

## RESEARCH ARTICLE

# The role of plantigrady and heel-strike in the mechanics and energetics of human walking with implications for the evolution of the human foot

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**ABSTRACT**

Human bipedal locomotion is characterized by a habitual heel-strike (HS) plantigrade gait, yet the significance of walking foot-posture is not well understood. To date, researchers have not fully investigated the costs of non-heel-strike (NHS) walking. Therefore, we examined walking speed, walk-to-run transition speed, estimated locomotor costs (lower limb muscle volume activated during walking), impact transient (rapid increase in ground force at touchdown) and effective limb length (ELL) in subjects ( $n=14$ ) who walked at self-selected speeds using HS and NHS gaits. HS walking increases ELL compared with NHS walking since the center of pressure translates anteriorly from heel touchdown to toe-off. NHS gaits led to decreased absolute walking speeds ( $P=0.012$ ) and walk-to-run transition speeds ( $P=0.0025$ ), and increased estimated locomotor energy costs ( $P<0.0001$ ) compared with HS gaits. These differences lost significance after using the dynamic similarity hypothesis to account for the effects of foot landing posture on ELL. Thus, reduced locomotor costs and increased maximum walking speeds in HS gaits are linked to the increased ELL compared with NHS gaits. However, HS walking significantly increases impact transient values at all speeds ( $P<0.0001$ ). These trade-offs may be key to understanding the functional benefits of HS walking. Given the current debate over the locomotor mechanics of early hominins and the range of foot landing postures used by nonhuman apes, we suggest the consistent use of HS gaits provides key locomotor advantages to striding bipeds and may have appeared early in hominin evolution.

**KEY WORDS:** Bipedalism, Heel-strike, Limb length, Locomotion, *Australopithecus sediba*, *Homo floresiensis*

**INTRODUCTION**

Plantigrady is rare among cursorial mammals (Hildebrand and Goslow, 1998), which typically utilize digitigrade or unguligrade gaits to maximize limb length, which is a key determinant of the energetic cost of locomotion (Hildebrand and Goslow, 1998; Kram and Taylor, 1990; Pontzer, 2007a). Humans represent an exception to this pattern (Cunningham et al., 2010) as we possess adaptations for endurance terrestrial running (Bramble and Lieberman, 2004; Carrier, 1984), combined with plantigrade feet and a prominent heel strike (HS), during walking gaits, where the foot touches down heel first on the calcaneal tuberosity in a dorsiflexed posture, without

mid- or forefoot contact. Given the importance of limb length to cursorial mammals, it is uncertain why humans use a plantigrade foot posture with a consistent HS during walking (Cunningham et al., 2010).

A popular hypothesis is that the human HS gait evolved to reduce the energy costs of walking (Cunningham et al., 2010; Usherwood et al., 2012). This hypothesis is supported by studies showing subjects had relatively high energy costs of locomotion (COL) when asked to walk with digitigrade foot postures compared with typical plantigrade HS walking (Cunningham et al., 2010). Yet, human lower limb anatomy is not adapted for full digitigrady and it is possible that these experiments captured the energetic costs of novel gaits. Non-human apes may offer more context into how and why habitual HS walking evolved in humans because we often assume that traits shared among apes may have been present in our pre-bipedal ancestors. Extant non-human apes use an array of plantigrade walking gaits, some of which lack consistent heel strikes (Schmitt and Larson, 1995). For example, researchers have shown that our closest living relatives, bonobos (*Pan paniscus*) and common chimpanzees (*Pan troglodytes*), use a wide range of landing postures, from a traditional human-like heel strike, to landings where the heel does not touch down until the second half of stance phase (see Elftman and Manter, 1935; Vereecke et al., 2003). Most often, these apes use gaits where the heel and mid-foot contact the ground simultaneously, which also differ from human HS walking where initial ground contact is made by the heel alone (Elftman and Manter, 1935; Vereecke et al., 2003). Thus, the key human evolutionary shift from the non-hominin ape foot landings appears to be the consistent use of heel-only landing postures.

