the pelvis, lower limbs and feet, as well as the muscular connections will demonstrate the similarities and relatedness of these three species.

- *Homo sapiens*

Humans have a muscular and skeletal system that is specialized for upright movement. Many aspects of the skeleton show similarities to other hominine species, but differences in the skeleton developed on account of redesigning the body to walk. The backbone and vertebrae are aligned vertically, and also increase in size to accommodate for greater weight demands from the body. The pelvis and sacrum have large areas for muscle attachment and are made of dense bone that can handle stresses from walking and keeping the body upright. The leg bones are very robust and also have large surface

attachment areas for muscles that are involved in movement. The entire leg is long which gives humans the ability to stride, move slowly or quickly, and conserve energy while doing so (Robinson 1978). The foot is one of the most uniquely adapted parts of the human body. It is able to function as a platform and as a spring, and compensate for the pressures of the body while walking, and even when standing. There are two arches, a medial arch and a longitudinal arch, which is a unique feature in humans. The arch is a distinctly human development that serves only for walking. All of the bones in the lower body have large surface area for muscle, tendon and ligament attachment. The muscles are arranged differently than in other hominines-the development of which can be seen in both living and extinct species (through muscle attachment sites).

• *Pan troglodytes*

The common chimpanzee is one of the most common research animals used in locomotor studies. One reason for its wide use is that the genetic makeup of the chimpanzee is between 95% and 99% that of humans (Stanford 2003). Chimpanzees (and other apes) have several modes of locomotion (Rose 1991), all of which hominids may have exhibited in their evolution and so it is inferred that chimpanzees are good models for study. Chimpanzee bone and muscle structure is similar to humans (Figure 4), but is adapted to quadrupedal and tree-life existence. Chimpanzees spend most of their day in trees, going to ground to feed (Stanford 2003). They most often stand or move bipedally when feeding (Hunt 1994) (Figure 5). When chimpanzees stand bipedally, they exhibit vast differences (from humans) that are due to their different musculature. In addition, they have different gait patterns that can be tested energetically and mechanically. Nevertheless, the differences are compelling when compared with australopithecine and

human musculature. Recent studies have also suggested using apes other than *Pan troglodytes*, as there are other locomotor patterns that are similar to upright walking, especially the mechanics of arboreal climbing (Schmitt 2003). Chimpanzees show exhibit different electromyographic patterns in muscle use than humans (Ishida et al. 1985). However, since the majority of studies do use the chimpanzee, this makes it a reasonable choice for study in this paper.

- *Australopithecus afarensis*

Australopithecus afarensis is the most logical choice for looking at an ancient ancestor for three reasons. First, most research is based on *A. afarensis*. Second, it is the most complete skeleton of an ancient human ancestor to date. Third, *A. afarensis* is the earliest known hominid ancestor that has demonstrated adaptations for bipedal movement. Prior to the discovery of Lucy in 1973, the fossil record was a conglomerate of several hominids, that were studied together to determine morphology (Day 1978). I will be analyzing research based on specimen A.L. 288-1, "Lucy", which was found in 1973 in the Hadar Formation, Ethiopia, by a team headed by Donald Johanson (Johanson and Taieb 1978). The skeleton is 40% complete (Figure 6). Other specimens of *A. afarensis* have been found, but none are as complete as A.L. 288-1 (Alemseged et al. 2006, Reno et al. 2005). The specimen was found in a sandy channel fill with grain sizes suggesting a slow moving stream (Johanson et al 1982b). The bones do not exhibit prefossilization weathering, suggesting that the skeleton floated away from the death site (Johanson et al 1982b). The skeleton is complete enough to estimate body weight at about 60 lbs (Jungers 1982) and that there was sexual dimorphism shown by comparisons with several of the other specimens (McHenry 1980). Evidence of skeletal anatomy from

Lucy shows that *Australopithecus afarensis* had made a complete shift to bipedalism, although it is not the fully human bipedalism experienced today (Wolpoff 1983). Several studies of Lucy's limbs have concluded that she probably walked in an upright manner, although the manner of her bipedalism was probably a fusion of both ape-like and human-like motion (Crompton et al. 1998, Hunt 1994, McHenry 1986, Stern and Susman 1991). The femur has a neck shaft angle that is comparable to that of modern man. The tibia is straight-shafted, and fibula demonstrates features that are necessary for human bipedalism. A study by Berge (1994) compared muscle attachment sites of humans and apes with *A. afarensis* and found that the sites, if discernible, showed a mosaic pattern.

Bone Morphology

Several bones are useful for comparing *Homo sapiens*, *Pan troglodytes* and *Australopithecus afarensis*. The bones that are compared were: the pelvis, consisting of ischium, ilium, pubis; the sacrum; the femur; the tibia; the fibula; and the calcaneus.

• *Pelvis*

The human pelvis is short and basin shaped, while the ape pelvis is long and narrow (Aiello and Dean 1990) (Figure 7). When in normal posture with the vertebrae, the pelvis in humans is at a 90º angle, and in chimpanzee is at 45º. The sacrum is at an angle to the vertebrae in humans and follows a straight line in chimpanzees. The three nominal bones of the pelvis differ in shape, reflecting the ability of humans to navigate bipedally and of a chimpanzee's quadrupedalism. The most notable feature that differs is the size of the ilium. In humans, the ilium is smoothly rounded, and very wide, whereas in chimpanzees it is elongate, angular and narrow. The ischium in humans is wide, and has a greater ischial tuberosity, which provides an area of attachment for the hamstring

muscles (ibid). The chimpanzee ischium is not as wide, but is long in comparison with a human's ischium. The ape ischium is adapted better for powering movements than speed, which is reflected in basic movement. The human pubis is also wide, and has a greater region of muscle attachment for trunk support. The ape pubis body is deeper than that seen in humans. Humans also exhibit a wider sciatic notch. In *A. afarensis*, the ilium projects laterally from the body, similarly to the chimpanzee (ibid). The ischium is longer than that seen typically in humans, and the tuberosity lacks the pulled up appearance seen in human ischia. The pubis is also relatively longer. The Lucy pelvis shows the same marks as typical australopithecine pelves. It shows a deep lesser sciatic notch and well formed greater sciatic notch, and also exhibits similar angles to human notches (Johanson et al. 1982b).

