



## Muscle force production during bent-knee, bent-hip walking in humans



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### ABSTRACT

Researchers have long debated the locomotor posture used by the earliest bipeds. While many agree that by 3–4 Ma (millions of years ago), hominins walked with an extended-limb human style of bipedalism, researchers are still divided over whether the earliest bipeds walked like modern humans, or walked with a more bent-knee, bent-hip (BKBH) ape-like form of locomotion. Since more flexed postures are associated with higher energy costs, reconstructing early bipedal mechanics has implications for the selection pressures that led to upright walking. The purpose of this study is to determine how modern human anatomy functions in BKBH walking to clarify the links between morphology and energy costs in different mechanical regimes. Using inverse dynamics, we calculated muscle force production at the major limb joints in humans walking in two modes, both with extended limbs and BKBH. We found that in BKBH walking, humans must produce large muscle forces at the knee to support body weight, leading to higher estimated energy costs. However, muscle forces at the hip remained similar in BKBH and extended limb walking, suggesting that anatomical adaptations for hip extension in humans do not necessarily diminish the effective mechanical advantage at the hip in more flexed postures. We conclude that the key adaptations for economical walking, regardless of joint posture, seem to center on maintaining low muscle forces at the hip, primarily by keeping low external moments at the hip. We explore the implications of these results for interpreting locomotor energetics in early hominins, including australopithecines and *Ardipithecus ramidus*.

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### Introduction

The selection pressures that led to the origins of upright bipedalism, a hallmark trait of the human lineage, remain a point of major debate among paleoanthropologists (e.g., Stern and Susman, 1983; Susman et al., 1984; Wheeler, 1991; Hunt, 1996; Lovejoy et al., 1999; Stern, 2000; Richmond et al., 2001; Ward, 2002; Thorpe et al., 2007; Crompton et al., 2008; Lovejoy et al., 2009a, b). One model for the evolution of bipedalism suggests that hominins shifted to walking upright to reduce the energy cost of locomotion compared with a chimpanzee-like quadrupedal ancestor (e.g., Rodman and McHenry, 1980; Sockol et al., 2007). This model is supported by evidence that humans, and early hominins such as australopithecines, have morphological adaptations for walking on an extended hind limb, which reduce the energy cost of locomotion compared

with chimpanzees walking both quadrupedally and bipedally (Sockol et al., 2007; Pontzer et al., 2009). Others have suggested that early hominins walked bipedally in a way that involved more flexed hips and knees (bent-hip, bent-knee or BKBH), which likely leads to higher energy costs, but may still have offered an energetic advantage compared with chimpanzee-like locomotion (e.g., Stern and Susman, 1983; Susman et al., 1984; Stern, 1999, 2000).

While recent work on the Laetoli footprints supports the hypothesis that extended limb bipedalism had evolved by 3.6 Ma (millions of years ago) (Raichlen et al., 2010; Crompton et al., 2012), the form of bipedalism used by the earliest hominins remains unclear (e.g., Richmond et al., 2001; Thorpe et al., 2007; Lovejoy et al., 2009b). Reconstructing locomotion in early hominins is complicated because we do not fully understand how anatomical traits in humans and earlier bipeds function under different locomotor regimes, and it is therefore difficult to determine the adaptive value of specific morphologies. For example, Carey and Crompton (2005) demonstrated that when humans adopt chimpanzee-like limb joint angles (i.e., BKBH bipedalism), their energy costs remain lower than

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chimpanzees walking bipedally, even though energy costs are higher than in normal human walking (see Sockol et al., 2007). This is in some ways an unexpected result, since one might predict that human anatomy is not well suited for locomotion in more ape-like postures, and could therefore lead to higher energy costs than those of apes. To better understand how bipedal anatomy evolved, and to identify the key features that led to the evolution of lower energy costs in our ancestors, it is essential to develop a more complete understanding of how human anatomy performs in different locomotor postures. The purpose of this study is to use our current understanding of the biomechanical determinants of energy costs to explore how human anatomy functions during BKBH walking.

### Linking anatomy to cost

Previous work has shown that locomotor costs are well explained by the amount and rate of muscle volume activated to support the body against the force of gravity (e.g., Kram and Taylor, 1990; Taylor, 1994; Roberts et al., 1998a, b; Griffin et al., 2003; Biewener et al., 2004; Pontzer, 2005, 2007; Sockol et al., 2007; Pontzer et al., 2009; Weyand et al., 2010). Thus, an experimental approach using inverse dynamics (estimating muscle forces from kinematic, kinetic, and anatomical data) can help us determine how morphology impacts the energetic cost of locomotion (COL; kCal/s). During walking, hind limb joints experience a moment equal to the product of the ground reaction force (the force exerted by the ground; GRF) and the moment arm of the GRF (the perpendicular distance from the GRF vector to the joint center; i.e.,  $\text{moment}_{\text{ext}} = \text{GRF} \times \text{moment arm}_{\text{GRF}}$ ), combined with inertial and gravitational moments due to segmental accelerations. In general, the effects of segment accelerations on these moments are small relative to the effects of the GRF at walking speeds (Biewener et al., 2004). Extensor muscles must resist this flexion moment by producing an opposing moment that is equal in magnitude and opposite in direction to the external moment acting on the joint ( $\text{moment}_{\text{muscle}} = \text{muscle force} \times \text{moment arm}_{\text{muscle}}$ ) (Kram and Taylor, 1990; Roberts et al., 1998a, b; Pontzer et al., 2009). Producing muscle force requires the recruitment and activation of muscle, which ultimately costs metabolic energy (Kram and Taylor, 1990).

Since inertial and gravitational moments are small relative to the moment of the GRF, the amount of muscle force produced, and therefore energy expended, to resist external moments during walking is determined mostly by three main factors: 1) the magnitude of the GRF, 2) the length of the GRF moment arm, and 3) the length of the extensor muscle moment arms that must resist the external moment. First, the magnitude of the GRF is affected by the amount of time the foot is on the ground in stance phase (contact time). All else being equal, the shorter the contact time, the greater the magnitude of the GRF, and therefore the greater the magnitude of the external moment acting on a joint (Kram and Taylor, 1990; Pontzer, 2005, 2007). Second, the length of the GRF moment arm is determined, in large part, by the orientation of the GRF vector and its distance from hind limb joint centers (e.g., Biewener et al., 2004). For example, during extended limb walking, the GRF vector passes close to the knee and hip joint centers, leading to shorter moment arms and thus smaller external moments compared with walking with flexed limbs (Kram and Taylor, 1990; Roberts et al., 1998a, b; Sockol et al., 2007; Pontzer et al., 2009). Finally, the length of the moment arm for the muscle(s) that must resist the external moment will determine how much muscle force is required to support the body. For any given combination of GRF magnitude and GRF moment arm at a given joint, a larger extensor muscle moment arm will allow an individual to resist an external moment with lower amounts of muscle force.

