The Bent Hip and Bent Knee Gait and its Possible Role in the

Evolution of Modern Human Bipedalism

by

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Thesis submitted in partial fulfillment of the
requirements for the degree of Master of
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ABSTRACT

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Abstract

The relatively stiff gait of modern humans minimizes the muscular work done to move the lower limbs and the center of mass. Nonhuman primates, and perhaps our earliest ancestors, use a form of bipedalism in which the hip and knee are held in a flexed position. This thesis follows up on other studies examining loading and energetic costs of these compliant walking gaits by examining the effects of increased hip and knee flexion on kinetic, kinematic, and energy exchange variables. The bipedal gait of twelve human subjects using normal and bent hip and bent knee gait were compared. The subjects walked along force plates embedded in the ground while 3D kinematic data was simultaneously gathered. The data was then processed using EvaRT, Orthotrak, and Matlab to evaluate the variables used. During the bent hip and bent knee bipedal locomotion subjects demonstrated lower peak vertical and parallel ground reaction forces, much higher ankle flexion, less hip extension, and less energy recovery during a full stride. These data provide novel insight into the nature and costs of locomotion in bipedal primates and the earliest human ancestors.

Contents

List of Tables

List of Figures

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1. Introduction

1.1 Experimental Proposal

Upright, striding bipedalism distinguishes modern humans from all other extant animals (Alexander 2004). Bipedal locomotion as practiced by modern humans involves numerous specializations in the anatomy of the lower limbs such as long lower limbs, adducted femora, and a stable rigid foot, which allows humans to support and balance the weight of the upper body in an erect posture. In addition to stabilizing the body, the highly derived anatomy of humans facilitates long strides with fully extended legs and regulation of whole body oscillations, both of which may reduce metabolic costs of locomotion (Cavagna and Kaneko 1977). Mapping the evolutionary pathway to modern human bipedalism has proven challenging because of the scarcity of the fossil record and the difficulty inherent in interpreting the life of the animal from a few fragmented fossils. Laboratory-based studies on the biomechanics of bipedalism in modern humans such as those conducted by Li and Colleagues (1996), Schmitt (2003), and the one presented here can shine light on some of the factors that should be considered when reconstructing the locomotor habits of an extinct animal and give clues about the functional anatomy of modern human bipedalism.

The central questions in this project are, how has the mechanics and functional anatomy of bipedal locomotion changed in the more than six million years over which it evolved and how does this connection between mechanics and anatomy inform our interpretation of bipedal locomotion in early hominins? In that context, it is worth beginning by describing the mechanics of bipedalism in modern humans.
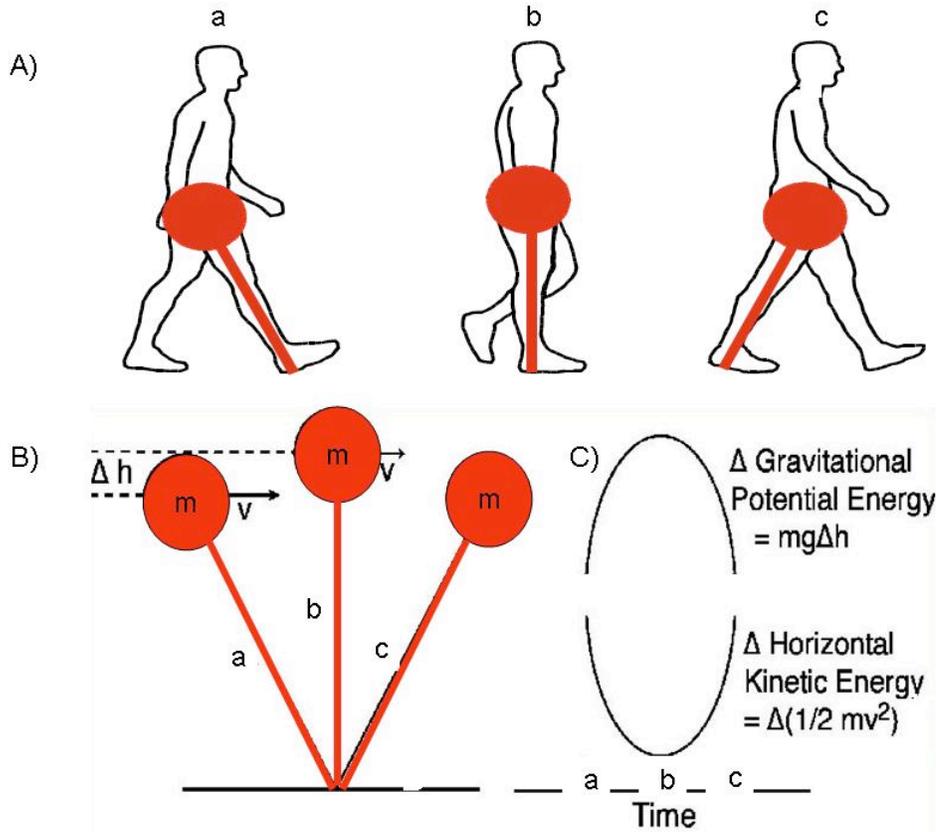
Figure 1: A schematic representation of the inverted pendulum model of human walking and its effects on the potential energy (PE) and kinetic energy (KE). In all section a = heel-strike, b = midstance, c = cotralateral heel-strike. A. The mass of the person is modeled as a single point concentrated around the natural center of mass (COM). The COM is supported by a massless stiff strut indicated by the red line running along the lower limb. As the step proceeds this mass-strut reaches its highest vertical point at midstance. B. Placing the point of contact at a single place the movement of the mass-strut system approximates an inverted pendulum. The change in height from heel-strike to mid-stance is described as delta-h and approximates the change in the PE in the system. C. The fluctuations of the curves in PE and KE due to change in height and forward motion. In a stiff pendular model like this one PE is highest when KE is lowest.

Human beings walk on stiff, straight legs (Inman 1944). As a result, as modern humans walk, their center of mass rises and falls throughout the stride (figure 1a). At heel strike the center of mass is at its lowest point. Then the body vaults over the relatively stiff stance leg and the center of mass reaches its zenith during midstance

2

(Cavagna et al. 1977 ; Geyer et al. 2006; Lee and Farley 1998). The energetics of the periodic fluctuation of the center of mass can be modeled with an inverted pendulum (Cavagna et al. 1976). First described by Cavagna and colleagues in 1976, the pattern involves storage and release of potential and kinetic energy in the manner indicated in figure 1b,c. When the center of mass rises from heel strike to single support, kinetic energy is transferred into gravitational potential energy. When the center of mass is highest the available gravitational potential energy is at its maximum and available kinetic energy is at its minimum. Once the stride goes through the highest point the gravitational potential energy is converted into kinetic energy that can be used to drive the center of mass forward and back up again because the contrateral leg remains stiff and the horizontal kinetic energy drives the center of mass forward and up (Cavagna et al. 1977 ; Cavagna et al. 1976). Without the conversion of gravitation potential energy into kinetic energy muscles would have to do all the work of redirecting the center of mass from generally downward to generally upward at the step-to-step transition, although the mechanics of that redirection also induces some costs as well so that the energy savings of pendular exchange are slightly reduced by the need to redirect the center of mass at all (Adamczyk et al. 2006; Cavagna et al. 1976; Donelan et al. 2002; Ruina et al. 2005). Thus, the ability to exchange kinetic and gravitational potential energy can reduce the work required by muscles and could potentially lower metabolic costs of locomotion. Although direct measures of energy exchange and metabolic costs are limited, this relationship has been supported (Griffin et al. 2004a; Ortega and Farley 2005). Humans have been show to recover close to 70% of the potential energy as kinetic energy when they are walking at moderate speeds (Cavagna et al. 1977 ; Cavagna et al. 1976; Griffin et al. 2004a), which means less muscular effort is required from the limbs to move the center of mass forward. At slow and fast speeds that energy recovery is

3

reduced but never below 50%. The high level of exchange at moderate walking speeds is only achieved once a child reaches 10 years old (Schepens et al. 2004) because of required changes in skeletal mass and length as well as neuromuscular control.

The potential and kinetic energy of the center of mass is determined from ground reaction forces which are a direct measure of acceleration of the COM which in turn can be used to calculate COM velocity and displacemement (Cavagna et al. 1977). Ground reaction forces reflect the style of locomotion (Alexander and Jayes 1978). The pendular locomotion of modern humans yields a distinct ground reaction force curve different from that of other primates (Kimura et al. 1979; Li et al. 1996; Schmitt 2003) that has two peaks greater than the mass of the body separated by a shallow valley (Alexander and Jayes 1978).

The use of the inverted pendulum style of locomotion is seen in many other animals including dogs, horses, and large birds (Cavagna et al. 1977 ; Griffin et al. 2004a), but to a much lesser degree in our closest relatives, the primates (Kimura 1996; Kimura et al. 1979; Schmitt 2003).   Many extant primates, instead, use compliant bipedal or quadrupedal locomotion, meaning they use a deeply yielding (large angular change from touchdown to midsupport (Schmitt 1999)) elbow or hip and knee while moving (Kimura 1996; Schmitt 1999; Vereecke et al. 2006). Yielding at the hip and knee allows for a smoother gait with no up to down transitions but with less exchange of energy (Alexander and Jayes 1978; Kimura 1996; Schmitt 2003). Therefore, compliant locomotion has little to no exchange of kinetic and gravitational potential energy and does not benefit from its potential efficiency.[1] The shape of the ground reaction force

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[1] This is less clear for quadrupeds see Griffin TM, Wicker SJ, Hoyt DF, Garcia S, and Kram R. 2004b. Determinants of Walk-trot Transition in Horses. Durham: Duke University. 30 p. for discussion of pendular mechanics in dogs and see alternative perspective for *Lemur catta* in O'Neill M. 2009. Musculoskeletal design predicts locomotor cost: a test of the force production model across speed and gait in nonhuman primate.

curve during compliant locomotion (high values of joint yield) is substantially different from the two-peaked curve seen in pendular locomotion (Kimura 1996; Li et al. 1996; Schmitt 2003). When moving compliantly, animals have a ground reaction force curve that is fairly flat and only barely reaches or just surpasses the body mass of the individual (Alexander and Jayes 1978; Kimura 1996; Li et al. 1996; Schmitt 2003).