•*Sacrum*

In humans, the sacrum is composed of five fused sacral vertebral bones (White 1991). It functions to support the weight of the upper body and position the trunk with the lower limbs. The human sacrum is wider than the chimpanzee, and has a more acute angle with the pelvis. These two features function for bipedalism, which increases the distance between the sacroiliac joint and positions the hip more vertically over the femurs (Aiello and Dean 1990). In apes, the sacrum has a more variable number of fused lumbar vertebrae. The sacrum is much narrower than that seen in humans, and has a less acute angle. There is less articulation at the sacroiliac joints, which reflects the greater difficulty of chimpanzees in walking. The *Australopithecus* sacrum reflects the human sacrum, in width and angle of articulation with the ilium. It sits at a lesser angle than in

humans. This suggests that australopithecines may have had difficulty in stabilizing their body when upright (ibid).

•*Femur*

The human femur is longer than the chimpanzee femur. The bicondylar angle is an important measure in differentiating between the two species. This is the angle that the shaft of the femur makes with a 90º angle when the femoral condyles are resting on a horizontal surface. Humans have a larger angle than apes, which positions the leg closer to mid-line (Figure 4). The result is that the center of gravity in the body only moves a small distance with each step (Aiello and Dean 1990). The head of the femur in humans is larger than chimpanzees, and the placement of the head on the neck is centered, while in chimpanzees it is posterior (ibid). Cortical bone around the neck is thicker in human femora, due to the muscle attachment. Human femora often exhibit a pilaster while apes do not. Condyles on human femora are larger and square in shape, while chimpanzees are asymmetrical, reflecting the amount of weight transferred in movement. Australopithecine femora are rarely found complete. The A.L. 288-1 femur is whole, and shows a smaller head size compared to humans, a larger neck length and smaller neck angle. It is thought that this resembles chimpanzees, but may in fact reveal some sexual dimorphism instead (ibid). The bicondylar angle of australopithecines is often greater than that found in humans (Lovejoy 1978). There are few other similarities between humans and australopithecine femora.

•*Tibia*

The retroversion angle is important in determining the angle at which the tibia articulates with the femur (Figure 4). It varies greatly in different human populations,

which are accounted for in populations that do a lot of squatting activities or sit in chairs, etc. It does not necessarily justify an ape-like or human-like movement pattern, although apes are generally found with a higher angle than humans (Aiello and Dean 1990). Many features of the human and ape tibia are distinct for musculature. The tibial epicondyles in apes are much narrower than in humans, and the shaft is narrower, giving the head a platform appearance. The shape of the shaft in humans is concave superiorly and convex inferiorly, while in chimpanzees the shaft is entirely concave. The ape shaft is more robust relative to length than in humans. The tibial joint surface is perpendicularly oriented to the long axis of the shaft while in apes it is more lateral (Aiello and Dean). The distal joint surface also shows more torsion in humans than in apes. Both of these differences between human and ape tibia reflect the amount of movement the tibia and talus can exhibit. The tibia of *Australopithecus afarensis* is more chimpanzee-like in morphology than human-like. The tibial epicondyles are very similar to chimpanzees. The shaft also shows the same shape as a chimpanzee, resulting in the head of the tibia having a raised appearance (Johanson et al. 1982a).

- *Fibula*

The fibula in humans and apes are comparable, only differing in robusticity and in the shape of the styloid process (Figure 4). The ape fibula is generally much more robust, and convex in shape. In humans, the bone is usually concave or straight, but morphological differences are highly variable in humans. The styloid process that is shown on human fibula is often missing on ape fibula. The head on the ape fibula appears flat compared with that of a human. The articular facet (with the talus) faces medially in humans while in apes it faces anteromedially (Aiello and Dean 1990). This reflects that

the fibula stabilizes the ankle in humans, and in apes supports more weight. The ape

malleolar fossa appears expanded and the peroneal groove is wide. In humans, the

malleolar fossa and peroneal groove is shorter and smaller. This limits the range of

flexion of the human ankle. The Lucy specimen shows a malleolar expansion and large

peroneal groove (Johanson et al. 1982a), almost identical to that of a chimpanzee.

- *Calcaneus*

The human calcaneus is unique in that the muscle and tendon attachments to it

create an arch that is longitudinal and transverse. Apes have an arch that is only

transverse. The calcaneus of humans is more robust than humans. It is also straighter in

horizontal and medial axis than in apes. The peroneal trochlea is well developed in apes,

while in humans the plantar trochlea is more developed. The calcaneocuboid facet in

humans is highly assymetrical, which allows for a close-packed postion when the foot is

in stance phase (Aiello and Dean 1990). In apes, the facet is more symmetrical, and does

not have the locking mechanism needed for human-like walking. The calcaneus of

Australopithecus afarensis is robust, and shows a fibular trochlea that is similar to a

chimpanzee (Latimer and Lovejoy 1989).

Musculature

To adequately describe the muscular connections required for bipedal movement

is an immense task, again requiring a thesis of itself. To expedite the requirement of

examining muscle attachments and connections, I will only focus on the attachments of

the pelvis and femur (hip), femur and tibia (knee) (Figure 8), and tibia and foot. Trying to

describe the muscles separately is futile, as all the muscles work together in the body to

create movement. Therefore, grouping the different muscles by activity will further advance the discussion.

- *Hip Muscles*
  - Flexors

Flexor muscles move the bones of the hip closer to the femur. The iliopsoas is the main flexor muscle of the hip, and is composed of two muscles, the psoas major and the iliacus. In apes there is a third muscle, the psoas minor, which is used to flex the trunk in the lumbar region. The psoas major inserts on the lesser trochanter, and the iliacus within the iliac fossa. The rectus femoris is one of four muscles of the quadriceps femoris, and flexes the hip in addition to extending the knee. The tensor fascia latae stretches into the iliotibial tract, which connects to the tibia on the lateral side. The gluteus maximus is the largest and most posterior of the gluteal muscles. It produces the extension and lateral rotation of the hip joint. With the iliotibial tract, the two flex the hip and extend the knee. In apes, the two muscles flex the knee and hip joint. The tensor fascia latae in apes extends under the gluteus maximus, instead of under as in humans, which gives it the different flexing mechanism. The sartorius muscle flexes the knee and rotates the leg medially, enabling the "cross-legged" position (Martini 2006). Apes also have a small muscle called the iliotrochanetricus, which is a flexor of the thigh.