The goal of this study is to better understand the advantages and disadvantages of this shift to consistent HS gaits. To accomplish this goal, we measured the mechanics and energetics of human walking with the two footfall extremes seen in ape-like plantigrade walking: an HS, where touchdown occurs with the heel only, and a non-heel strike (NHS), where initial ground contact occurs at mid-foot and the heel lands later in stance. Interestingly, although humans do not habitually walk with either digitigrade or more ape-like gaits, Lieberman et al. (2010) found that many individuals adopt NHS gaits at running speeds, similar to those used at times by nonhuman apes. Running with an HS foot posture produces rapid and potentially dangerous increases in the ground reaction force (GRF), known as an impact transient (IT), just after the heel impacts the ground (Lieberman et al., 2010). NHS footfalls seem to benefit runners by reducing ITs at higher locomotor speeds (Lieberman et al., 2010), possibly decreasing injury rates (Lieberman, 2012) without increasing locomotor costs (Divert et al., 2005, 2008; Franz et al., 2012; Kram and Franz, 2012). By specifically exploring the possible benefits of using an HS at slow locomotor speeds, we hope to better understand why a consistent

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**List of symbols and abbreviations**

COL	cost of locomotion
COP	center of pressure
COP <sub>c</sub>	change in center of pressure (m)
DC	dynamically calculated
DSH	dynamic similarity hypothesis
$\dot{E}_{COL}$	estimated cost of locomotion ( $\text{cm}^3 \text{N s}^{-1}$ )
ELL	effective limb length (m)
$F_{\text{musc}}$	muscle force
$Fr$	Froude number
$Fr'$	plantigrade adjusted Froude number
GRF	ground reaction force (N)
HS	heel-strike
IT	impact transient
$l_{\text{fasc}}$	muscle fascicle length
$L$	limb length (m)
$L'$	plantigrade adjusted limb length (m)
$M$	moment
NHS	non-heel-strike
$t_c$	foot contact time (s)
$V_{\text{musc}}$	volume of active muscle ( $\text{cm}^3 \text{N}^{-1}$ )
WTR	walk-to-run

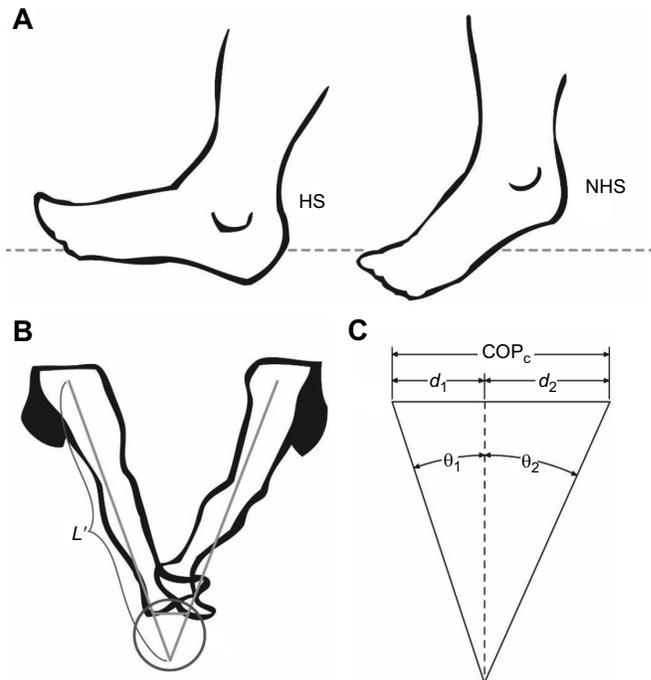
HS evolved in our bipedal ancestors, and whether NHS gaits offer any advantages that may explain their occasional use in other apes.

**Plantigrade walking and effective limb length**

As noted by Cunningham et al. (2010), human use of plantigrade foot postures is unique among organisms adapted for long distance travel since plantigrade reduces hindlimb length compared with digitigrade postures. Limb length is a key determinant of walking mechanics and energetics because when modeled as an inverted pendulum, the limb acts as a strut during stance phase, with the center of mass vaulting over the point of ground contact (Alexander, 1976; Gray, 1944; Kuo, 2001; Pontzer, 2005). Long limbs reduce energy costs in this model by increasing step lengths, which leads to longer time periods for accelerating the center of mass and reduced rates of force generation (Pontzer, 2007a).

Characterizing the effects of plantigrade HS walking on the length of the pendulum strut may help to explain why this footfall pattern evolved. Researchers typically use either a linear sum of skeletal elements (Stuedel and Beattie, 1995), the height of the hip in quiet stance (Pontzer, 2007a) or hip height at mid-stance during locomotion to describe effective limb length (ELL: average length of the strut over a step). These lengths assume the pivot point of the inverted pendulum is fixed at ground contact and therefore plantigrade should reduce ELL compared with digitigrade foot postures. However, the pivot point translates anteriorly during a step [i.e. the center of pressure (COP) shifts continuously throughout the stance phase] in plantigrade walkers. Pontzer (2007b) suggested that a significant anterior shift in the COP throughout the step (COP<sub>c</sub>; see Fig. 1) may actually increase the ELL because the pivot point of the inverted pendulum strut would occur significantly below the foot (see Fig. 1B; Pontzer, 2007b). Additionally, Pontzer (2007b) showed that an estimate of ELL that took COP translation into account ( $L'$ ) was a significantly better predictor of the force required to accelerate the center of mass during walking than hip height alone in humans.