Although compliant locomotion during bipedalism in most examples and quadrupedalism in at least *Eulemur fulvus* severely limits exchange of kinetic and gravitational potential energy, there are thought to be benefits to this type of locomotion. In arboreal primates, it has been argued that a compliant gait may lead to smoother, easier movement on tree branches without bouncing (Schmitt 1999). An additional potential benefit of the flat ground reaction force curve associated with compliant locomotion is that it may reduce the transient impact force and resulting shock wave (Schmitt 2003; Voloshin et al. 1981) that passes through the joints of the body during each step (Schmitt 2003; Schmitt et al. 1996). A bipedal animal using compliant locomotion would have a reduced opportunity to take advantage of energy exchange, but it may benefit from longer stride lengths (due to large angular excursion of a limb landing and pushing off in an extended position and yielding during stance) and faster walking speeds (Schmitt 2003). Lastly, although oscillations of the COM allow energy exchange they also require redirection of the COM (Ruina et al. 2005) that represents another cost, although on the whole the energy exchange may be worth this additional cost and there are mechanisms such as overlapping support phases and creation of pseudoelastic redirections that can reduce redirection costs in a pendular model

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American Journal of Physical Anthropology 138:282. and O'Neill and Schmitt, submitted in which *L. catta* can achieve high values of energy exchange as well as very low levels.

(Adamczyk et al. 2006; Ruina et al. 2005). Bishop et al. (2008) argued that the stealthy locomotion of cats may benefit somewhat from reduced redirection costs. Therefore, the potential benefits of compliant locomotion are broad and seem to vary in different animals that are exposed to an assortment of environmental pressures. This variation highlights the fact that to understand potential selective pressures on animal locomotion it is important to take the animal's whole lifestyle into consideration. Energy efficiency is very important to cursorial animals, but may not be the most important consideration in animals that do not move quickly or travel great distances (Bishop et al. 2008). Therefore, when recreating locomotor scenarios for extinct animals with few fossils for reference an expansive perspective of their environment and evolutionary pressures is necessary to make a reasonable hypothesis.

The fact that primates, our closest living relatives, use relatively compliant (yielding) gaits brings to question whether modern human bipedalism went through a compliant locomotion phase (Schmitt 2003). The fossil record does little to answer this question. Indicators of bipedalism such as an obturator externus groove, elongated femoral neck, and large, vertical gluteal tuberosity are seen in the femur as early as 6 million years ago in *Orrorin tugenensis* (Pickford et al. 2002; Richmond and Jungers 2008). When the morphology of the proximal femur of *Orrorin tugenensis* is compared to the proximal femur of great apes, modern humans, fossil *Homo*, and early hominins using a cluster analysis, it falls within a distinct early hominin cluster (Richmond and Jungers 2008). This cluster is characterized by a very wide iliac blade and long femoral neck, which creates a greater gluteal muscle moment arm (Richmond and Jungers 2008). The unique femoral morphology and associated mechanical peculiarities of early hominins seems to have persisted for 4 million years from 6 million years ago in *Orrorin* to 2 million years ago in Australopithecines (Richmond and Jungers 2008) and are associated

6

with the origins of bipedalism. A full understanding of how this suite of anatomical features could affect locomotion is crucial to reconstructing the evolution of bipedalism.

The most complete, early example of a biped is the recently described *Ardipithecus ramidus* from 4.4 million years ago (Lovejoy et al. 2009b). The anatomy of *A. ramidus* shows a combination of both bipedal and arboreal characteristics (Lovejoy et al. 2009b) The short, broad iliac spine and ankle morphology indicate that this animal was able to walk upright and propel itself forward with its feet, but the placement of the ischial surface and abduction of the big toe suggest that *A. ramidus* was also somewhat arboreal (Lovejoy et al. 2009a; Lovejoy et al. 2009c). This important fossil find was only recently described in a peer-reviewed publication and the interpretation of its functional anatomy has not been discussed at the level of detail applied to *Australopitheucs afarensis* fossils from 3.2 million years ago. These fossils also display a combination of arboreal and bipedal characters (Crompton et al. 2008; Lovejoy 1988; Schmitt 2003; Stern 2000; Stern and Susman 1983 ; Susman et al. 1984 ; Ward 2002), although how these features are interpreted varies widely.

Since its discovery in 1974, the *A. afarensis* fossils have spurred a debate concerning the origins of bipedalism. Features associated with bipedalism found in the *A. afarensis* fossils include short, broad iliac blades and valgus knees (Lovejoy 1988; Stern and Susman 1983 ; Susman et al. 1984). Anatomical features generally associated with an arboreal lifestyle are the long upper limbs, relatively short hindlimbs, rod-shaped pisiform, curved phalanges, and cranially-oriented glenoid fossa (Lovejoy 1988; Stern and Susman 1983 ; Susman et al. 1984). This combination of characters brings to light the question of whether the mere presence of bipedal traits indicate full, upright, striding bipedalism like modern humans or whether the presence of arboreal traits may indicate a lifestyle compromised between bipedalism and arborealism with a bent hip

7

and bent knee, compliant type of locomotion (Crompton et al. 2008; Lovejoy 1988; Schmitt 2003; Stern 2000; Stern and Susman 1983 ; Susman et al. 1984 ; Ward 2002). Some features that may specifically indicate a bent hip and bent knee type of locomotion include the tibiotalar joint that appears well suited to withstand large anteriorly directed shear forces from increased ankle flexion, orientation of the iliac blade more laterally, reorientation of the hamstrings, the diminutive size of the anterior horn of the acetabular surface indicating a more flexed position of the femur, and a flat sacrum (Stern 2000; Stern and Susman 1983 ; Susman et al. 1984). Additionally, the joints of the lower limbs of *Australopithecus afarensis* are loose and poorly stabilized. For instance, the hip joint is small with small femoral ligaments, the lateral lip of the patellar groove is not well developed compared to modern humans, and the sacrum does not have developed upper lateral angles for sacroiliac ligaments (Stern 2000; Stern and Susman 1983 ; Susman et al. 1984). These weak joints of the lower limbs may have been adequate for a bent hip and bent knee gait and not a stiff-legged vaulting gait because a bent hip and bent knee gait has a reduced peak vertical and transient impact force felt at the joints (Schmitt 2003; Susman et al. 1984). Although these fossils have been extensively analyzed, bringing life to partial fossils has proven very difficult and there has been no consensus about the locomotion of *A. afarensis*.

Even as more fossils are discovered in the future, recreating the bipedalism of our ancestors will always be a challenge. Bones can provide a broad framework for interpreting locomotor ability, but without empirical data on living animals, one can only speculate about the specific movements and behaviors of an animal. This study attempts to understand the implications of compliant locomotion in a bipedal ancestor to determine if this type of locomotion is consistent with the fossil evidence. In this study, I compare, lower limb joint flexion angles, ground reaction forces, stride

8

parameters, toe clearance, and mechanical work variables in humans walking normally and with a bent hip and bent knee. These data provide novel insight that should be taken into consideration when reconstructing the wide spectrum of possibilities for the bipedalism of early hominins.

1.2 Expectations

In the study, locomotor variables were compared when humans walked with an upright, striding form of bipedalism and then with a bent hip and bent knee form of bipedalism. Knee yield and sacral displacement (the change in the height of L5-sacral joint during the stride) were measured to confirm that participants were in fact using a compliant (yielding) bent hip and bent knee gait. When walking with a yielding gait it is expected that knee yield would be higher and sacral displacement would be lower than when walking with a normal gait. It is predicted that when walking with a bent hip and bent knee gait subjects will show increased flexion in the ankle, knee, and hip during both stance and swing phase. In addition, subjects will show less hip extension because the leg is not fully extended.

Based on previously published data (Li et al. 1996; Schmitt 2003) subjects walking with a bent hip and knee should demonstrate lower vertical ground reaction forces as well as lower mediolateral and fore-aft ground reaction forces. This decrease in ground reaction force is predicted to keep moments about the ankle and knee at similar levels as they are in normal walking.

The spatiotemporal variables examined are velocity, stride length, cadence, double support time, and single support time. Schmitt (2003) reported increased velocity, stride length, and single support time in subjects walking with a bent hip and

bent knee. This study anticipates similar results. In addition, cadence should be lower and double support time longer when walking with a bent hip and bent knee gait because this gait is laboring and cumbersome to use. The toe clearance is expected to be lower when walking with a bent hip and bent knee gait because subjects do not have as much space to clear the substrate when walking with a bent hip and bent knee.

Along with the kinetic and kinematic analysis of bent hip and bent knee gait an analysis of the mechanical work used during both types of gaits was done. Variables considered where change in potential energy, change in kinetic energy, percent of recovery of potential energy, and congruence of the potential and kinetic energy curves. A yielding form of locomotion is expected to have similar changes in potential and kinetic energy, but the curves of the two should be aligned differently. The bent hip and bent knee form of locomotion should show more congruence between the two energy curves and less energy recovery between the two types of energy because it moderates the oscillation of the center of mass compared to normal walking (Alexander and Jayes 1978; Schmitt 1999).

The examination of these variables provides a full comparison between the compliant, bent hip and bent knee gait and the modern, striding gait. This allows for conclusions about how the bent hip and bent knee gait affect the biomechanics of locomotion and the costs and benefits of this type of locomotion. The skeletal anatomy, locomotor needs of the animal, and the effects the locomotion has on the biomechanics must be taken into consideration when reconstructing the behavior of an extinct animal as each plays a role in an animal's behavior.