  - Extensors

Extensor muscles move the bones of the hip and femur away from each other. The hamstrings, which are a conglomeration of three muscles, are the major extensors of the thigh. The biceps femoris, semimembranosus and semitendinosus extend the hip joint and flex the knee. The muscles have the same function in chimpanzees, but because the

chimpanzee is in a continual flexed postion, the muscles are much larger and have a

better lever advantage (Aiello and Dean 1990). The gluteus maximus functions in

extending the hip, and is not active during walking. In apes, the muscle has a larger area

of attachment, and is called the gluteus maximus proprius. It extends to the

ischiofemoralis; in humans, it stretches to the iliotibial tract.

    o Abductors

       Abductors move the leg away from the midline of the body (Martini 2006). The

gluteus medius and gluteus minimus are the primary abductors of the hip and thigh. The

gluteus medius covers the minumus. The position of the muscles on the lateral side of the

hip, and the function as abductors of the thigh make them unique to bipedal walking

(Aiello and Dean 1990). In apes, the scansorius muscle draws the leg up towards the

body, and is probably important in climbing.

    o Adductors

       Adductors move the leg toward the midline of the body. The adductors of the

thigh are similar in apes and humans. The adductor magnus is the largest of the

adductors, and can flex, and rotate the thigh medially and laterally to the body. The

adductor longus, adductor brevis, pectinus and gracilis, or collectively the quadriceps, all

rotate the femur at the hip and differ in their position of insertion (Martini 2006). These

muscles are all present in humans and apes, but in apes the gracilis muscle is much larger

and wider.

    o Lateral Rotators

       The six lateral rotators move the thigh at the hip joint. These are short muscles

that are all connected at the ischium or pubis and at the greater and lesser trochanters of

the femur. The piriformis, obturatur internus, superior gemellus, inferior gemellus and quadratus femoris all have insertions that are directly connected to the pelvis and femur. The obturator externus weaves around the pelvis and connects to the posterior side of the femur. When the leg is flexed, the muscle runs in a direct line to the femur (Martini 2006).

In humans and apes, the hip muscles allow the leg to move forward and backwards, and to the sides laterally. The hip joint and its muscle attachments are one of the best indicators of locomotion patterns (Lovejoy et al. 2002). The small differences in muscle insertion and origin are apparent in the gluteus maximus muscle, which in apes has a greater area of attachment (Figure 9). In *A. afarensis*, the markings for muscle attachments show a greater similarity to humans than apes, especially for the vastus medialus muscle (Johanson et al. 1982a).

- *Knee Muscles*

There are four muscles that act directly on the knee joint; other muscles move the knee incidentally while moving the hip or knee.

o Extensors

Three muscles act as extensors of the knee. These are the vastus lateralis, vastus medialus and vastus intermedialus. The rectus femoris is also connected as an extensor of the knee. These four muscles together are the quadriceps femoris. These four muscles combine at the quadriceps tendon, which inserts at the patellar ligament. The popliteus muscle rotates leg at the knee, and flexes the knee. It locks the leg so it is stable when standing and may assist in stabilization (Langdon 2005). It is the muscle that lies closest to the posterior of the tibial bone. Humans and apes both have similar musculature in the knee region. The

meniscus is also an important feature in the knee, as it pads the femur and tibia when in articulation.

The human knee joint allows for full stabilization of the body, while in apes the knee has more features that give it more movement. The patella is the most frontal bone of the knee, and it "floats" above the femur, connected by ligaments to the femur and tibia. It increases the lever advantage of the quadriceps femoris, especially when the knee is approaching full extension (Aiello and Dean 1990). In apes, the patella is smaller, and reflects the smaller quadriceps muscle. The patella also shows a distinct change over time in australopithecine morphology.

oKnee Ligaments

Ligaments keep the femur, patella and tibia in articulation (Figure 10). The collateral ligaments are located on the medial and lateral sides; the cruciate ligaments are located within the joint. The two collateral ligaments hold the joint together and limit rotation and extension. The two cruciate ligaments cross and keep the femur from sliding off the tibia when the joint is flexed or extended (Aiello and Dean 1990).

The ligaments in apes are similar but are arranged to allow for more flexion and rotation of the femur and tibia. The chimpanzee also lacks the locking mechanism that the quadriceps muscle allows humans. In "Lucy", the area for the posterior cruciate ligament and meniscus is well marked (Johanson et al 1982a).

• *Foot Muscles*

The foot muscles are divided into two groups, the extrinsic and intrinsic, or long and short muscles. The long muscles originate on the tibia or fibula, and insert onto the tarsal or metatarsal bones (Figure 11). These are the muscles that are responsible for

gross movement of the foot. The short muscles originate and insert on the foot bones (Figure 11). These are the muscles that position the foot during the stance and stride phases of locomotion. The human foot exhibits two arches, a medial arch and a longitudinal arch, which is unique to humans. All hominids have shown a medial arch (Wang and Crompton 2004).

    o Long Muscles

        ▪ Dorsiflexion

Dorsiflexion occurs when the superior surface of the foot is closer to the tibia through flexion at the ankle. The major muscle is the tibialis anterior. It opposes the gastroncnemius muscle and can also invert the foot.

        ▪Inversion

Inversion turns the foot inward toward the midline of the body. The tibialis posterior inverts the foot. The muscle inserts on all the talus bones and four metatarsals. The muscle also meets a tendon of the short muscle flexor hallucis brevis and stabilizes the longitudinal arch.