This relationship between the muscle moment arm and the amount of muscle force required to resist external moments is a key element linking anatomy to cost. Walking in ways that increase external moments (e.g., on more flexed hind limb joints) will necessarily lead to higher energy costs because muscles produce more force by recruiting larger amounts of muscle volume, and the energy costs of muscle activity are correlated with the amount of muscle volume activated (e.g., Kram and Taylor, 1990; Roberts et al., 1998a, b; Pontzer, 2005, 2007; Pontzer et al., 2009). However, over evolutionary time, selection can alter skeletal anatomy to increase muscle moment arms, effectively reducing muscle forces required to support the body against external moments in a given posture.

An important example of this type of selection acting on the human skeleton is the human ischium. Previous work has linked the low energy costs of human walking to the relatively low muscle forces produced at the hip joint to resist external moments. In humans, and earlier hominins such as the australopithecines, a dorsally oriented ischial tuberosity maintains large muscle moment arms in extended-limb postures, allowing for full hip extension, and therefore small external moments from the GRF, during bipedal walking (Robinson, 1972; Sockol et al., 2007; Pontzer et al., 2009). This configuration differs from apes, where the ischial tuberosity is oriented caudally, increasing the extensor muscle moment arm when the hip is in highly flexed postures (such as climbing), but decreasing the extensor muscle moment arm when the hip is in an extended posture. The ape ischial orientation acts as a constraint on their ability to walk on extended hind limbs, since their muscles cannot generate extensor moments in these limb postures (Sockol et al., 2007). Thus, previous work suggests that the human ischium is an adaptation for reducing energy costs in extended-limb walking (Robinson, 1972; Fleagle and Anapol, 1992; Sockol et al., 2007), and the ape-ischium is an adaptation for extensor moment production in the more flexed hip postures experienced during vertical climbing (e.g., Isler, 2005).

While these types of adaptive explanations are plausible, they are generally based on comparative biomechanical studies (e.g., Sockol et al., 2007). Here, we use an experimental alteration of walking mechanics to examine how human anatomy performs using different limb postures (i.e., flexed limb walking versus extended limb walking). These data are compared to biomechanical data collected in a previous study of chimpanzee locomotion (Sockol et al., 2007) to provide insight into how selection has acted on human anatomy to generate low energy cost extended limb bipedalism. We hypothesize that human anatomical adaptations to extended limb bipedalism, such as the dorsally oriented ischial tuberosity, will lead to higher muscle forces in more flexed limb postures, contributing to the higher energy costs of BKBH walking (see Carey and Crompton, 2005).

### Methods

To test how human anatomy performs during BKBH bipedalism, we collected kinetic and kinematic data from eight recreationally fit adult humans and utilized previously collected chimpanzee kinematic and kinetic data from Sockol et al. (2007). The human sample consisted of five females and three males between the ages of 24 and 30 (mean body mass [S.D.] =  $66.3 \pm 11.8$  kg). Institutional Review Board approval was obtained by The University of Arizona prior to the study and subjects gave informed consent prior to their participation.

Subjects walked barefoot across a trackway at self-determined slow, preferred, and fast speeds under two experimental conditions: 1) extended-limb bipedal walking, and 2) BKBH posture using a hip angle of  $\sim 130^\circ$  and knee angle of  $\sim 150^\circ$  (following Carey and Crompton, 2005). A goniometer was used to find a posture with

the appropriate degree of flexion for each subject and a visual guide was constructed to ensure that each subject maintained the appropriate joint angles throughout each trial. The guide consisted of a string that ran along the trackway, parallel to the floor, and was set at shoulder level when each subject was at  $\sim 130^\circ$  of hip flexion and  $\sim 150^\circ$  of knee flexion. Subject speeds were standardized using Froude numbers [ $\text{velocity}^2/(\text{gravitational acceleration} \times \text{limb length})$ ] (Alexander and Jayes, 1983). Here, we calculate limb length as the distance from the hip to the ground while standing for extended-limb and at midstance for BKBH walking (i.e., effective limb length; see Pontzer, 2005, 2007).

Kinetic data were collected using a force-plate (AMTI, Watertown, MA) embedded in a 4 m trackway recording at 4 kHz. Kinematic data were recorded using a 6-camera motion capture system (Vicon, Los Angeles, CA) capturing at 200 Hz with reflective markers fixed to hind limb joint centers. Kinetic and kinematic data were processed using custom-designed software in MATLAB (MathWorks, Natick, MA). A zero-lag Butterworth, low-pass filter was used to smooth kinematic (fourth-order filter with a 6 Hz cutoff) and kinetic (ninth-order with a 100 Hz cutoff) data (Winter, 2004).

An inverse dynamics approach was used to estimate muscle force production to determine how anatomy and posture interact to generate energy costs (Kram and Taylor, 1990; Taylor, 1994; Roberts et al., 1998a, b). This method assumes that the metabolic COL is equal to the rate at which muscle volume is activated to support body weight (Taylor et al., 1980; Kram and Taylor, 1990; Taylor, 1994; Roberts et al., 1998a, b; Pontzer, 2005, 2007; Sockol et al., 2007):

$$\dot{E}_{\text{metab}} = (V_{\text{muscle}}/t_c)k \quad (1)$$

where  $\dot{E}_{\text{metab}}$  ( $\text{J N}^{-1} \text{ s}^{-1}$ ) is estimated metabolic cost,  $V_{\text{muscle}}$  ( $\text{cm}^3 \text{ N}^{-1}$ ) is the mass-specific volume of muscle activated over a single step,  $t_c$  ( $\text{s}^{-1}$ ) is the duration that the foot is on the ground,  $k$  ( $\text{J cm}^{-3}$ ) is a constant that describes the rate at which a unit volume of muscle uses energy (Roberts et al., 1998a, b), and  $g$  is gravitational acceleration. This method described by Eq. (1) results in an estimation of net metabolic COL (after subtracting resting metabolic rate). The value of  $k$  is assumed to be constant across species (Roberts et al., 1998b), and is constant in humans at walking speeds between 0.5 and 1.5 m/s (Griffin et al., 2003). While  $k$  may differ between extended limb and BKBH walking, for the purpose of this study, we assume  $k$  is also constant across locomotor modes in humans. The impact of this assumption was tested by comparing the difference in  $V_{\text{muscle}}/t_c$  between locomotor modes with the difference in COL ( $\dot{E}_{\text{metab}}$  measured by respirometry) between locomotor modes in Carey and Crompton (2005). If the proportional difference in  $V_{\text{muscle}}/t_c$  between locomotor modes is similar to the measured difference in  $\dot{E}_{\text{metab}}$ , then the assumption that  $k$  is similar across locomotor modes is supported (see eq. (1)).