10

2. Materials and Methods

Twelve subjects (5 male, 7 female) ranging in age from 18 to 50 and weight from 46.7kg to 119.8kg participated in the study. Three-dimensional kinematic and force data were collected as each subject walked with both a normal human bipedal gait and with a bent hip and bent knee gait. The instructions for maintaining a bent hip and bent knee gait were to walk as smoothly as possible without bobbing the head up and down. Each subject experimented with these instructions and finally settled on the bent hip and bent knee walking. The speed, step length, and degree of flexion were not controlled and subjects moved as they felt comfortable in the bent hip and bent knee gait.

The three-dimensional kinematic data was collected using a motion analysis system (Motion Analysis Inc, Santa Rosa, CA). In preparation for data collection, reflective markers were placed bilaterally on the following anatomical landmarks: acromion process, lateral epicondyle of humerus, wrist, anterior superior iliac spine, greater trochanter of femur, posterior superior iliac spine, thigh, lateral knee, shank, lateral malleolus, lateral calcaneus, lower calcaneus, upper calcaneus, and 2nd webspace of the foot. A marker was also placed at the superior aspect of the L5-sacral interface and asymmetrically on the back. During the static trials, additional markers were placed on the medial femoral condyle and the medial malleolus for identification of joint centers during collection of static trials. These markers were removed once the static trial was performed. Kinematic data were collected at 60 Hz.

Each subject was asked to walk along a 30-meter walkway with embedded 1200Hz AMTI force plates (Advanced Medical Technologies Inc., Watertown, MA). First, the participants walked regularly with a speed that they comfortably use in every day life. They were asked to walk back and forth on the walkway until ten trials could be captured when a full stride was completed from heel strike of one foot to its next heel

strike. This same procedure was repeated while walking with a bent hip and bent knee style of locomotion. Subjects chose their own walking speed in both types of trials.

EvaRT (Motion Analysis Inc, Santa Rosa CA) software was used to track the reflective markers and condition the data. The raw data was smoothed using a 4th order, recursive Butterworth filter with a 6Hz cutoff frequency. Three trials of normal and bent hip bent and knee walking in which all markers were identified and the subject had clean contact with the force plate were averaged to yield kinematic and kinetic data. The following twenty-one variables were examined: sacral displacement (the change in height of the L5-sacral interface marker during one full stride), knee yield (change in knee flexion angle from heel strike to midstance), cadence, double support time, single support time, vertical ground reaction force, mediolateral ground reaction force, fore-aft ground reaction force, ankle moment, ankle moment arm, knee moment, velocity, stride length, ankle flexion angle during stance phase, ankle flexion angle during swing phase, knee flexion angle during stance phase, knee flexion angle during swing phase, hip flexion angle during stance phase, hip flexion angle during swing phase, hip extension angle, and toe clearance (the distance from the substrate to the second webspace of the foot). Data such as hip flexion, knee flexion, ankle flexion and toe clearance were found using EvaRT. Spatiotemporal variables (velocity, stride frequency, stride length, and support time) as well as ground reaction forces and moments were computed using OrthoTrak (Motion Analysis Inc, Santa Rosa, CA).   Stride length and sacral displacement data were normalized to subject height; force data were normalized to subject weight.

Energetic data was computed using a Matlab 7.0 (Mathworks, Nadick, MA) script written specifically for this purpose by Kristen Bishop. Methods are derived from Cavagna et. al. (1976, 1977), Ahn et. al. (2004), and Bishop et. al. (2008). The change in

potential energy (PE) and kinetic energy (KE) from midstance to midstance for one full

stride was calculated. Midstance is when the center of mass is at its lowest point. The

potential energy was calculated from the vertical component of the displacement of the

center of mass from the formula:

$$PE = mgh$$

where m is body mass, g is gravitational acceleration (9.8 ms^{-2}), and h is the vertical

position of the center of mass relative to its starting position.   The kinetic energy was

calculated using the formula:

$$KE = \tfrac{1}{2}\, mv^2$$

where m is body mass and v is the resultant velocity vector. The total mechanical

energy (TME) is the addition of the potential energy and kinetic energy. The percent of

energy recovery was calculated with the formula:

$$\% \text{ Recovery} = \frac{\sum PE + \sum KE - \sum TME}{\sum PE + \sum KE} \times 100$$

The phase relationship of the potential and kinetic energy curves is a major factor

in the amount of energy that can be exchanged. A quantity called congruity is a

calculation that allows for a quantitative comparison in the phase relationship of the

potential and kinetic energy (Ahn et al. 2004). It is calculated by multiplying the slope of

the potential energy curve by the slope of the kinetic energy curve for each value

collected (Ahn et al. 2004; Bishop et al. 2008). Therefore, congruity is positive when the

potential and kinetic energy change in the same direction and negative when they

change in opposite directions. The reported congruity value is the percent of the stride

when the congruity is positive.

Although the sampling of individuals is random and independent, the variables

were not always normally distributed and did not demonstrate equal variance. This

13

could be attributed to a relatively small sample size. For this reason, both parametric and non-parametric statistics were used to analyze the data (Sokal and Rohlf 1995) to provide the widest range of statistical information. Because the paired data (comparison of normal to compliant) from each individual was treated as a random sample and did not have influence on the paired data from another individual the Wilcoxon's Signed-Rank test was used to analyze the data, with a p-value of .05 used as a measure of significance (Sokal and Rohlf 1995). The Wilcoxon's Signed-Rank test examines values of the normal mean minus the bent hip and bent knee mean for every variable. These differences are then compared for all the subjects to determine if the pattern of positive or negative differences is significant. In addition to the Wilcoxon's Signed-Ranked test, T-tests where performed to compare the means of each subject during bent hip and bent knee walking and the means of the whole sample. Before statistical testing, a priori assumptions were made about the data based on previously reported and unreported samples. This allowed the use of one-tailed tests. Because many comparisons between the normal and bent hip and bent knee locomotion were made and the variables collected could not be assumed to be independent, a conservative conversion of the data was done to decrease type 1 error (Sokal and Rohlf 1995). The Dunn-Sidák method was used to convert the data and lower the type 1 error in each test so that the overall probably of making the type 1 error in the whole sample will be lowered (Sokal and Rohlf 1995). Statistical Analysis was performed using JMP 7 (version 7.0.1 for Macintosh, SAS Institute Inc., Cary, NC).

      All materials and methods were approved by the Duke University IRB; protocol number 2240.

3. Results

3.1 Kinetic and Kinematic Data

Table 1: Mean, standard deviation, and significanec for all kinetic and kinematic data values. P-values were calculated using the Wilcoxon Sign-Rank testing. An asterisk indicates significance at p-value = .05. Bolded items are significant variables once the Dunn-Sidak method adjusted the p-value. 1. Knee Yield is the difference in knee angle from heel strike to midstance. 2. Toe clearance is the distance from the 2nd webspace to the floor. 3. Ankle angle is the angle between the lateral knee, lateral malleolus and 2nd webspace. 4. Knee angle is the angle between greater trochanter, lateral knee, and lateral malleolus. 5. Hip angle is defined as angle between ASIS, greater trochanter, and lateral knee.

	Normal Walking		Bent Hip and Bent Knee Walking		p value
Variable	Mean	St. Dev.	Mean	St. Dev.	
Sacral Displacement	**0.26**	**0.09**	**0.19**	**0.05**	**0.0024***
Knee Yield[1]	22.1	12.5	31.4	9.9	0.0081*
Velocity (cm/s)	141.8	28.7	139.4	27.6	0.3188
Stride Length (cm)	139.1	17.0	146.0	24.2	0.1392
Cadence (strides/min)	121.2	11.7	113.6	11.3	0.0337*
Double Support Time (s)	10.3	1.6	11.3	2.9	0.3188
Single Support Time (s)	60.4	1.6	61.8	2.4	0.0737
Vertical GRF (% Body Weight)	**1.19**	**0.14**	**1.08**	**0.11**	**0.0005***
Mediolateral GRF (% Body Weight)	0.06	0.02	0.06	0.02	0.3386
Fore-aft GRF (%Body Weight)	**0.22**	**0.03**	**0.18**	**0.0**	**0.0044***
Toe Clearance (mm)[2]	122.2	31.1	109.8	24.3	0.0320*
Ankle Moment (N*cm)	2.4	1.8	2.1	1.6	0.1018
Ankle Moment Arm (cm)	3.3	2.8	3.5	3.0	0.4548
Knee Moment (N*cm)	3.0	3.2	3.3	2.9	0.1902
Stance Ankle Flexion Angle[3]	**92.3**	**4.1**	**112.3**	**5.7**	**0.0002***
Swing Ankle Flexion Angle[3]	**86.9**	**2.7**	**95.7**	**7.5**	**0.0012***
Stance Knee Flexion Angle[4]	**33.7**	**9.2**	**59.0**	**9.2**	**0.000***
Swing Knee Flexion Angle[4]	**65.1**	**5.4**	**82.5**	**6.8**	**0.0002***
Stance Hip Flexion Angle[5]	**76.1**	**11.6**	**96.2**	**12.7**	**0.0002***
Swing Hip Flexion Angle[5]	**75.9**	**11.2**	**96.9**	**13.0**	**0.0002***
Hip Extension Angle[5]	**52.3**	**11.1**	**61.7**	**10.7**	**0.0024***

Table 1 summarizes the mean and standard deviation for the normal and bent hip and bent knee gait for each variable. The p-value (test statistic from the Wilcoxon's Signed-Rank test) is reported as well. The values in table 1 indicated with an asterisk are

significant at a p-value of .05 and the bolded variables are those that maintained a

statistically significant pattern of change within the population once the Dunn-Sidák

conversion method was used with an adjusted p-value to decrease type 1 error. There is

a statistically significant difference between the normal and bent hip and bent knee trials

in sacral displacement and knee yield, although the significance of the latter is reduced

by the Dunn-Sidak adjustment (table 1).