        ▪Eversion

Eversion moves the foot toward the lateral sides of the body. There are two muscles, the fibularis longus and fibularis brevis. The muscles originate at the fibula, giving rise to the peroneal groove on the fibula. A third muscle, the fibularis tertius, may occur in humans. These muscles are active in the stance phase of walking in humans, but inactive in chimpanzees. However, in arboreal locomotion the muscles are active in chimpanzees (Aiello and Dean 1990).

        ▪Plantarflexion

This is the movement that lifts the entire weight of the body over the foot as the heel lifts off the substrate during locomotion. The muscle is the triceps surae, and is divided into two muscles, the gastrocnemius and the soleus. The gastrocnemius is the larger of the two muscles, and originates on the two femoral condyles. The soleus lies underneath the gastrocnemius and originates at the fibula. The muscles combine to form the Achilles tendon. The tendon is about 65% of the muscle length (Aiello and Dean 1990), and attaches to the calcaneal tuberosity. The plantaris muscle is associated with the triceps surae.

- Extensors and Flexors

These are muscles that extend and flex the toes. They are the extensor hallucis longus, the extensor digitorum longus, the flexor hallucis longus, and the flexor digitorum longus. In humans, these muscles flex or extend the toes, and the flexors can also plantarflex the ankle. In humans, the flexor hallucis longus is separate from the other flexor muscle. In apes, there is an additional muscle which moves the hallux (great toe). This is the abductor hallucis longus, and allows for the opposable toe in apes.

o Short Muscles

The short muscles are arranged in layers from most superficial to most deep. There is one muscle that is on the superior surface of the foot, the extensor digitorum brevis. This muscle extends the toes.

- First Layer

These are the most superficial of the short foot muscles. They are comprised of the flexor digitorum brevis, the abductor hallucis and the abductor digiti quinti. These

muscles help stabilize the foot in locomotion, especially the anterior to the posterior part of the foot and leg (Aiello and Dean 1990).

▪Second Layer

There are four muscles, called lumbricals and the flexor accessorius. These muscles are more strongly developed in the apes than in humans, and flex the metatarsophalangeal joints.

▪Third Layer

The muscles are the flexor hallucis brevis, flexor digiti minimi brevis and adductor hallucis. These muscles assist in flexion of the great toe in locomotion, and shape the foot for the arches.

▪Fourth Layer

The interosseous muscles make up this last layer. There are two types of muscles: the plantar interosseous which adduct the toes; and the dorsal interosseous, which abduct the toes.

Given the muscle and bone attachments, in addition to body proportions, the human foot exhibits the "proportions and basic geometry…more suitable for bipedal standing," (Wang and Crompton 2004).

Locomotion and Walking Phases

Walking involves a heel strike, placing the foot down directly over the arch, and pushing off from the big toe (Klein 2002). A complete cycle is measured from heel-strike to heel-strike, or toe-off to toe-off of the same foot (Napier 1967) (Figure 12). In human walking, the lower limb essentially vaults over the foot and transfers the center of gravity with each foot step, resembling a pendulum that is alternatively inverted and suspended

(Preuschoft and Witte 1991). The center of gravity in humans is ventral to the sacro-iliac joint (Kummer 1991). The body must keep the center of gravity balanced on one foot during a step, and so is always in danger of falling over to the side. The muscles and bones of the lower appendicular skeleton prevent this from happening by their very nature. The mass is always over the heel-strike at its lowest point and reaches the highest point at mid-stance (McMahon et al. 1987, Schmitt 2003). When a human is walking, the back foot is pushing backwards and the front foot is pushing forwards with the heel. In the second phase, the back foot is lifting, and all weight is centered on the front foot, with the foot squarely on the substrate. In the third phase, the back foot is swinging forward above the substrate, and the front foot is still holding the center of mass. In the fourth stage, the front foot has become the back foot, and the back foot is the front foot. The center of mass is transferring to the ball of the first (front) foot. In the last phase, the weight of the body is on the ball of the back foot, and the frontal foot is transferring weight onto the heel of the foot (Alexander 1992a). The legs are kept relatively straight, and the transfer of weight oscillates from the right to left side of the body. The transfer of weight converts to force when a person walks on force plates. When humans walk, hip extension occurs from heel strike and knees are not flexed until mid stance. The opposite pattern is seen in apes, with a flexed hip and straighter hip (Okada 1985). More energy is used when humans use a bent-hip gait, and less energy when in a normal gait (Wang et al. 2003).

Analysis of Force Plate Data

"…The total force exerted by an animal is found by measuring the forces exerted by the contacting extremities on the ground…Force at the extremities can be measured by

means of force plates" (Kimura 1985). The force plate data collected in Spring 2006 was analyzed to show the amount of force applied by the human body, and measure the angle of the foot when in stride phase. Each subject (Table 1) was instructed to walk normally and in a "bent-hip, bent-knee" pattern, which resembles the ape pattern of bipedal walking. As the subject walked across the force plates, measurements of the amount of force and foot angle were recorded into a computer, using the program EvART. Force plates locate the center of pressure by measuring the force, in this case, pressure, of the foot against it (Alexander 1992b). The center of pressure is under the center of gravity and moves with the movement of the body. When walking, the forces on the feet are twice as high in standing because there is more pressure pushing on part of the foot during the walking phases (Alexander 1992b). The different forces are due to body weight.

By comparing the results of the data in graphical form to that of established graphs (Kimura 1985) (Figure 13), it is possible to determine if humans can imitate the bipedal walking pattern of apes. Then it is possible to extrapolate if australopithecines also walked in a more human or ape-like pattern using data from the Laetoli footprints, which can be measured as force plate data.

Foot forces are recorded in three dimensions: vertical, anterior-posterior, and medial-lateral. The vertical force is recorded in a strict horizontal movement, specifically when the foot strikes the force plate. The anterior-posterior force is associated with starting and stopping the limb during a stride. The posterior force occurs when the toe-off pushes off from the ground, and anterior force occurs when the heel hits the ground, with

associated angles. The medial-lateral forces are measured with the sides of the foot and balance.

• Normal Walking: Vertical

The pattern of vertical walking follows the expected forces, with a two humped pattern. The data reveals that approximately 100% of body weight is applied to the foot in normal walking. The two peaks are associated with heel-strike and toe-off. (Figure 14).