The amount of muscle volume ( $V_{\text{muscle}}$ ) activated over a step was calculated following methods reported in detail by Sockol et al. (2007). Briefly, for a given muscle group (i.e., hip, knee, and ankle extensors),  $V_{\text{muscle}}$  is the product of muscle fascicle length ( $l_{\text{fasc}}$ ) and the active cross sectional area of the muscle ( $A$ ) (see Sockol et al., 2007; Pontzer et al., 2009). We used mean  $l_{\text{fasc}}$  for a given muscle group scaled to subject body mass from the literature (Biewener et al., 2004).  $A$  is the product of the extensor muscle force ( $F_{\text{muscle}}$ ) required to counter flexing moments at each hind limb joint, and  $\sigma$ , a constant relating muscle force to muscle cross-sectional area, typically  $20 \text{ N/cm}^2$  for all species (Biewener et al., 2004).  $F_{\text{muscle}}$  was found by estimating the net joint moments resisted by a given extensor muscle group. The net joint moments were calculated using the combination of the ground

reaction force (GRF) vector, limb segment accelerations, and the flexor moments generated by two-joint muscles following Biewener et al. (2004) and Winter (2004). Extensor muscles at each joint were chosen following Biewener et al. (2004). Weighted mean muscle fascicle lengths for each extensor muscle group were taken from Biewener et al. (2004) and were scaled to body masses of each subject in our study. Segment accelerations were calculated using the second-order finite differences method (Winter, 2004). Net moments,  $M$ , were determined for each kinematic frame at each joint using the free-body method described in Winter (2004), and segment inertial properties were estimated from equations in Winter (2004). Extensor muscle forces ( $F_{\text{ankle}}$ ,  $F_{\text{knee}}$ , and  $F_{\text{hip}}$ ) to generate these moments were determined by solving the system of equations given in Biewener et al. (2004):

$$M_{\text{ankle}} = F_{\text{ankle}}r_{\text{ankle}} \quad (2)$$

$$M_{\text{knee}} = F_{\text{knee}}r_{\text{knee}} - F_{\text{G,knee}}r_{\text{G,knee}} - F_{\text{H,knee}}r_{\text{H,knee}} \quad (3)$$

$$M_{\text{hip}} = F_{\text{hip}}r_{\text{hip}} - F_{\text{RF,hip}}r_{\text{RF,hip}} \quad (4)$$

where the bi-articular muscles are gastrocnemius (G), hamstrings (H), and rectus femoris (RF). Human extensor muscle moment arms ( $r_{\text{ankle}}$ ,  $r_{\text{knee}}$ , and  $r_{\text{hip}}$ ) were calculated using equations that relate moment arms to joint angle from the literature for the hamstrings, quadriceps, and gastrocnemius (Rugg et al., 1990; Visser et al., 1990). Moment arms were scaled to each subject by body mass (hip and knee) or segment length (ankle). These values provide an estimation of extensor muscle moment arms as they change with joint angle, better reflecting muscle performance during locomotion. Chimpanzee extensor moment arms were assumed to be constant across a normal range of flexion (see Thorpe et al., 1999). Flexor moments generated by two-joint muscles (gastrocnemius and hamstrings) were calculated assuming the force produced by each muscle in an extensor group is proportional to its physiological cross sectional area (PCSA; Biewener et al., 2004) and using moment arms for these muscles,  $r$ , scaled to body mass, taken from Biewener et al. (2004). Following Biewener et al. (2004), muscle force impulses were divided by GRF impulses, and these values were used to determine total limb  $V_{\text{muscle}}$  as follows:

$$V_{\text{muscle}} = 1/\sigma \left( \frac{l_{\text{fasc,hip}} \int F_{\text{hip}}}{\int \text{GRF}} + \frac{l_{\text{fasc,knee}} \int F_{\text{knee}}}{\int \text{GRF}} + \frac{l_{\text{fasc,ankle}} \int F_{\text{ankle}}}{\int \text{GRF}} \right) \quad (5)$$

As outlined above,  $V_{\text{muscle}}$  has units  $\text{cm}^3 \text{ N}^{-1}$  and is the volume of muscle required to produce 1 N of ground force. Note that  $(\int F_{\text{muscle}}/\int \text{GRF})$  is equal to the inverse of the effective mechanical advantage for a given joint, since  $R/r = \int F_{\text{muscle}}/\int \text{GRF}$ ; we used the convention  $l_{\text{fasc}}/\text{EMA}$  in a previous analysis (see Eq. (2) in Pontzer et al., 2009). This method also accounts for segmental and gravitational acceleration, which is especially important for determining the correct moments at proximal joints, particularly at the hip (Biewener et al., 2004; Winter, 2004). All statistical comparisons between BKBH and normal walking using the variables outlined above were made using a two-tailed, paired Student's  $t$ -test.