Table 2: P-value for each kinetic and kinematic variable using t-test. The variables indicated with an asterisk are considered significantly different with a p-value of .05. The bolded variables are significantly different between the bent hip and bent knee and normal walking when the p-value is adjusted using the Dunn-Sidak conversion.

Variable	p-value
Sacral Displacement	**0.0020***
Knee Yield	0.0083*
Velocity (cm/s)	0.3526
Stride Length (cm)	0.1117
Cadence (strides/min)	0.0307*
Double Support Time (s)	0.1740
Single Support Time (s)	0.0449*
Vertical GRF	**0.0004***
Mediolateral GRF	0.3350
Fore-aft GRF	**0.0031***
Toe Clearance (mm)	0.0303*
Ankle Moment	0.0992
Ankle Moment Arm (cm)	0.3526
Knee Moment	0.3987
Stance Ankle Flexion Angle	**0.0000***
Swing Ankle Flexion Angle	**0.0006***
Stance Knee Flexion Angle	**0.0000***
Swing Knee Flexion Angle	**0.0000***
Stance Hip Flexion Angle	**0.0001***
Swing Hip Flexion Angle	**0.0001***
Hip Extension Angle	0.0109*

Table 2 reports the test statistic for each variable for the T-test comparing means.

Again, significant differences are indicated with an asterick and are significant at a p-

value of .05. The bolded variables are those that maintained statistically significant

16

differences in mean once the Dunn-Sidak conversion method was used to adjust the p-value to decrease type 1 error. This data is similar to the Wilcoxon's Sign-Ranked test data.

There are no statistically significant differences in speed, double support, contact time, or stride length when comparing normal and bent hip and bent knee walking. The cadence, however, was significantly different between normal and compliant walking, but not once the Dunn-Sidák method was used to convert the p-value. The lack of difference in spatiotemporal parameters allowed for a more straightforward comparison of kinematic and kinetic parameters without having to adjust for the effect of speed and other variables.

Figure 2a demonstrates that the peak vertical forces are significantly (see Table 1) lower when walking with a bent hip and bent knee. On average, the peak vertical forces decrease by 10% of body weight when subjects walked with a compliant gait. The fore-aft forces are significantly different between trials when using the Wilcoxon's Signed-Rank test and Dunn-Sidak p-value conversion (figure 2c; Table 1). The fore-aft forces are also considered significantly lower when the subjects walked with a bent hip and bent knee gait compared to walking normally when using the T-tests to analyze the difference in means. Also, 6 of the 12 individual comparisons of fore-aft forces are significantly lower with a sample size of 3 for each individual. The difference in fore-aft forces is on average 4% of body weight across gait types. There are no statistically significant differences between the two samples in mediolateral forces.
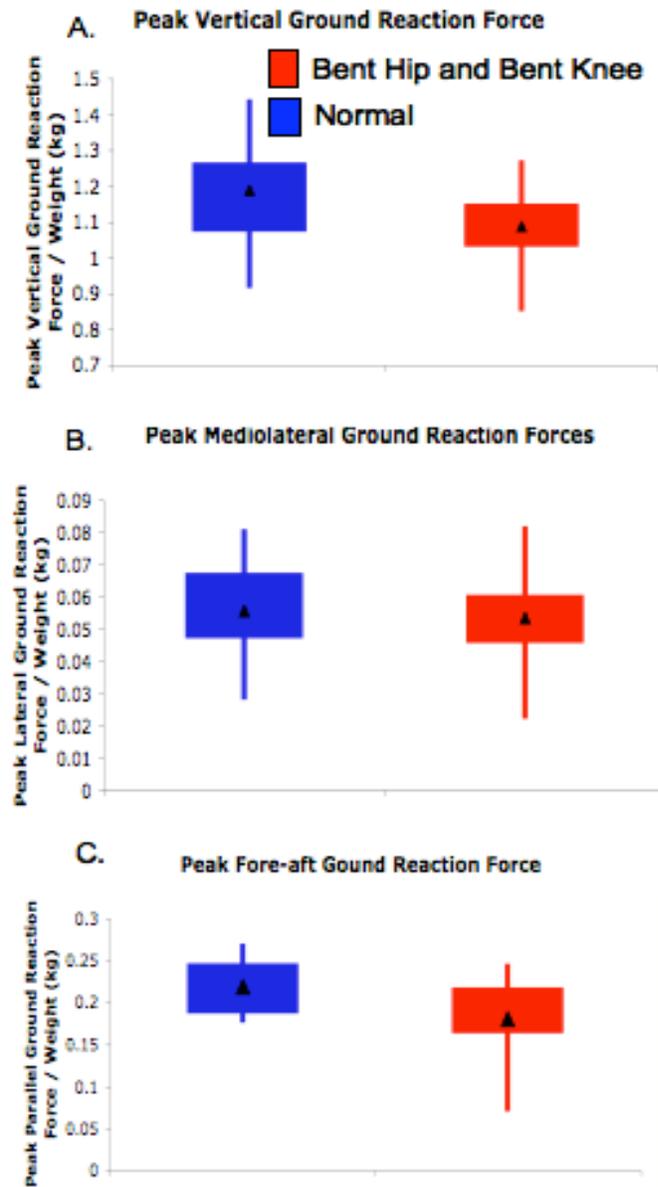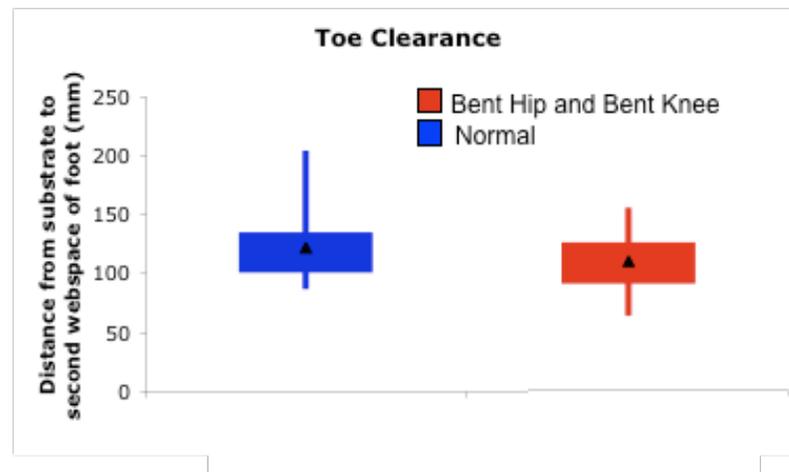
Figure 2: Normal and Bent Hip and Bent Knee Peak Forces. A. This graph illustrates the distribution of peak vertical ground reaction forces shown while walking normally and walking with a bent hip and knee. B. This graph illustrates the distribution of mediolateral ground reaction forces shown while walking normally and with a bent hip and bent knee. C. This graph illustrates the distribution of peak parallel ground reaction forces shown while walking normally and with a bent hip and bent knee.

Figure 3 shows the difference between bent hip and bent knee and normal trials in toe clearance. These differences are not statistically significant (Table 1, Table 2). Along with the bent hip and bent knee trials having lower toe clearance, they also had a much smaller standard deviation. There is no statistical difference between the ankle moment, ankle moment arms or knee moments in normal and bent hip and bent knee trials (Table 1, Table 2).

Figure 3: Toe clearance over substrate. This graph illustrates the distribution of maximum toe clearance for normal and bent hip and bent knee trials.

Ankle dorsiflexion angles increase significantly in swing and stance phase during bent hip and bent knee trials compared to normal trials as seen in table 1 and figure 4a. During stance, the ankle angle increases an average of 20 degrees and during swing it increases an average of 8 degrees. In fact, the ankle was more flexed throughout the whole stride when walking with a bent hip and bent knee gait (figure 4b). Knee flexion was also significantly higher in bent hip and bent knee locomotion during swing phase (table 1). The knee angle increased by an average of 25 degrees during stance phase and 17 degrees during swing phase.
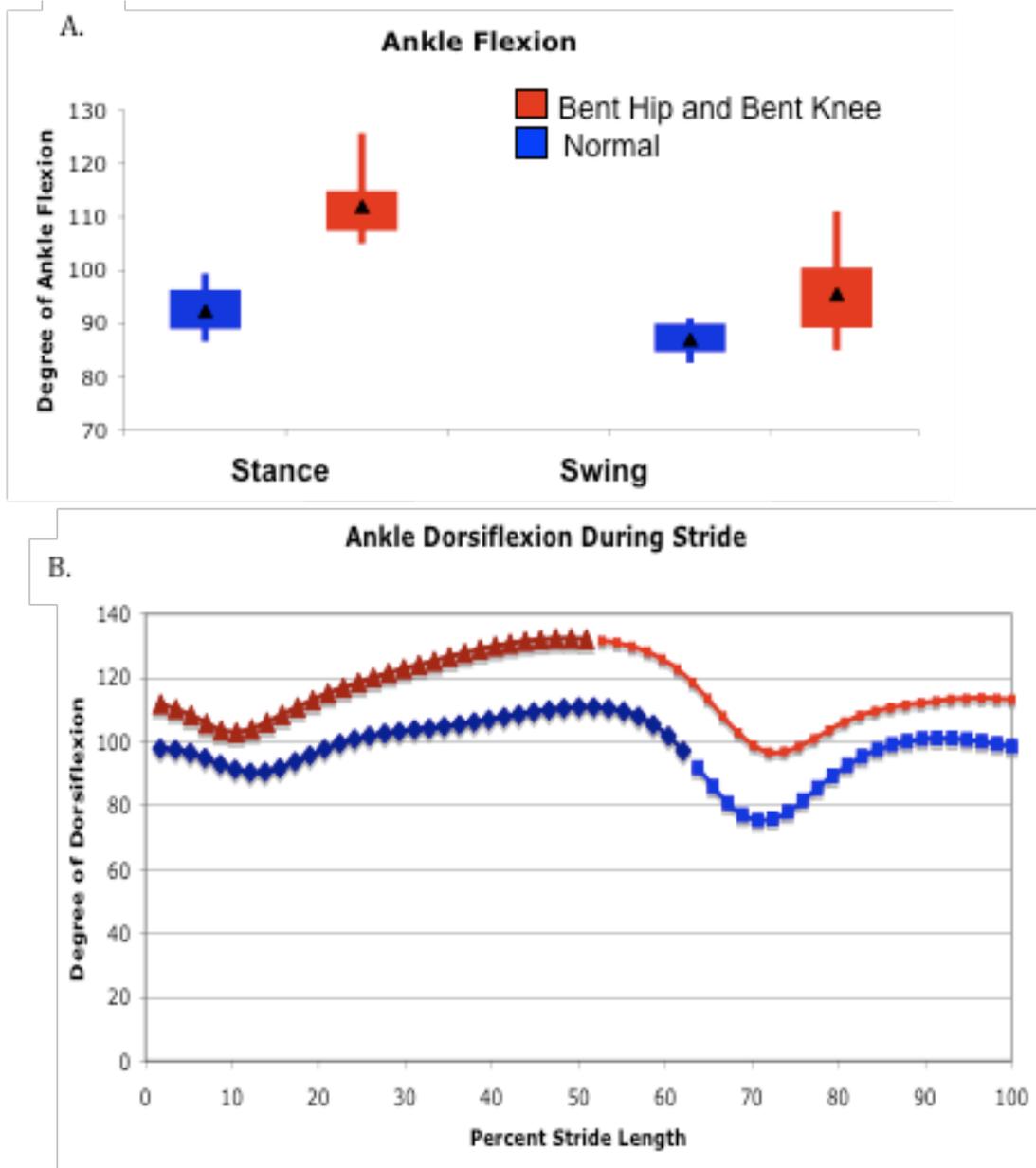
Figure 4: Ankle flexion in normal and bent hip and bent knee trials. A. Distribution of maximum ankle flexion angles for normal and bent hip and bent knee trials during both stance and swing phase. A higher angle value indicates more dorsiflexion. B. Representative trials comparing ankle flexion during normal and bent hip and bent knee. At 90 degrees the foot is neutral and neither dorsiflexed nor plantarflexed. Above 90 degrees is dorsiflexion and below 90 degrees is plantarflexion. The ankle is dorsiflexed more throughout the whole stride in bent hip and bent knee locomotion.