• Normal Walking: Anterior-Posterior

The anterior-posterior forces follow the expected pattern, with the high peak representing the force of the heel and the dip the force of the hallux. (Figure 15).

• Normal Walking: Medial-Lateral

The lateral forces have a peak pattern opposite that of the anterior-posterior forces. The graph follows the expected pattern. More force is being applied in the latter half of the phase when the hallux is contacting the plate. (Figure 16).

•Bent-Hip, Bent-Knee: Vertical

The graph represents the force used to move in an apelike pattern. The subjects were able to successfully imitate the ape-like movement resulting in a one-humped peak. The graph shows that the amount of force on the foot was nearly twice that of body weight. (Figure 17).

•Bent-Hip, Bent-Knee: Anterior-Posterior

The graph of subjects imitating bent-hip, bent-knee forces resembles that of the apes in anterior-posterior aspect. This shows that it is possible for humans to mimic apes in two planes of movement. (Figure 18).

•Bent-Hip, Bent-Knee: Medial-Lateral

The graph shows a different pattern than that for ape movement. In apes, the forces are stable and then dip, while in human imitation, the forces dip and then peak. The third aspect of moving like an ape is not replicated. (Figure 19).

Discussion

Humans are able to imitate ape like bipedal motion in the vertical and anterior-posterior forces. The inability of humans to successfully imitate the medial-lateral forces suggests that more force is still used to push off the foot on the sides of the foot. In apes the medial side of the foot is used to push off. The arch of the human foot is probably responsible for the opposite forces.

Comparing the forces used in human bipedalism to impressions left at Laetoli may reveal clues as to how australopithecines walked.

The Laetoli footprints have several impressions of the heel, sole and ball and hallucal aspect (Tuttle et al. 1991) (Figure 20). The impressions reveal longitudinal arches, which is clearly a human foot feature (Langdon 2005), as well as a hallux that is positioned relatively closer to the second toe than it is in chimpanzees. These two features suggest that the australopithecines that left the impressions had a human type foot. In studies that compare human foot impressions with those from Laetoli (Day and Wickens 1980, 1991; Tuttle et al. 1990, Tuttle et al. 1991), the indications are that the impressions are similar and may reflect an advanced state of bipedality (Day and Wickens 1980).

Summary of Results

1. The human body is adapted to standing, and subsequently walking, because of the arrangement of muscle connections of the hip and leg. Adductors and abductors move the leg forward and backward, while extensors and flexors lift the leg.

2. Australopithecine skeletons have a mosaic form, combining features of human and chimpanzee morphology. The pelvis is more human like, while the femur is more ape like. The tibia and fibula are ape like, while muscle attachment sites are located in a human orientation. The calcaneous is distinctly human. This makes *Australopithecus afarensis* a good model for looking at bipedalism studies.

3. Humans are able to imitate an ape-like gait in vertical and anterior-posterior dimensions. They are unable to imitate the lateral forces. This may be a result of the unique arch of the human foot.

4. The similarities of the australopithecine skeleton to human shows that the evolution of skeletal and musculature occurred. *A. afarensis* was able to walk, but not the way modern humans do. Comparisons of the Laetoli footprints show that australopithcines had a similar foot-fall pattern to that of modern humans.

Conclusions

In researching the morphology of humans, chimpanzees and *A. afarensis*, the family resemblance is apparent. Bones from each of the three species shows that there are unique features to each, and that *A. afarensis* has a mosaic pattern that utilizes musculature and bone morphology that lends itself to a different mode of upright walking. *A. afarensis* may have walked with a gait pattern that was more upright than chimpanzees, but had more bounce in it than humans. Examining force plate data of the

locomotor patterns shows that humans are only able to imitate ape patterns in certain ways. This result indicates that the distinctive gaits of humans and apes are different from each other in their morphology. Hypothesizing that *A. afarensis* also has a unique pattern, and more similar to that of humans based on its bone and muscular morphology is not an unreasonable deduction.

Acknowledgments

Tables

Table 1. Subject data of force plate experiments from Spring 2006.

Subject	Sex	Age	Weight
Subject 5	Female	Age 20	158 lbs
Subject 6	Female	Age 20	137 lbs
Subject 7	Female	Age 20	128 lbs
Subject 8	Male	Age 47	178 lbs
Subject 10	Male	Age 19	180 lbs
Subject 11	Female	Age 21	174 lbs

Figures
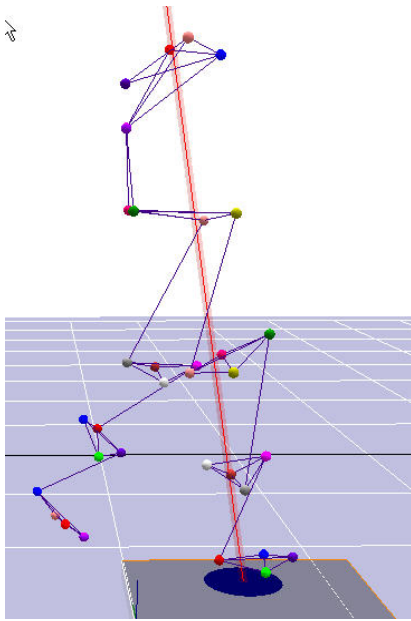
Figure 1. EvART live motion data capture of straight leg gait. Each point represents a reflective marker on the subject's body. The nearly vertical line is the force projected onto the force plate.
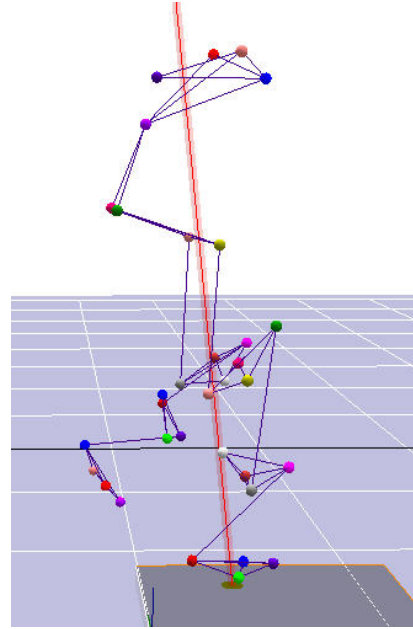
Figure 2. EvART live motion data capture of bent-hip, bent-knee gait.