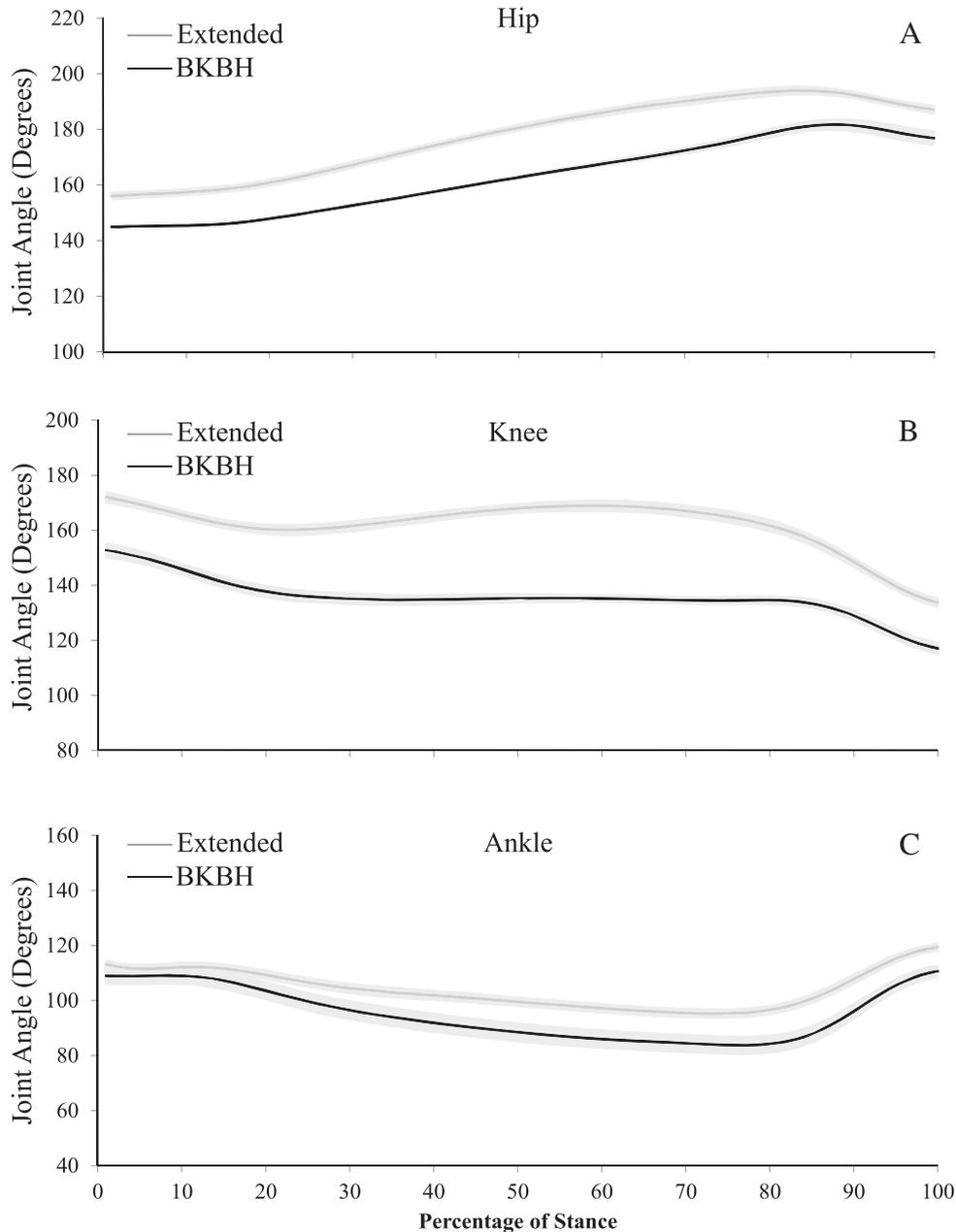
## Results

During BKBH walking, subjects held their joints in consistently more flexed postures than during normal walking, as expected

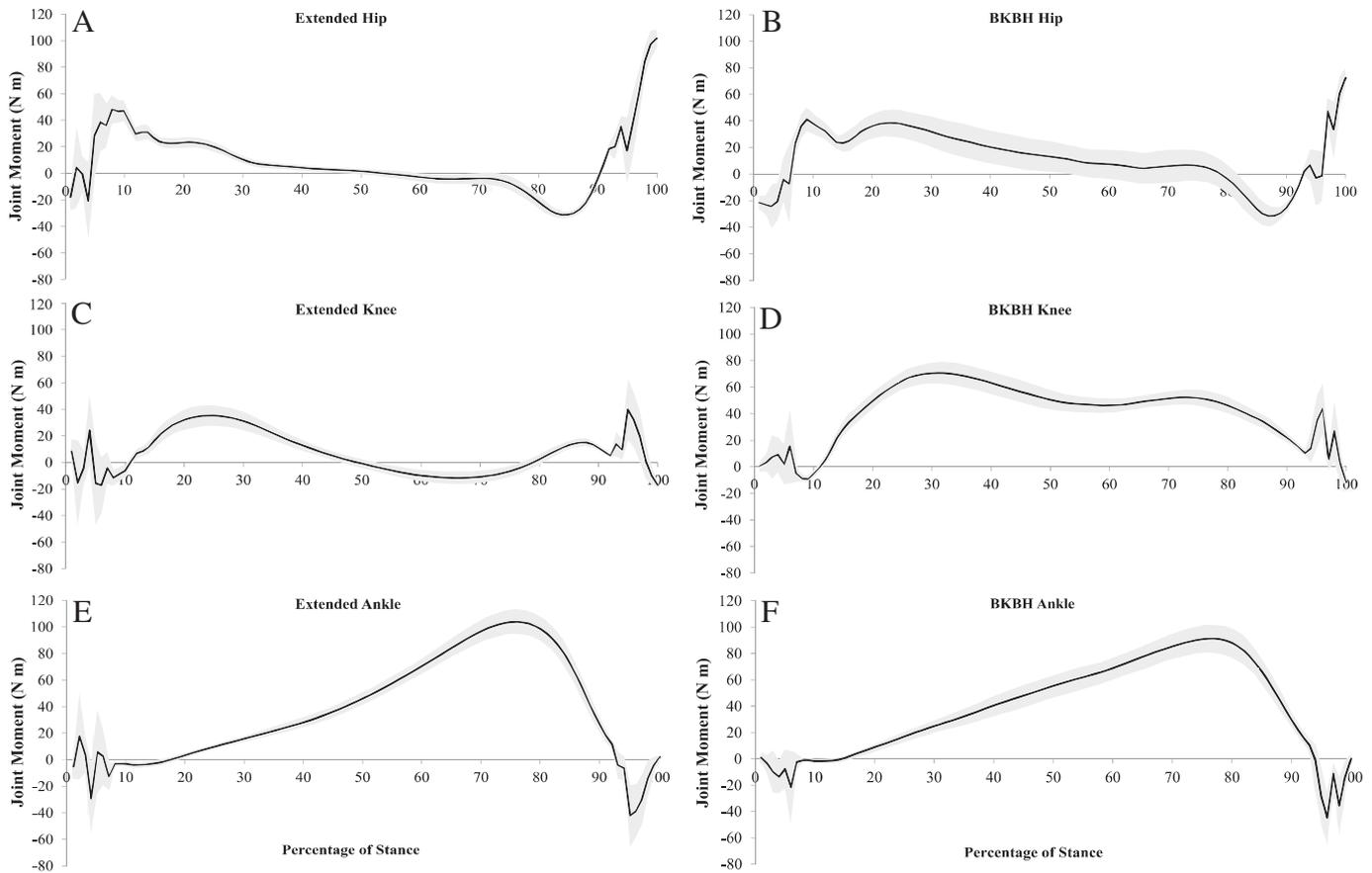
(Fig. 1). Despite these differences in joint angles, external joint moments were broadly similar between the two modes at the hip and the ankle, however external moments at the knee differ in magnitude (see Fig. 2). Differences in external moments led to increased values of  $V_{\text{muscle}}/t_c$  during BKBH walking.  $V_{\text{muscle}}/t_c$  increased significantly in BKBH walking for slow, preferred and fast speeds by  $58.1\% \pm 13.0\%$ ,  $47.1\% \pm 9.5\%$  and  $43.1\% \pm 7.3\%$ , respectively (Table 1; Fig. 3). Averaged overall speeds,  $V_{\text{muscle}}/t_c$  increased by  $47.8\% \pm 8.3\%$  in BKBH compared with extended-limb walking. The difference in  $V_{\text{muscle}}/t_c$  in BKBH and extended-limb trials is not due to a difference in velocity between experimental conditions. Froude numbers were not significantly different between modes of walking within slow ( $p = 0.12$ ) and fast ( $p = 0.14$ ) speed categories (see Table 1). However, Froude numbers in the preferred speed