There is a statistically significant difference between hip flexion during both stance and swing phase in the normal and bent hip and bent knee trials (table 1). Figure 5 shows the difference between the two. While walking with a bent hip and bent knee, subjects increased their flexion by an average of 20 degrees during stance phase and 17 degrees during swing phase. Also, figure 4 shows the statistically significant (table 1) difference in hip extension between normal and bent hip and bent knee trials. The normal trials demonstrated much more hip extension with an average of 9 degrees more hip extension than the bent hip and bent knee trials.
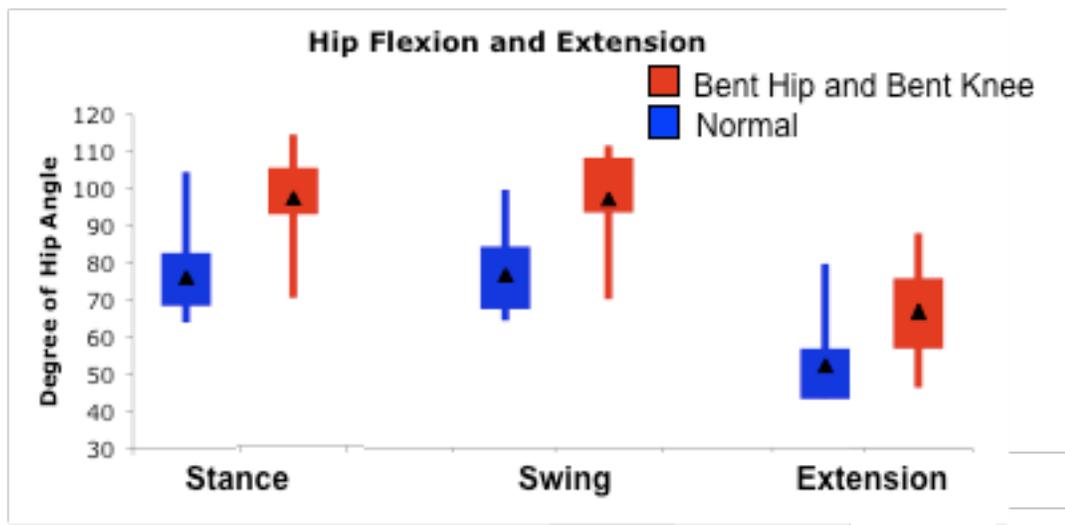

Figure 5: Hip flexion and extension. This graph shows the distribution of maximum and minimum hip angle values. Hip angles were measured as the angle between the anterior superior iliac spine, greater trochanter, and lateral knee. A smaller angle value indicates more hip extension. A larger angle value indicates more hip flexion.

3.2 Energy Exchange

The mean, test statistic for the Wilcoxon's Signed-Rank test, and test statistic for T-test are reported for each variable in table 3. Significant values with a p-value of .05 are indicated with an asterick while bolded values remain significant after the Dunn-Sidak conversion of p-values. The change in kinetic energy, congruence, and percent of

energy recovery are significantly different in the bent hip and bent knee style of walking compared to normal walking. The change in kinetic energy is not significantly different between the two samples.

Table 3: Mean, p-value for the Wilcoxon Sign-Ranked test, and p-value for t-test for energy exchange variables. The significant p-values at p-value of .05 are indicated with an asterisk. The bolded values indicate significant differences between the normal and bent hip and bent knee walking once the p-value is converted using the Dunn-Sidak method. 1. The delta KE variable represents the change in kinetic energy during one full stride from midstance to midstance. 2. The delta PE variable represents the change in potential energy during one full stride from midstance to midstance.

Variable	Normal Walking Mean	Bent Hip and Bent Knee Mean	Wilcoxon Sign-Ranked p-value	T-test p-value
Delta KE[1]	19.747	28.212	**0.0024***	**0.0022***
Delta PE[2]	22.858	17.087	0.0737	0.0870
Congruence	16.361	59.993	**0.0005***	**0.0000***
Percent Recovery	62.701	25.566	**0.0005***	**0.0000***

The change in kinetic energy is an average of 8.5 Kilojoules lower in normal walking than in bent hip and bent knee walking. The kinetic and potential energy curves of bent hip and bent knee walking are an average of 38% more congruent, or having similar slopes than the energy curves of normal walking. The difference in congruence allows for the normal trials to demonstrate an average of 37% more energy recovery during a stride than the bent hip and bent knee trials.

4. Discussion

This study attempts to understand how walking with a bent hip and bent knee gait affects the angles of the lower limb, stride parameters, ground reaction forces, toe clearance, and energy exchange. Changes in these variables and the constraints of the skeletal morphology should be considered when recreating the locomotor behavior of extant bipedal hominins.

4.1 Kinetic and Kinematic Data

The bent hip and bent knee mode of locomotion does not have an effect on most spatiotemporal gait parameters; velocity, stride length, double support time, single support time, and cadence all remain statistically equivalent between the two types of locomotion. Previously, it has been reported that when subjects are asked to walk quickly, subjects are significantly faster while using the bent hip and bent knee mode of locomotion (Daegling and Schmitt 1999). It is probable that this study did not see these differences in speed because we asked participants to walk as they felt comfortable and did not control speed in any way. The bent hip and bent knee style of locomotion is not a hindrance to spatiotemporal stride parameters such as speed and stride length.

There was a significant decrease of 10% of body weight in peak vertical ground reaction forces when walking with a bent hip and bent knee, a value consistent with that reported by Li et al. (1996) and Schmitt (2003). This difference indicates less of a peak load experienced by the body during walking. Upright, striding bipedalism creates a peak ground reaction force much larger than body weight (Alexander and Jayes 1978). The modern human skeleton is able to sustain this peak load with heavily fortified joints in the ankle, knee, and pelvis. The loosely stabilized joints of *Austalopithecus afarensis* and other early hominins may reflect a relatively low peak load compared to full,

upright, striding bipedalism. Walking with a bent hip and bent knee may have been the only mode of locomotion the joints of *Australopitheucs afarensis* would have been able to handle on a daily basis, an argument articulated by Stern and Susman (1983) and Schmitt (2003) and supported by the data here.
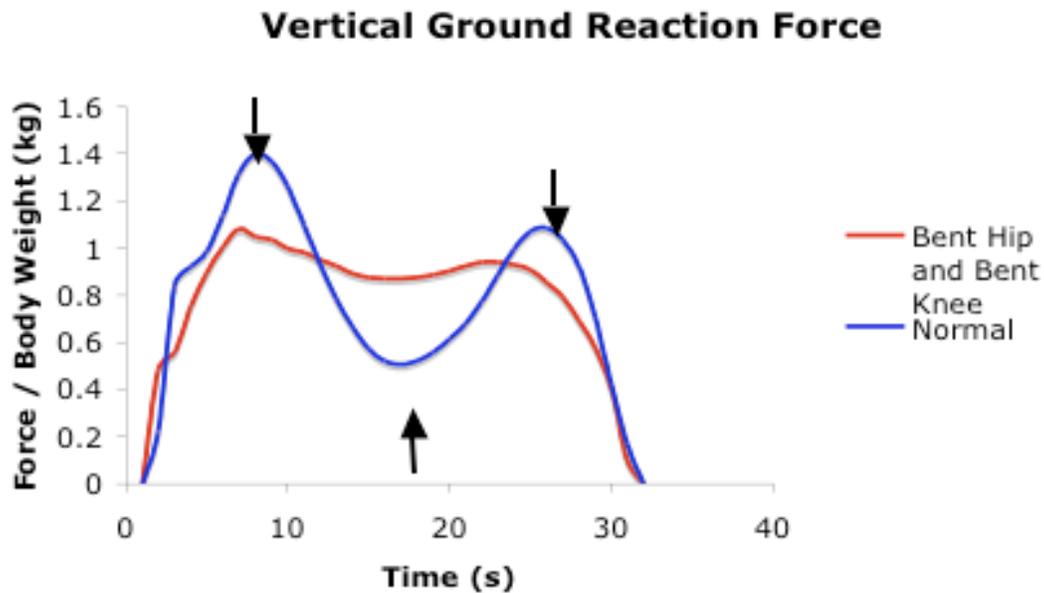
Figure 6: Change in vertical ground reaction force curve. The figure shows a representative vertical ground reaction force trace from subject 4 using the normal and bent hip and bent knee style of bipedalism. The arrows indicate the change from the normal force trace to the bent hip and bent knee force trace. These are the changes predicted in Stern et. al. (2004) with an increased change in the contact point of the foot.