Figure 3. Laetoli footprints (Trails G-2 and G-3) located in Laetoli, Tanzania.
Source: www.modernhumanorigins.net
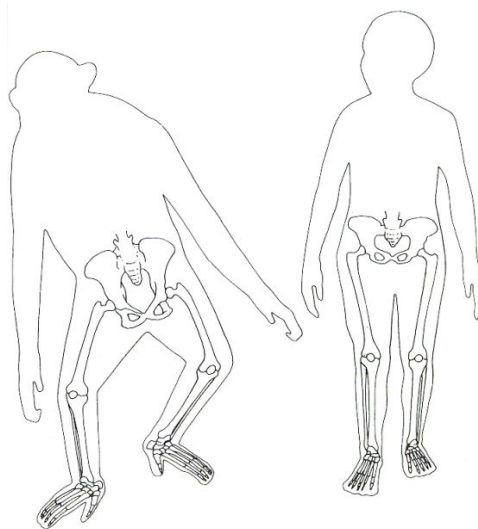
Figure 4. Comparison of chimpanzee and human lower skeleton. Not to scale. After Tardieu, 1991.

Figure 5. A bonobo (*Pan paniscus)* walking bipedally. Source: http://pin.primate.wisc.-edu/av/images.

Figure 6. A.L. 288-1 "Lucy". Source: www.modernhuman-origins.net

Figure 7. Pelves from chimpanzee, *Australopithecus afarensis* and human. After Langdon, 2005.
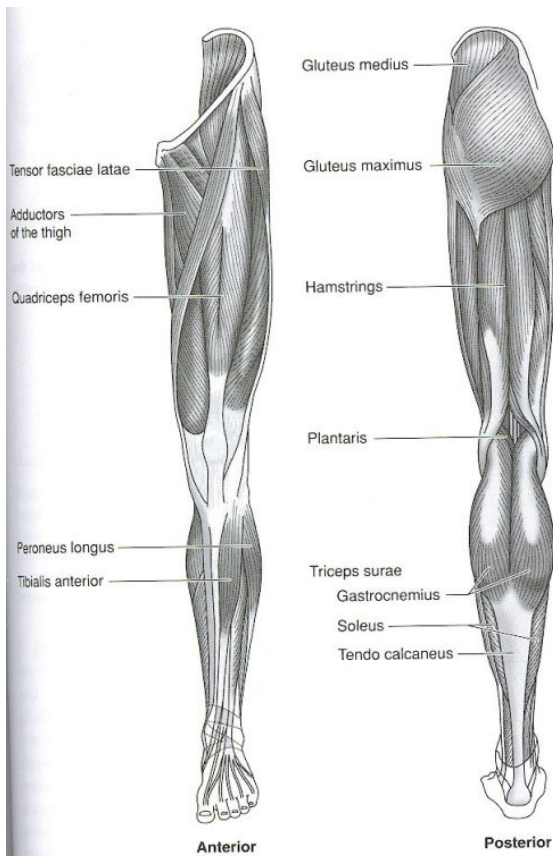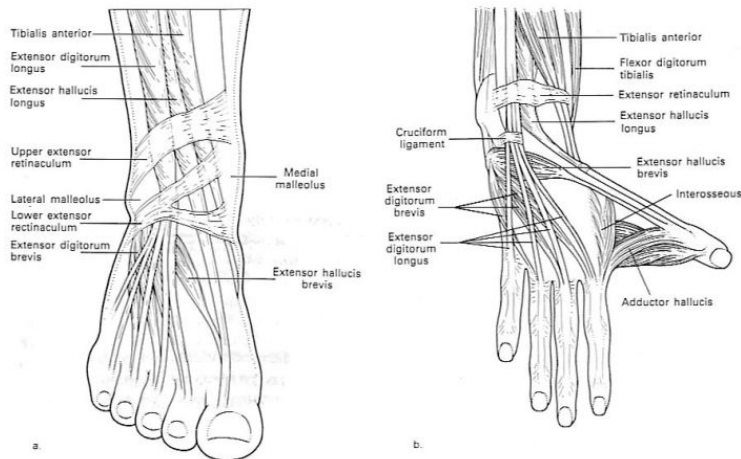
**Figure 8. Human muscle morphology of the thigh and leg. After Langdon, 2005.**
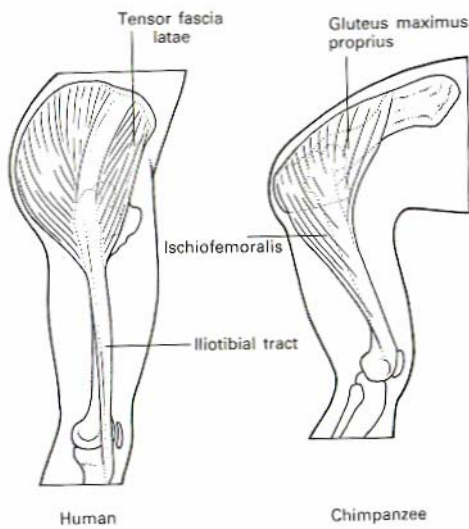
Figure 9. Human and chimpanzee muscle differences in the gluteus maximux and angle of thigh and leg. After Aiello and Dean, 1990.
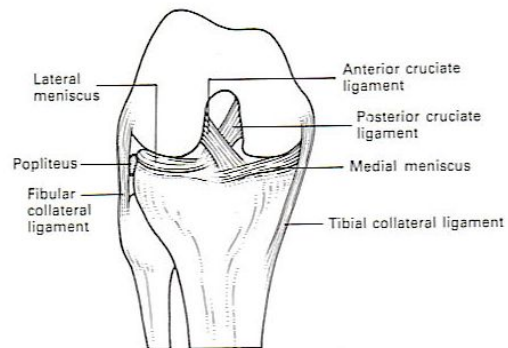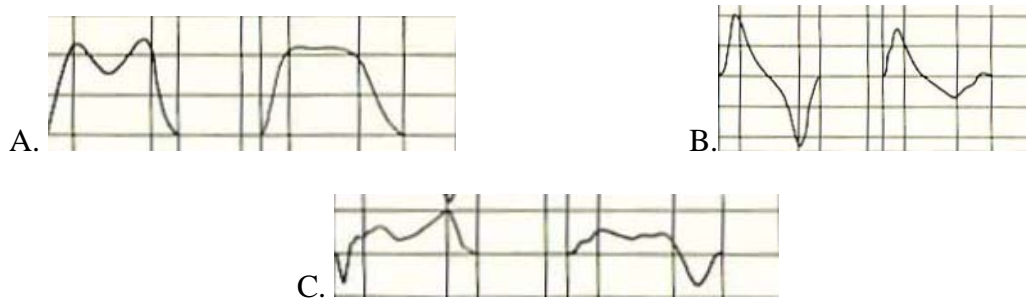