category were significantly faster in extended-limb trials compared with BKBH trials (Table 1). Since  $V_{\text{muscle}}/t_c$  tends to increase with higher Froude numbers (Table 1), the higher Froude numbers in extended-limb preferred speed trials compared with BKBH preferred speed trials serves to reduce the observed difference in  $V_{\text{muscle}}/t_c$  between these two modes.

$V_{\text{muscle}}/t_c$  is determined by both active muscle volume ( $V_{\text{muscle}}$ ) and contact time ( $t_c$ ) as described in Eq. (1). In this study, contact times do not significantly differ between walking modes at slow or fast speeds, but are significantly larger in BKBH trials at preferred speeds (Table 1). This difference is likely due to subjects selecting slower preferred speeds in BKBH trials relative to extended limb trials. However, even with the slower speed and longer contact times,  $V_{\text{muscle}}/t_c$  is still larger in BKBH trials.



**Figure 1.** Joint angles in extended limb and BKBH walking. Average joint angles across all individuals at preferred speeds from 1 to 100% of stance phase in both extended and BKBH modes (gray line indicates extended limb, black line indicates BKBH) at the hip (A), knee (B), and ankle (C). The shaded portion represents the standard error of the mean (SEM). For all joints, smaller angles are more flexed joints.



**Figure 2.** Joint moments in extended limb and BKBH walking. Average joint moments across all individuals at preferred speeds from 1 to 100% of stance phase for extended hip (A), BKBH hip (B), extended knee (C), BKBH knee (D), extended ankle (E) and BKBH ankle (F). The black line indicates the average while the shaded portion represents the SEM. Positive moment values indicate flexion while negative values indicate extension.

Thus, increases in  $V_{\text{muscle}}/t_c$  values during BKBH walking were due largely to increased whole limb active muscle volume in BKBH walking (see Table 1; Fig. 4). However, the contributions of active muscle volume to estimated locomotor costs are not evenly distributed across the major joints. Reflecting the pattern of

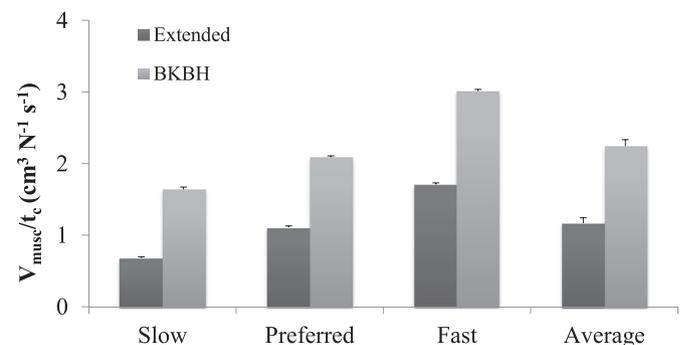
**Table 1**  
Kinematics and muscle volume data for extended limb and BKBH walking in humans.

Variable	Speed	Extended	S.D.	BKBH	S.D.	P-value
Froude number	Slow	0.07	0.03	0.07	0.02	0.12
Froude number	Preferred	0.17	0.03	0.13	0.03	<0.05
Froude number	Fast	0.27	0.05	0.26	0.07	0.14
$(V_{\text{muscle}}/t_c)$	Slow	0.69	0.23	1.64	0.44	<0.05
$(V_{\text{muscle}}/t_c)$	Preferred	1.11	0.26	2.09	0.26	<0.05
$(V_{\text{muscle}}/t_c)$	Fast	1.71	0.29	3.01	0.35	<0.05
Contact time (sec)	Slow	0.92	0.20	0.96	0.23	0.40
Contact time (sec)	Preferred	0.65	0.08	0.74	0.09	<0.05
Contact time (sec)	Fast	0.50	0.04	0.56	0.05	0.11
Hip $V_{\text{muscle}}$	Slow	0.06	0.03	0.18	0.15	0.06
Knee $V_{\text{muscle}}$	Slow	0.18	0.14	0.94	0.30	<0.05
Ankle $V_{\text{muscle}}$	Slow	0.37	0.04	0.38	0.05	0.28
Total $V_{\text{muscle}}$	Slow	0.61	0.16	1.50	0.20	<0.05
Hip $V_{\text{muscle}}$	Preferred	0.10	0.03	0.19	0.15	0.12
Knee $V_{\text{muscle}}$	Preferred	0.23	0.11	0.95	0.28	<0.05
Ankle $V_{\text{muscle}}$	Preferred	0.38	0.02	0.39	0.07	0.73
Total $V_{\text{muscle}}$	Preferred	0.71	0.14	1.52	0.17	<0.05
Hip $V_{\text{muscle}}$	Fast	0.13	0.05	0.21	0.13	0.08
Knee $V_{\text{muscle}}$	Fast	0.37	0.18	1.08	0.21	<0.05
Ankle $V_{\text{muscle}}$	Fast	0.36	0.02	0.37	0.04	0.84
Total $V_{\text{muscle}}$	Fast	0.87	0.17	1.66	0.12	<0.05

P-values are from paired student's *t*-tests. S.D. is the standard deviation.

external moments at hind limb joints, active muscle volume ( $V_{\text{muscle}}$ ) at the knee increased significantly in BKBH walking and represented the largest component of total limb  $V_{\text{muscle}}/t_c$  across all speeds, comprising more than half of the total active limb muscle volume. In contrast, active muscle volume at the hip and at the ankle was not significantly different between the two modes at any speed (see Table 1). Therefore, the difference in  $V_{\text{muscle}}/t_c$  between BKBH and extended-limb bipedalism is explained by increased active muscle volume at the knee.