Generally, a decreased peak vertical ground reaction force is attributed to a longer support time (Schmitt 1999; Schmitt 2003), but in this case there is no difference in support time between the two samples. Although, it should be noted that the difference in single support phase closely approaches significance in the t-test comparing normal and bent hip and bent knee means. In 2004, Stern and colleagues suggested an alternative way to decrease the peak vertical ground reaction force by moving the contact point during the stride. The authors created computer models to determine how

different parameters such as limb length, hip rotation, and movement of the contact point affect the vertical ground reaction force curve. They found that when the contact point moved during support phase the vertical ground reaction force maximum lessened and minimum increased. In effect, the vertical ground reaction force curve lost its two distinct peaks and became more of a plateau (Stern et al. 2004). The vertical ground reaction force curves from the subjects walking with a bent hip and bent knee show this pattern (Figure 6). When walking with a bent hip and bent knee, subjects may have moved the point of pressure on their foot more substantially than they do when walking normally to decrease the peak vertical ground reaction force without significantly changing the support time. Moving the center of pressure on the foot during stance phase shifts the ground reaction force vector forward and increases the distance to the limb while walking normally (Carrier et al. 1994; Gruss 2007). This shift is expected to have effects on the moments experienced at the joints. The long feet in *Australopithecus afarensis* would have made it possible to move the point of pressure even more during stance phase, thereby possibly lessening the peak vertical forces even more than is seen in this study and further affecting the joint moments.
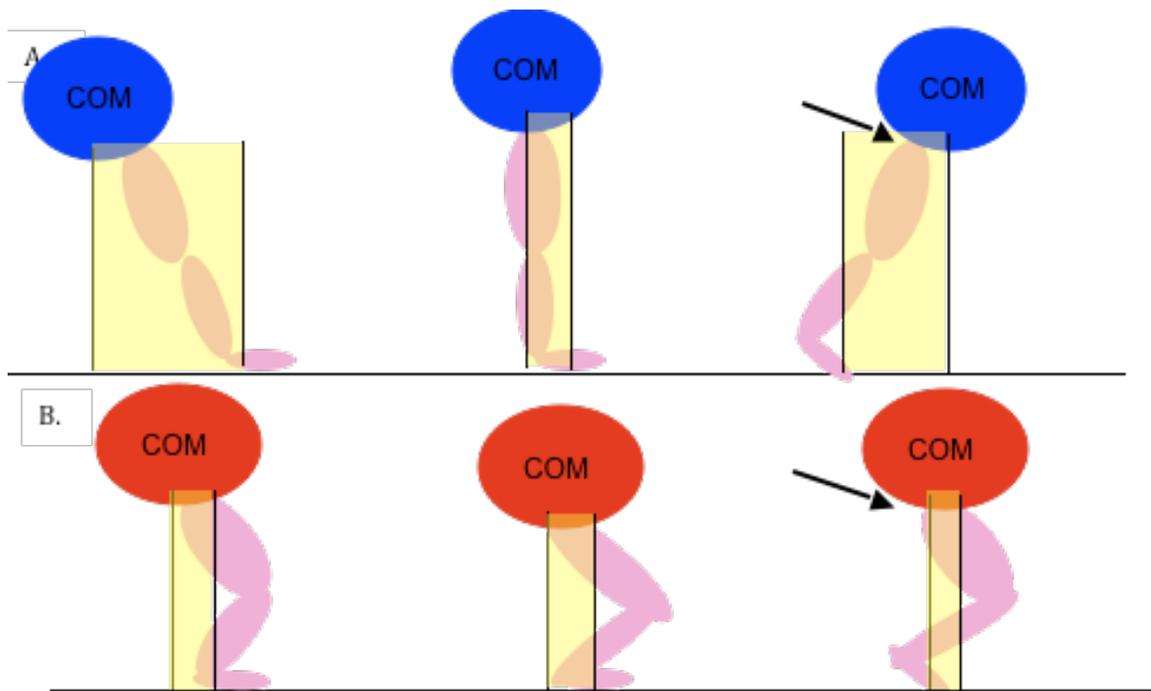
Figure 7: Effect of bipedal style on parallel forces. A. The distance from the point of pressure to the center of mass is highlighted in yellow. The full extension of the lower limb during normal gait, especially during single support, creates a significant distance between the center of pressure on the foot and the center of mass. B. During the bent hip and bent knee style of bipedalism the hip joint stays in a flexed position throughout the stride. The flexion of the lower limbs decreases the distance from the point of pressure on the foot and the center of mass. This decreases the parallel forces experienced while using this type of locomotion.

The fore-aft (braking and propulsive) forces are also significantly different between the bent hip and bent knee and normal trials. These forces decreased an average of 4% of body weight when walking with a bent hip and bent knee. The magnitude of braking and propulsive forces is influenced by the distance of the center of mass from the point of pressure of the foot. When the point of pressure of the foot is very close to the center of mass the force needed to brake or propulse the center of mass is very low. Alternatively, when the point of pressure of the foot is far from the center of mass the braking and propulsive forces required increase substantially. Lower fore-aft forces may indicate the subject is more "balanced" around the center of mass (that is

26

there is a shorter horizontal distance between center of mass, pelvis, and point of contact [figure 7]), and is therefore using a stable form of locomotion that may minimize braking and propulsive forces with each step. *Australopitehcus afarensis* appears to have been walking bipedally while maintaining skeletal adaptations for arboreal locomotion. Full, striding bipedal locomotion as practiced by modern humans requires a strong, reinforced skeleton to handle frequent large forces, while arboreal locomotion requires loose, mobile joints to facilitate a wide range of limb motion. It is possible that the bent hip and bent knee mode of locomotion allowed *Australopithecus afarensis* to move in a stable manner, with the center of mass balanced closer to the center of pressure of the foot while walking. This would decrease the required braking and propulsive forces. Lower fore-aft and vertical forces may have further facilitated bipedal locomotion with a mobile skeletal associated also with arboreal travel.

The ankle moments and ankle moment arms of the two gait styles are not significantly different. Ankle moment arms are defined as a line from the center of rotation (the ankle joint) perpendicular to the ground reaction force vector. The ankle moment arm changes throughout stance phase of the stride with plantarflexion of the foot as it moves from heel strike to toe off (Carrier et al. 1994; Gruss 2007; Stauffer et al. 1977; Stern and Susman 1983). Plantarflexion brings the center of rotation closer to the point of pressure while it moves down the foot, thereby decreasing the distance from the center of rotation to the ground reaction force vector. While walking with a bent hip and bent knee subjects demonstrated much more dorsiflexion at the ankle. Although this did not change the ankle moment arm significantly, the ankle moment arm average is slightly higher when walking bipedally with a bent hip and bent knee because the increased dorsiflexion of the ankle opposes the effect of the plantarflexion during toe off and keeps the center of rotation further from the point of pressure. Even with larger

27

ankle moment arms, the ankle moments stay the same or a little lower in the bent hip and bent knee trials. This is because the ankle moment is defined as the ankle moment arm times the force vector. The lower forces seen while walking with a bent hip and bent knee compensated for the increased ankle moment arm, so that both forms of locomotion have similar ankle moments. Maintaining manageable ankle moments is important, because much larger ankle moments would require stronger plantarflexors to prevent the lower limb from collapsing. Balancing the slightly increased ankle moment arm with the decreased ground reaction forces would be vital to maintain similar ankle moments. It seems that the bent hip and bent knee mode of bipedal locomotion would allow *Australopithecus afarensis* to balance these two variables and keep the ankle moments at manageable levels.

Knee moments were the same when subjects walked with a normal gait and with a bent hip and bent knee gait. As stated earlier, increasing the changes in the point of pressure of the foot will move the force vector further from the center of mass (Carrier et al. 1994; Gruss 2007). When the center of mass is in line with the joints, such as in erect, striding bipedalism, this means that the moments could be increased at each joint as the center of pressure moves away from the center of mass and increases the length of moment arms from joints. This change in the relationship between the ground reaction force vector and the center of rotation was diminished by the plantarflexion of the foot during toe off. It seems that the yielding at the knee during stance phase helps to maintain low moment arms from this joint. Although the point of pressure moves further out during bent hip and bent knee walking, increased knee yield along with lower vertical forces mitigates the effects of this movement and maintains the knee moments at reasonable levels. In fact, walking with upright, striding bipedalism and the long feet of early hominins would increase moment arms at the knee without the

28

compensation of knee yield. Larger knee moments would require more stabilization at the joint, so preserving lower knee moments during bent hip and bent knee walking is consistent with the skeletal anatomy of *Australopithecus afarensis*.