Figure 10. Ligaments of the human knee joint. After Aiello and Dean, 1990.

Figure 11. a: Human foot muscles and ligaments. b. Chimpanzee foot muscles and ligaments. After Aiello and Dean, 1990.

---------Toe Off----------→---------------Midswing--------→-------Heel Strike----------
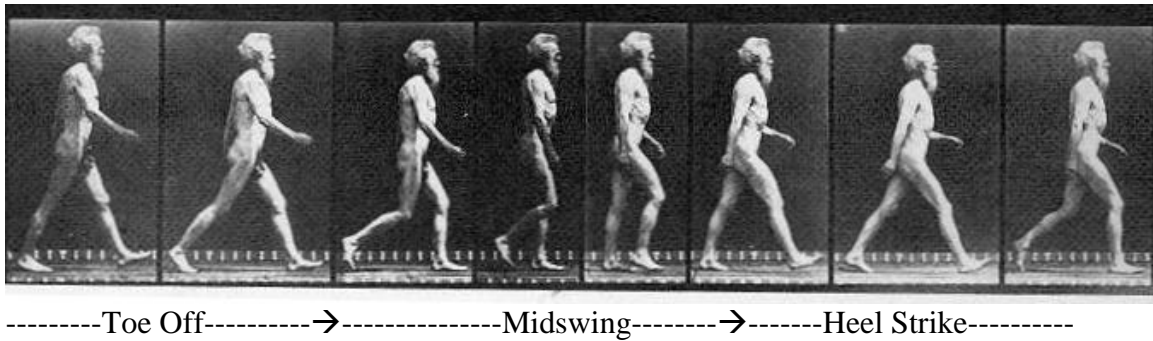
Figure 12. Phases of walking from Eadward Muybridge studies. After Muybridge, 1979


Figure 13. Established force plate gait patterns. The left line is for humans, the right line is for chimpanzees. 13-A shows vertical forces. 13-B shows anterior-posterior forces. 13-C shows medial-lateral forces. After Kimura, 1985.
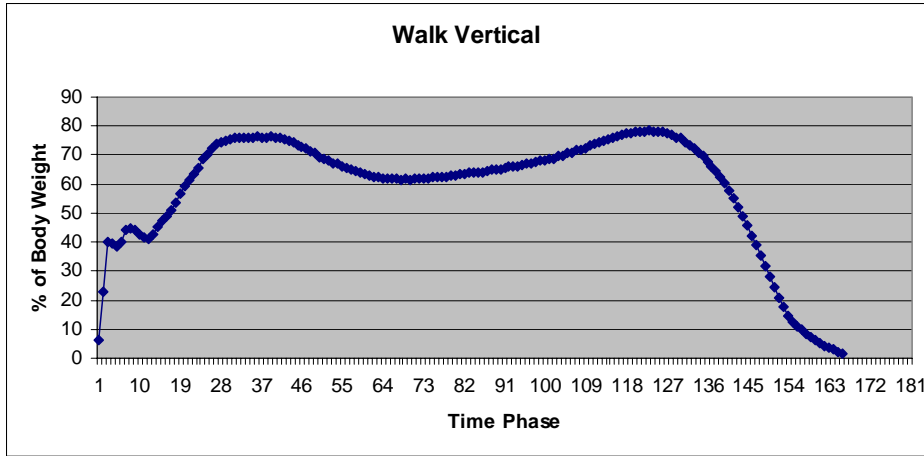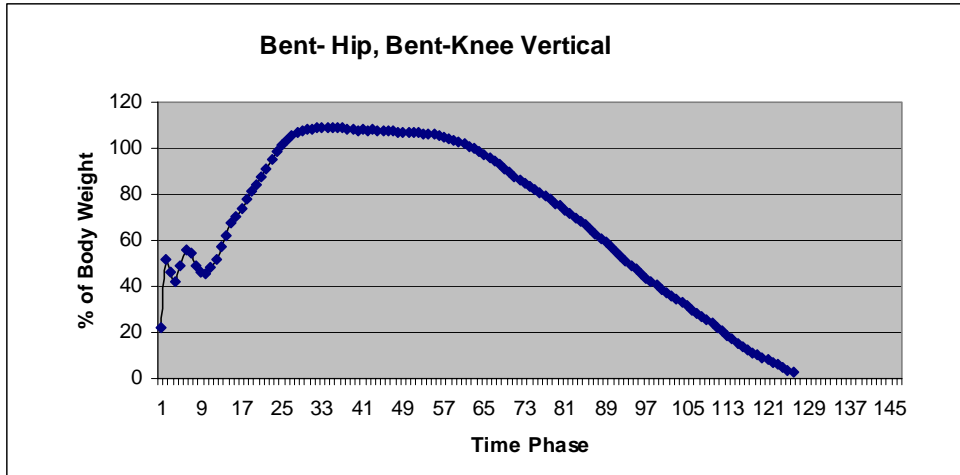
Figure 14. Force plate data of vertical forces, normalized for foot angle and weight. Data is from a representative subject.
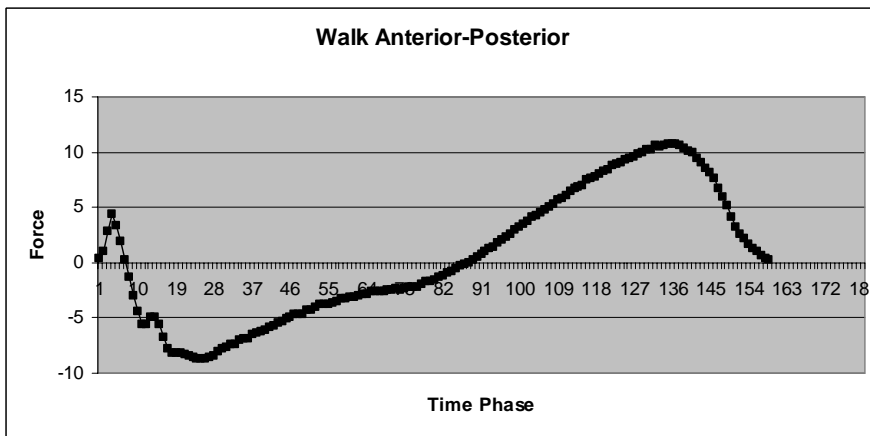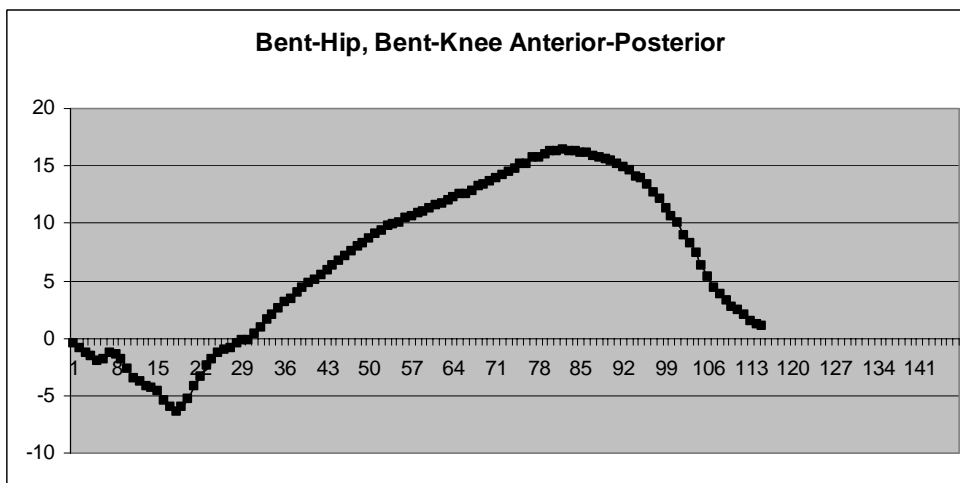