$V_{\text{muscle}}/t_c$  is higher in chimpanzees (either bipedal or quadrupedal) than in human BKBH walking (Table 2; Fig. 5). Only



**Figure 3.**  $V_{\text{muscle}}/t_c$  across speeds in humans. Average ( $V_{\text{muscle}}/t_c$ ;  $\text{cm}^3 \text{N}^{-1} \text{s}^{-1}$ ) values for all individuals for slow, preferred, fast walks, and an average across all speeds in extended and BKBH modes. The error bar is the SEM.

preferred speeds were used to compare across species because these data represent self-selected speeds for humans and chimpanzees. On a mass-specific basis (i.e., per kg of body mass), bipedal chimpanzees use 63.4% more total limb active muscle volume, while quadrupedal chimpanzees use 52.6% more active muscle volume than human BKBH walking at preferred speeds (note that reliable statistical analyses are not possible due to the small sample size of the chimpanzee dataset). The majority of this difference comes from elevated muscle volumes at the hip in chimpanzees (Fig. 6; Table 3).

## Discussion

Compared with chimpanzees, human anatomy reduces  $V_{\text{muscle}}/t_c$  across a range of postures.  $V_{\text{muscle}}/t_c$  values for human BKBH bipedalism, while  $47.8\% \pm 8.3\%$  higher than for normal human walking, are lower than  $V_{\text{muscle}}/t_c$  values for chimpanzees walking quadrupedally. These results agree remarkably well with data from Carey and Crompton (2005) showing that BKBH walking in humans was 52% more energetically expensive than normal extended limb bipedalism. Thus, the energetic difference between these locomotor modes is robust and not sensitive to sample composition or methodology. In addition, this comparison between studies acts as a check on our assumption that  $k$  in eq. (1) (the variable that describes the rate at which a unit volume of muscle uses energy) is constant across BKBH and normal walking. Since the difference in  $V_{\text{muscle}}/t_c$  is similar to the difference in  $\dot{E}_{\text{metab}}$  measured by oxygen consumption (Carey and Crompton, 2005),  $k$  is not expected to differ between BKBH and normal walking. While we believe these results suggest that  $k$  does not change within an individual across locomotor modes, we suggest this hypothesis requires further direct testing in future work.

Using inverse dynamics, we identified increased active muscle volume at the knee as the main source of increased energy costs in human BKBH walking. This finding corroborates a recent forward dynamics simulation, which found that crouched walking required significantly higher knee extensor muscle force generating capacity (Steele et al., 2012). One way to interpret our results is to consider the position of the GRF vector relative to the knee and hip across these locomotor modes. The knee is the primary source of increased energy costs because during stance phase in BKBH locomotion, the GRF vector is positioned posterior to the knee joint but passes directly through the hip joint (see Fig. 7), resulting in large external knee moments and requiring an increase in the amount of force produced by the knee extensor muscles. Because the GRF vector remains close to the hip joint in both extended-limb and BKBH walking, muscle forces and therefore active muscle volumes at the hip are low in both forms of locomotion. It is

**Table 2**

$V_{\text{muscle}}/t_c$  and contact time for chimpanzees and humans.

Variable	Chimpanzees				Humans			
	Bipedal	S.D.	Quadrupedal	S.D.	Extended	S.D.	BKBH	S.D.
$(V_{\text{muscle}}/t_c)$	6.35	1.19	3.92	1.15	1.11	0.26	2.09	0.26
Contact time (sec)	0.68	0.07	0.80	0.03	0.65	0.06	0.74	0.07

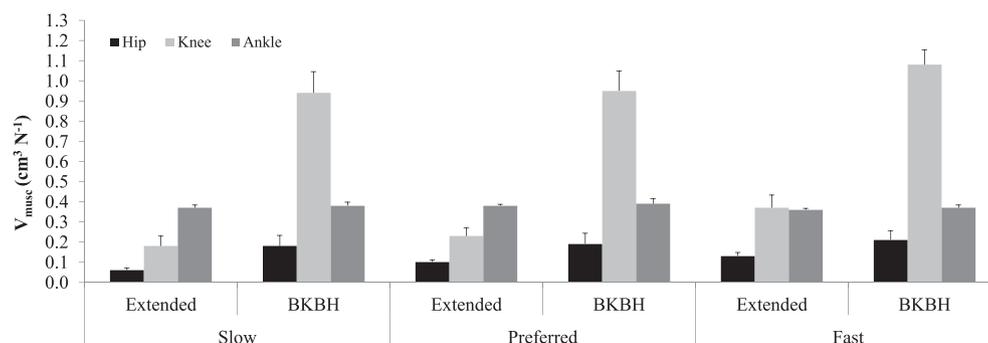
Note: values for  $V_{\text{muscle}}/t_c$  ( $\text{cm}^3 \text{N}^{-1} \text{s}^{-1}$ ) and contact times ( $\text{s}^{-1}$ ) for chimpanzees walking quadrupedally and bipedally and humans BKBH and extended limb bipedalism. All individuals are walking at preferred speeds. The contact time for the quadrupedal chimpanzees is represented by a single number because it was the same value for both fore- and hind limbs. S.D. is the standard deviation.

important to note that reductions in inertial and gravitational moments due to segment accelerations could also lead to lower hip relative to knee moments. Future experiments may explore the effects of inertial properties on joint moments in different locomotor modes by experimentally altering segment mass distributions using added mass.