Toe clearance is the same when subjects walk with a bent hip and bent knee and when they walk normally. Although, when walking with a bent hip and bent knee the distribution of toe clearance values had a much lower standard deviation than when walking normally. This may indicate that walking with a bent hip and bent knee comes close to the boundary for the lowest attainable toe clearance while walking bipedally. *Australopithecus afarensis* had particularly long toes, which may have required even more flexion at the ankle, knee, and hip joint to maintain toe clearance. Increased flexion would require additional muscular effort. It is possible that even with these compensatory methods, the long, curved toes of *Austalopithecus afarensis* would have had difficulty clearing the substrate and would have needed to curl their toes to gain adequate toe clearance over the substrate. Increased lower limb flexion and possibly curling the toes are behaviors that would be used in both bent hip and bent knee and upright, striding bipedalism to mitigate the long, curved toes seen in early bipedal hominins. The adjustments to maintain toe clearance while walking with a bent hip and bent knee or while walking with an upright, striding form of bipedalism in *Austalopithecus afarensis* would require more muscular effort to maintain. Although, this is a potential energetic cost of bent hip and bent knee locomotion, it would be an energetic cost added to upright, striding locomotion as well. It is possible that relatively short feet and toes seen in modern humans allow for efficient clearance of the substrate while walking bipedally.

When subjects walked with a bent hip and bent knee they showed increased flexion at the hip and knee when compared to walking normally. This is consistent with

previous studies (Schmitt 2003). Subjects who walked with a bent hip and bent knee gait also have more dorsiflexion at the ankle during both stance and swing phase than subjects who walked normally. More muscular effort may be required to maintain the deep dorsiflexion of the ankle throughout the stride than for normal walking. During stance phase, more muscular effort would be needed to maintain stability in the ankle when it is bearing body weight in a deeply flexed position as in bent hip and bent knee walking. This problem is exacerbated for apes and early humans that had highly mobile ankle joints (Stern and Susman 1983). Similarly, swing phase might also involve increased muscular effort that would require more energy to maintain a dorsiflexed ankle in order for the toe to clear the substrate. Maintaining increased dorsiflexion of the ankle is an obvious area of energetic expenditure seen while walking with a bent hip and bent knee mode of bipedal locomotion; upright, striding locomotion avoids this energetic cost.
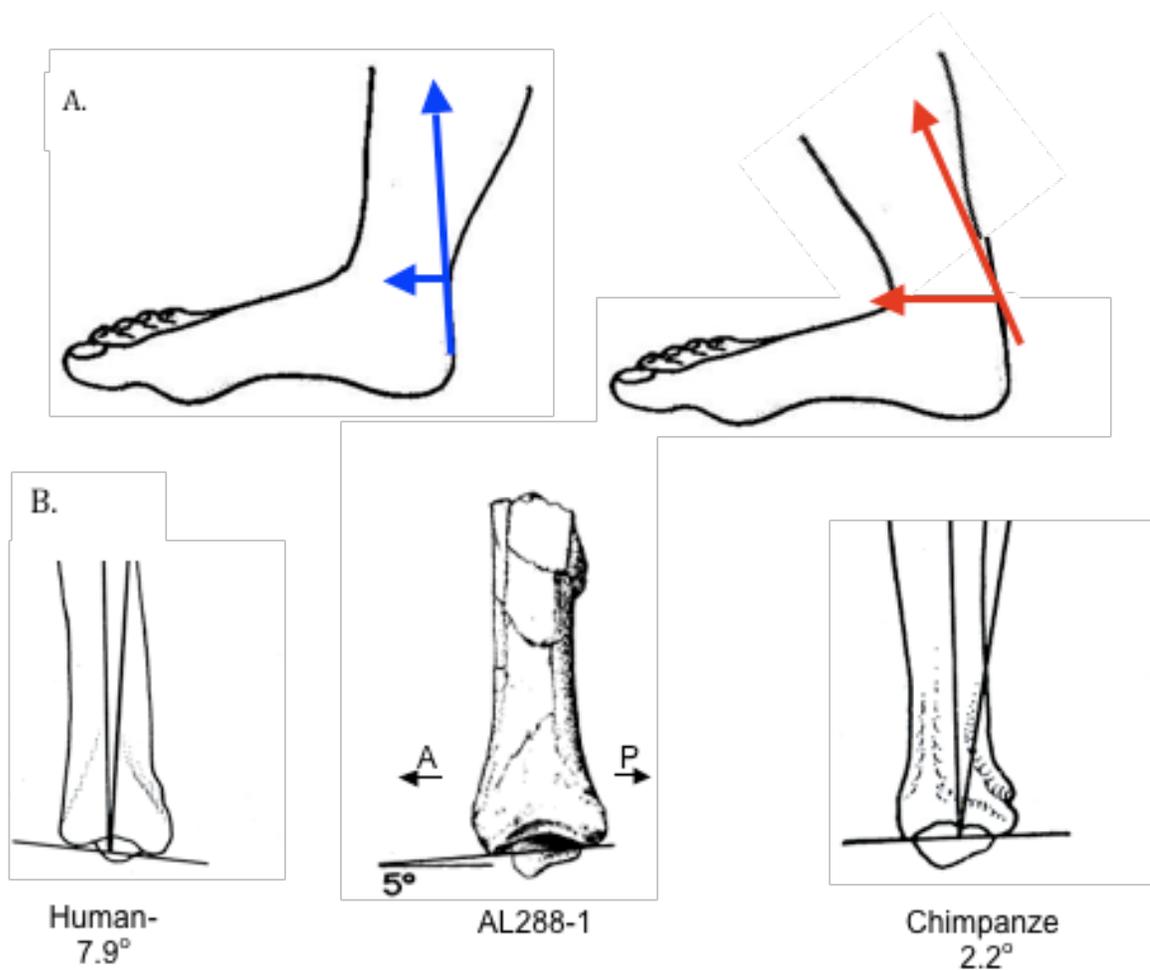
Figure 8: Demonstration of shear force on tibiotalar joint. A. Increased dorsiflexion at the ankle increases the anteriorly directed shear force at the tibiotalar joint. Changing the direction of the Achille's tendon force vector increases the anteriorly directed portion of the Achille's tendon force vector. This vector is translated onto the tibiotalar joint. B. Anteriorly tilted talar surface of the tibia in AL288-1 (from Stern and Susman, 1983). This is similar to the chimpanzee distal tibia and opposite form the human distal tibia. Two other *Australopithecus afarensis* show the opposite orientation of this one and are oriented as the human distal tibia.

A deeply dorsiflexed ankle could also have an impact on the skeletal anatomy of early hominins. Increasing dorsiflexion at the ankle increases the anteriorly directed shear force at the tibiotalar joint (figure 8). The Achilles tendon force vector is the major force vector on the posterior of the tibiotalar joint (Stauffer et al. 1977). This force vector keeps the tibia from collapsing on the foot during stance phase. When the tibia is

31

directed more anteriorly and the foot is dorsiflexed as it is in bent hip and bent knee

locomotion the horizontal component of the Achilles tendon force vector increases. The

horizontal component can be translated onto the tibiotalar joint (Stauffer et al. 1977;

Stern and Susman 1983). Therefore, dorsiflexion of the foot increases the anteriorly

directed shear force at the tibiotalar joint. Increased shear at the tibiotalar joint would

need to be resisted by skeletal or cartilaginous features that strengthen the joint. The

anatomy of the tibiotalar joint in early hominins is not clear in this point. Stern and

Susman (1983) report an anteriorly inclined tibia in the AL288-1 (similar to that seen in

chimpanzees) but a posteriorly inclined tibia in AL333-6 and AL333-7 (similar to

humans). All three of these distal tibias belong to *Australopithecus afarensis*. It is possible

that the specimen that demonstrate posteriorly inclined tibias had other means of

resisting the anteriorly directed shear force such as strong anterior tibial tendons. If

early hominins walked with a bent hip and bent knee the anteriorly directed shear forces

would have been larger and there would need to be some resistant force in place to

prevent collapse of the tibia.

Lastly, subjects using the bent hip and bent knee style of locomotion

demonstrated significantly less hip extension than subjects walking normally. While

keeping the hip bent, subjects would not move their thigh as far backwards during toe

off as they do when they walk normally. With increased flexion at the knees and ankle,

decreased extension at the hip during toe off would be necessary to maintain low fore-

aft forces while walking with a bent hip and bent knee (Figure 6). Because our subjects

showed lower fore-aft forces during bent hip and knee locomotion, it is predicted that

they would also show less hip extension. Less extension at the hip joint during bent hip

and bent knee locomotion is consistent with predictions made from the *Australopithecus*

afarensis fossils. These fossils have a diminished anterior horn of the acetabulum, which

may have allowed for increased flexion and less extension at the hip joint. Decreasing the hip extension while walking with a bent hip and bent knee keeps the center of mass balanced over the point of pressure and further decreases the fore-aft forces.

4.2 Energy Exchange

With each step of normal, upright, striding bipedalism potential energy is created as the center of mass lifts leading into midstance. This potential energy is then converted into kinetic energy as the center of mass falls leading to toe off (Cavagna et al. 1976). The amount of energy recovery possible is determined by the change in potential and kinetic energy during the stride and the phase relationship of the two curves (Bishop et al. 2008). The change in kinetic energy was significantly different between the two gait types, while the change in potential energy showed no difference. When these potential and kinetic energy oscillations were compared the average congruence for bent hip and bent knee walking was 59.9. This is significantly different than the average congruence for upright, striding biepdalism, which was 16.3. Less congruence allows for more energy recovery. Our normal walking trials showed an averaged percent energy recovery of 62.7, which is consistent with previously reported results (Cavagna et al. 1976). The bent hip and bent knee trials had an average percent energy recovery of 25.5. This is significantly lower and indicates that while using the bent hip and bent knee style of locomotion there is little ability to recover potential energy to be used for kinetic energy. Because the bent hip and bent knee style of locomotion cannot exchange energy efficiently, muscular effort would be recruited to move the center of mass forward. This is a potential area of cost in bent hip and bent knee locomotion.