Figure 15. Force plate data of anterior-posterior forces, normalized for foot angle and weight. Data as above.
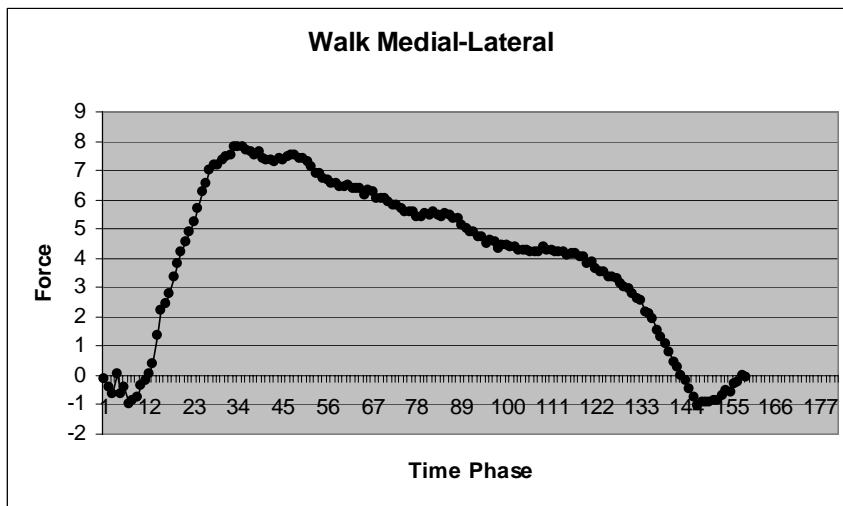
Figure 16. Force plate data for medial-lateral forces normalized for foot angle and weight. Data as above.

Figure 17. Force plate data for vertical forces in bent-hip, bent-knee motion normalized for foot angle and weight. Data as above.

Figure 18. Force plate data for anterior-posterior forces in bent-hip, bent-knee movement normalized for foot angle and weight. Data as above.
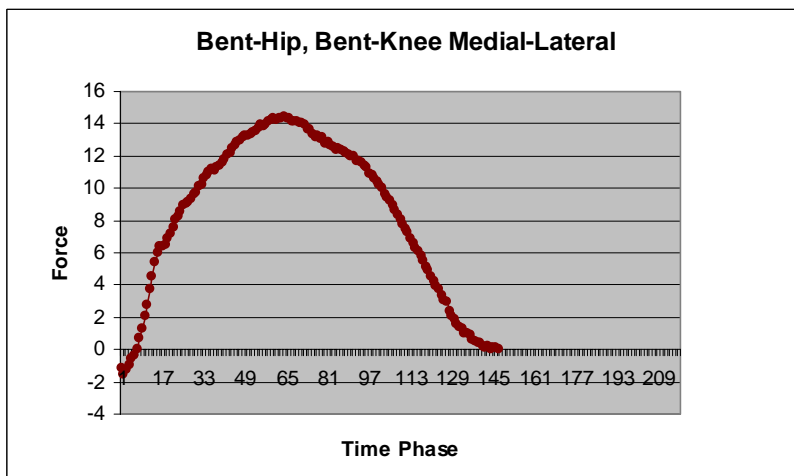
Figure 19. Force plate data for medial-lateral forces in bent-hip, bent-knee movement normalized for weight and foot angle. Data as above.

Figure 20. Close up of Laetoli footprint, showing clear impression of ball of foot and heel. After Tardieu, 1991.

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