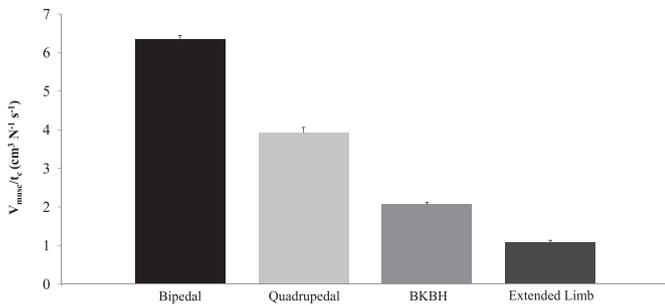
The higher values of  $V_{\text{muscle}}/t_c$  in human BKBH walking are consistent with the hypothesis that human anatomy is the product of selection to reduce energy costs of extended limb terrestrial locomotion (Rodman and McHenry, 1980; Sockol et al., 2007; Pontzer et al., 2009). However, human morphology leads to lower metabolic cost than chimpanzee anatomy even in flexed postures. Compared with humans, chimpanzees activate significantly more muscle volume at the hip, due primarily to the increased moment arms of the GRF in these postures (see Sockol et al., 2007). Thus humans walking with bent knees and hips do so in a way that still minimizes muscle volumes at the hip, while chimpanzees using similar locomotor postures have the greatest difference in muscle volume at the hip.

### Linking anatomy to cost

This difference between human and chimpanzee locomotion suggests that adaptations for reducing flexion moments at the hip were likely key drivers in the evolution of energetically economical bipedal walking. Since inertial and gravitational moments are generally small at walking speeds (Biewener et al., 2004), we believe adaptations that alter moments due to the GRF through increased hip and knee extension were likely responsible for generating the differences in cost between human and chimpanzee locomotion. Anatomical changes to the human pelvis clearly play a major role in the evolution of full hip extension during bipedalism (Robinson, 1972; Fleagle and Anapol, 1992; Sockol et al., 2007). Specifically, the dorsal orientation of the ischial tuberosity



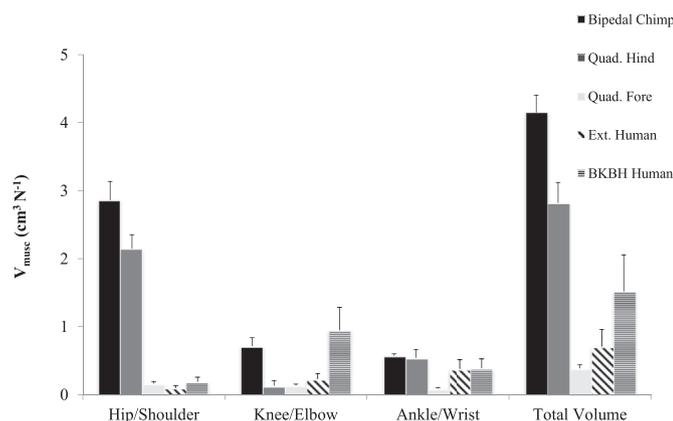
**Figure 4.** Active muscle volume in humans. Average activated muscle volume ( $V_{\text{muscle}}$ ;  $\text{cm}^3 \text{N}^{-1}$ ) for all individuals for slow, preferred, and fast walks in both extended and BKBH modes. The error bars are the SEM.



**Figure 5.**  $V_{musc}/t_c$  across species. Total limb (hip, knee, and ankle combined) average  $V_{musc}/t_c$  ( $\text{cm}^3 \text{N}^{-1} \text{s}^{-1}$ ) values across individuals for bipedal chimpanzees, quadrupedal chimpanzees (forelimb and hind limb values), BKBH humans, and extended limb humans. The error bars are the SEM.

increases the length of the hip extensor muscle moment arm in extended-limb postures, allowing for moment production when the hip is fully extended (Robinson, 1972; Fleagle and Anapol, 1992; Sockol et al., 2007). In chimpanzees, a more caudally oriented ischium increases hip extensor mechanical advantage in the more flexed hip postures used during climbing (e.g., ~130 degrees of flexion; Isler, 2005), but reduces mechanical advantage in more extended-postures (Robinson, 1972; McHenry, 1975), constraining joint angles to highly flexed positions during walking (Sockol et al., 2007).

Our results highlight the complexity of linking skeletal adaptations directly to reductions in energy costs. While human ischial anatomy is necessary for full hip extension, it does not lead to increased muscle forces at the hip during the moderate degrees of flexion used in BKBH walking, which suggests that a dorsally oriented ischial tuberosity can function well under a range of joint angles. Rather than ischial anatomy driving low energy costs in human BKBH walking, our results emphasize the importance of keeping the GRF vector close to the hip joint regardless of overall joint posture. When walking at a constant speed, the GRF vector is generally oriented from the center of pressure under the foot toward the center of mass of the body (Alexander, 2004). To maintain a GRF vector that passes near the hip joint center, the trunk (and therefore the center of mass of the trunk, head and arms) must



**Figure 6.** All species active muscle volume. Active muscle volume values ( $V_{musc}$ ;  $\text{cm}^3 \text{N}^{-1}$ ) at each joint for bipedal and quadrupedal chimpanzees, and extended limb and BKBH bipedalism in humans. Values for quadrupedal chimpanzees combine the hip and the shoulder, knee and elbow, and ankle and wrist since both are used during this form of locomotion and are analogous joints. Total limb values are a summation of all joints involved in that form of locomotion. The error bars are the SEM.

remain erect and centered over the pelvis. Thus, we hypothesize that this feature of human walking, whether it is with a flexed or extended hind limb, is made possible by specific anatomical adaptations in the lower back. Among the anatomical features that likely reduce costs during human walking, the lumbar lordosis is particularly important because it acts to maintain an erect trunk during stance phase (see Ward, 2002; Lovejoy, 2005). Without a lordosis, chimpanzees (and bonobos) walk with a trunk that slopes forward from the hip during bipedalism (D'Aouit et al., 2002; Alexander, 2004), leading to a GRF vector that passes anterior to the hip joint (Sockol et al., 2007). Although one might expect that this posture would simply bring the GRF vector closer to the knee in order to reduce moments at this joint, chimpanzees activate significantly more muscle volume at the knee as well as the hip compared with humans walking in BKBH or extended limb postures (see Fig. 6). Therefore, the results from this study suggest that the lack of a lumbar lordosis in chimpanzee bipedalism is likely a contributing factor in their increased energy COL compared with humans.