4.3 A Broader Prospective of the Evolution of Bipedalism

The data obtained in this study about bent hip and bent knee bipedal locomotion can be used to gain a full understanding of the evolution of the upright, striding form of bipedalism of modern humans. Bipedalism is an inherently unstable form of locomotion; balancing the body on two limbs instead of four provides less support and more balance issues for the animal. The animal must obtain behavioral and skeletal adaptations that allow it to move on two limbs without increasing their fore-aft or mediolateral forces too much and compromising their balance. Many animals demonstrate bipedal locomotion such as birds, kangaroos, and sometimes apes, but none of these animals are able to maintain an erect posture and straighten the knee at mid-stance to the degree found in humans (Alexander 2004). In birds that walk and run bipedallly there is deep flexion at the hip and knee throughout the stride (Gatesy and Biewener 1991). Kangaroos that bipedally hop also display a deeply flexed hip and knee. This flexion helps to balance the center of mass on a larger, more stable base. Most of a bipedal animal's mass is placed anteriorly in the thorax and abdomen. A large base assists in balancing the anterior and posterior masses on two limbs. In addition to increased flexion at the joints, all other habitually bipedal animals have tails, which serve to further balance the large anterior masses and the posterior mass on two limbs. The adaptations that increase balance help to reduce the fore-aft forces. If these forces were to become to high an animal would topple forward during single support phase, unable to create a breaking force that would stop the large, natural movement of the anterior mass forward and downward.

The erect, striding bipedalism of modern humans seems to break all the rules. The limb is relatively stiff and straight throughout the stride, providing a small, unstable base, and there is no tail to help balance the anterior forces. The anatomy of modern humans is transformed to bring the anterior and posterior masses very close to the

34

center of mass. Instead of creating a large base support, modern humans appear instead to bring mass closer to the center. Spinal curvature is one way this is accomplished. The lordosis of the cervical and lumbar portions of the spine counteract the kyphosis in the thoracic spine and help to bring the mass of the head, thorax, and abdomen more in line with the strong, reinforced pelvis. This helps to reduce mass that is placed purely anteriorly. In addition to bringing the anterior mass closer to the center, humans increase their posterior mass with a large gluteal region. Humans have a realtively large gluteus maximus that is pushed further posterior by the curvature of the sacrum (Bramble and Lieberman 2004; Sigmon and Farlow 1986 ; Stern and Susman 1983). The gluteal area that lies on the posterior surface of the pelvic bones is very muscular and oftentimes very fatty. The additional mass on the posterior surface of the pelvic bones form the gluteus maximus and associated fat creates more posterior mass and helps to balance the anterior mass. Modern humans are unique in their ability to use an upright, striding form of bipedalism because they bring the anterior mass close to the center with spinal curvature and create posterior mass with the gluteal region.
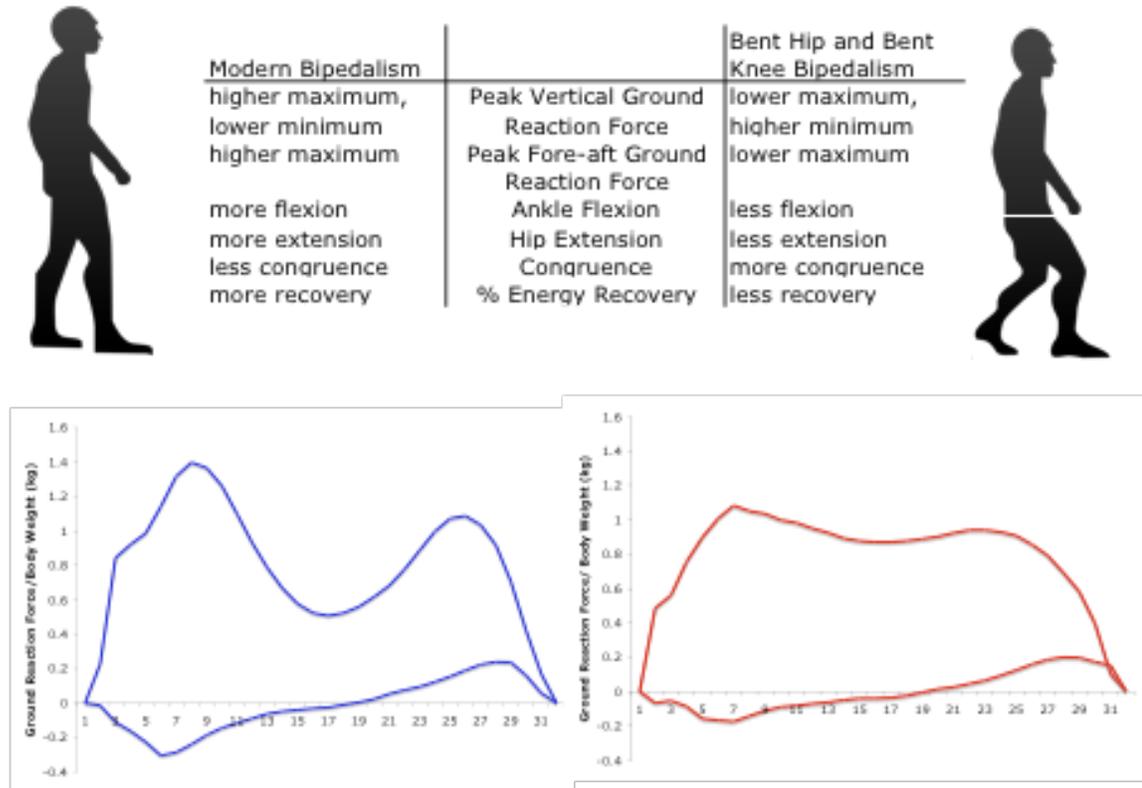
Applying these ideas about minimizing the fore-aft forces is revealing when considering the conception of obligate bipedalism. To maintain an erect, striding form of bipedalism hominins would need the ability to balance the anterior and posterior forces of the body on the pelvis. This problem would be exacerbated in early hominins because of their large, barrel-like chests adding anterior mass. To keep the fore-aft forces at a manageable level and to prevent toppling forward during single support, hominins would require lordosis in the cervical and lumbar vertebrae along with a massive, posteriorly positioned gluteal region. The sacrum of *Australopithecus afarensis* is very flat (Stern and Susman 1983), therefore negating its ability to position mass more posteriorly. It is possible that *Australopithecus afarensis* and other early bipedal hominins

35

still had massive gluteal regions, but this is difficult to determine given only fragmented fossil evidence. If early bipedal hominis did not have significant lordosis or some way to increase posterior mass, they would not have been able to use an erect form of bipedalism. If this is the case, bent hip and bent knee bipedalism would be the only option that would provide the needed stability and decrease the fore-aft forces. Although bent hip and bent knee bipedalism has many costs associated with it, it may be the only bipedal option available to an animal without the specialized anatomy of modern humans.

4.4 Conclusions

The many changes seen when subjects walk with a bent hip and bent knee gait are summarized in Figure 9. This type of locomotion lowers both the vertical and fore-aft forces experienced. Lowering the peak vertical force is attributed not to increasing the support time, but to increasing the changes in the point of pressure. While using bent hip and bent knee locomotion, the subjects move the point of pressure in the foot during stance phase slowly and fully, which allows for decreased peak pressures. Less hip extension seen while walking with a bent hip and bent knee decreases the fore-aft forces experienced by maintaining the center of mass balanced closely over the point of pressure of the foot. The lower forces seen with bent hip and bent knee locomotion help to mitigate the increased moment arms predicted with the *Australopithecus afarensis* skeleton and maintain equal ankle and knee moments. The compensatory methods required to clear the substrate would be required from both bent hip and bent knee and normal bipedal locomotion. A potential area of large energetic costs in bent hip and bent knee locomotion is the increased dorsiflexion throughout the stride. The loosely stabilized joints seen in early bipedal hominins exacerbate these costs. An additional

area of cost in bent hip and bent knee locomotion is the inability to exchange potential and kinetic energy efficiently.

	Modern Bipedalism		Bent Hip and Bent Knee Bipedalism
	higher maximum, lower minimum	Peak Vertical Ground Reaction Force	lower maximum, higher minimum
	higher maximum	Peak Fore-aft Ground Reaction Force	lower maximum
	more flexion	Ankle Flexion	less flexion
	more extension	Hip Extension	less extension
	less congruence	Congruence	more congruence
	more recovery	% Energy Recovery	less recovery

Figure 9: Summary of differences in normal and bent hip and bent knee style gaits.

Several aspects of early hominin morphology may be interpreted as strong indicators of arboreal locomotion such as long arms, loosely stabilized joints, and long, curved phalanges. Whether these arboreal characteristics were actually used for arboreal locomotion is irrelevant; they are present in the skeleton and would have affects on the mode of terrestrial locomotion used. The bent hip and bent knee style of bipedalism would 1.) lessen the forces on the body which is beneficial for a skeleton with loosely stabilized joints, 2.) lessen hip extension, which is consistent with acetabular anatomy, and 3.) increase changes in point of pressure of the foot, which

amplifies the benefits of decreased forces on the joints. Contrarily, the bent hip and bent knee style of locomotion maintains increased dorsiflexion throughout the stride which may require more muscular effort and therefore more energy to maintain while using bent hip and bent knee locomotion. Also, the muscular effort required to create kinetic energy during movement is very costly. The costs and benefits of this type of locomotion should be considered in the context of the skeletal adaptations and behavioral requirements of early bipedal hominins.

The costs and benefits of bent hip and bent knee locomotion cannot simply be compared to determine if this was a likely mode of locomotion for early hominins. Each species has a unique set of environmental factors that play a role their ultimate behavior. The cost of increased energy requirements and benefits of compatibility with a skeleton that has arboreal characteristics seen in bent hip and bent knee locomotion should be considered when reconstructing the locomotor behavior of extinct hominin ancestors. It is possible that although bent hip and bent knee locomotion is not the most efficient mode of locomotion, it was the best that could be done with a morphology that contained remnants of arboreal locomotion.

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