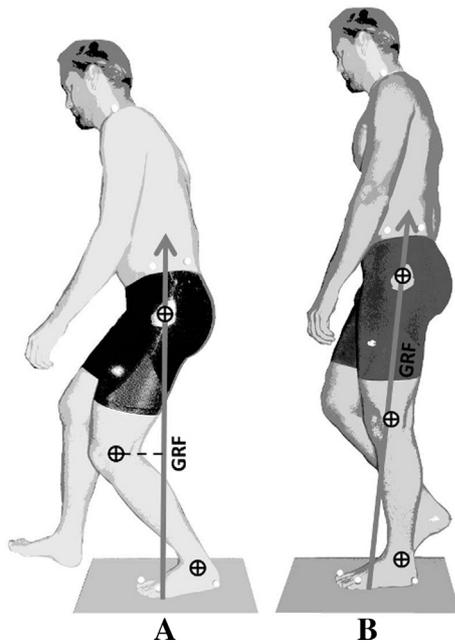
Although this direct connection between lumbar lordosis and lowering the energy costs of bipedalism in humans requires more detailed testing, the evolutionary history of the spine and pelvis in hominins provides a possible roadmap to the origins of energetically economical upright walking (e.g., Shapiro, 1993; Sanders, 1998; Lovejoy, 2005; Whitcome et al., 2007). An early purported hominin, *Ardipithecus ramidus*, is described as having 'situational' lumbar lordosis combined with a more chimpanzee-like ischial orientation (Lovejoy et al., 2009b). If this combination of features were present, the ischial orientation in *Ar. ramidus* seems well adapted to vertical climbing (i.e., high extensor moment production on flexed hips) and this species would not have been able to walk on a fully extended hip (i.e., lack of extensor moment production for hip extensors due to small moment arms). However, if *Ardipithecus* did have a lumbar lordosis, reduced external moments at the hip would have led to lower energy costs of BKBH walking in this taxon compared with chimpanzee-like locomotion. Since no lumbar or sacral vertebrae were found, and the anterior portion of the iliac blades are missing, it is impossible to confirm the presence of a lumbar lordosis. Thus, we must await future fossil discoveries to more fully understand the energetics of locomotion in this early hominin taxon.

In contrast, the presence of a human-like lumbar lordosis (Ward, 2002; Been et al., 2012) and a dorsally oriented ischial tuberosity (e.g., Robinson, 1972; Stern and Susman, 1983; Tague and Lovejoy, 1986) in australopithecines suggests a more complete transition to reduced energy costs in terrestrial locomotion, despite anatomical differences in the vertebrae of these taxa (e.g., Shapiro, 1993; Sanders, 1998). Based on our interpretation of ischial orientation and performance, this commitment to low energy costs in extended limb bipedalism may have led to a loss of vertical climbing performance in australopithecines compared with living apes due to reduced ability for force production when the hip joints are highly flexed. This emphasis on terrestrial behaviors does not downplay the potential importance of some arboreal behaviors as suggested by features such as a cranially oriented glenoid fossae and curved phalanges found in the australopithecine fossil record (e.g., Stern, 2000; Berger et al., 2010; Green and Alemseged, 2012). Additionally, although ankle anatomy reflects a shift away from arboreal adaptations (DeSilva, 2009), australopithecines may have retained soft tissue adaptations that would have allowed climbing similar to that seen in modern human hunter gatherers (see Venkataraman et al., 2013). Thus, changes in hip architecture likely reflect a shift in selection pressures towards increased terrestrial bipedal performance without fully compromising climbing capabilities.

**Table 3**  
Active muscle volume ( $V_{\text{musc}}$ ) for chimpanzees and humans.

Joint	Chimpanzees				Humans					
	Quad. hind limb	S.D.	Quad. forelimb	S.D.	Bipedal	S.D.	Extended	S.D.	BKBH	S.D.
Hip/shoulder	2.15	0.36	0.16	0.05	2.860	0.47	0.10	0.03	0.19	0.15
Knee/elbow	0.13	0.13	0.14	0.04	0.713	0.21	0.23	0.11	0.95	0.28
Ankle/wrist	0.54	0.21	0.09	0.02	0.574	0.04	0.38	0.20	0.39	0.07
Total	2.82	0.52	0.39	0.09	4.150	0.44	0.71	0.14	1.52	0.17

Values for active muscle volume ( $V_{\text{musc}}$ ;  $\text{cm}^3 \text{N}^{-1}$ ) for chimpanzee quadrupedalism and bipedalism and human BKBH and extended limb bipedalism. All individuals are walking at preferred speeds. S.D. is the standard deviation.



**Figure 7.** Midstance diagram. Human locomotion at midstance for BKBH (A) and extended limb (B) bipedalism. The vertical line represents the position of the ground reaction force (GRF) vector, which is approximated from the data. During extended limb bipedalism (B) the GRF is oriented through the knee and hip. During BKBH bipedalism (A), the GRF is also oriented through the hip, but is behind the knee, creating a joint moment.

## Conclusion

The results of this study highlight the importance of experimentally examining the performance of skeletal morphology in studies of human locomotor evolution. We found that differences in joint posture generate higher energy costs in humans due to an increase in active muscle volumes at the knee. These results lead to two conclusions important for understanding the evolution of human bipedalism. First, human hip anatomy linked to extended limb walking does not lead to the higher energy costs of BKBH walking. The dorsal orientation of the human ischium permits low muscle volumes at the hip during BKBH walking, and instead, the higher energy costs of humans walking with flexed limbs is mostly due to the increased moment arm of the GRF at the knee. Second, our results highlight the importance of orienting the GRF vector near the hip to maintain low energy costs of walking in humans compared with chimpanzees regardless of lower limb postures. We believe the orientation of the GRF vector is likely tied to an erect trunk posture, and therefore to the evolution of the lumbar lordosis, although this hypothesis requires more detailed testing.

Taken together, these conclusions help us better understand the evolutionary changes in locomotion that occurred during early

hominin evolution. The earliest fossil hominin pelvis, that of *Ar. ramidus*, suggests that hip extensor muscles optimized for climbing may have been combined with a lumbar spine capable of lordosis. If true, then this hominin may have walked terrestrially with lower energy costs than living chimpanzees even though it could not walk on a modern human-like extended hind limb (but see Lovejoy and McCollum, 2010). With the australopithecines, we see the first evidence of both dorsally oriented ischial tuberosities and true lumbar lordosis, indicating an abandonment of climbing capabilities similar to living apes and a commitment to reduced energy costs during bipedal walking. Future studies should focus on both the role of the lumbar lordosis in managing energy costs of bipedalism, and on interpretations of spinal anatomy in early hominins to best determine when selection produced low energy costs of walking during the evolution of bipedalism. Experimental studies focused on testing performance hypotheses for morphological adaptations will help us clarify the evolutionary scenarios that led to human walking biomechanics and to the evolution of the human skeleton.

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