Based on this view of ELL, an HS walking gait with a plantigrade foot may significantly increase the length of an inverted pendulum strut, even if this foot posture reduces hip height from the ground in quiet stance. Compared with the consistent use of an HS gait in



**Fig. 1. Differences in posture and limb length in heel-strike (HS) and non-heel-strike (NHS) gaits.** (A) Examples of foot posture at initial touchdown, HS and NHS. Dashed line indicates surface. (B) Depiction of  $L'$ , effective limb length (m), modeled as a point mass on the end of a rigid limb, taking into consideration COP<sub>c</sub>, the translation in COP during stance and hip excursion angle  $\theta$ . (C) Depiction of  $L'$  added limb length (region circled in B), see Materials and methods for details.

humans, many of the foot postures used by nonhuman apes lead to reduced total translation of the COP (Vereecke et al., 2003). For example, when bonobos land on both the heel and midfoot simultaneously (Elftman and Manter, 1935; Vereecke et al., 2003, 2005), the COP originates between the heel and forefoot, rather than directly under the heel. Therefore, a consistent HS landing posture that maximizes COP translation may be a novel evolutionary solution to lengthening inverted pendulum struts from an ape-like ancestral condition.

We use the dynamic similarity hypothesis (DSH) to test this model of inverted pendulum strut length. The DSH suggests that the motions of two animals are comparable if they can be made similar through dimensional scaling (Alexander and Jayes, 1983). Dimensionless parameters can be compared at speeds where the ratios of inertial to gravitational forces acting on two moving systems are equal. This condition is met when organisms walk at the same Froude number ( $Fr$ ; Alexander, 1989):

$$Fr = \frac{v^2}{gL}, \quad (1)$$

where  $v$  is velocity ( $\text{m s}^{-1}$ ),  $g$  is gravitational acceleration ( $9.81 \text{ m s}^{-2}$ ) and  $L$  is a characteristic length. Most researchers assume hip height represents the length of the pendulum strut when applying the DSH to animal locomotion. However, if Pontzer's (2007b) analysis is correct, researchers should instead use the length of the strut calculated from the true pivot point of the inverted pendulum ( $L'$ ). In this study we use both  $L$  and  $L'$  in calculations of  $Fr$  to compare HS and NHS human walking movements in the same subjects. This analysis will help us to determine whether differences

in mechanics and energetics between these gaits are due primarily to differences in the length of the inverted pendulum strut. If this hypothesis is supported, mechanical differences between footfall patterns found when calculating  $Fr$  using  $L$  should disappear when subjects walk at comparable  $Fr$  numbers calculated with  $L'$ .

Here, we examine two potential benefits of HS walking and one potential cost using this dynamic similarity analysis. First, since previous work suggests that ELL is a main determinant of the costs of locomotion (as described above, see Kram and Taylor, 1990; Pontzer, 2007b), we determined the effects of HS and NHS walking on estimates of the energy costs of locomotion. Second, we measured the effects of foot-contact posture on the walk-to-run (WTR) transition speed. Changes in ELL should affect WTR transitions because bipeds transition to running gaits at dynamically similar speeds, dependent largely on limb length and gravity (Kram et al., 1997; Raichlen, 2008; Usherwood, 2005). Finally, we explore the possibility that NHS gaits may reduce ITs at walking speeds, similar to the effects of NHS gaits on ITs at running speeds (see Lieberman et al., 2010).

## MATERIALS AND METHODS

### Subjects

Fourteen adults (7 men and 7 women) with a mean age of  $23.7 \pm 4.4$  years and body mass of  $69.2 \pm 16.6$  kg took part in this study. All subjects were healthy and free of injury at the time of the study. In order to avoid confounding variables, dancers and individuals with experience running barefoot or in minimalist shoes were not selected to participate in this study. Subjects performed all tasks barefoot. Prior to starting, the details of the study were explained to all participants and informed consent (approved by the University of Arizona Institutional Review Board) was provided.

### Foot posture kinematic and kinetic data collection

The study consisted of two separate experimental activities. The first task involved walking along a 4 m trackway across a range of speeds under two conditions: (1) landing with a HS (see Fig. 2A), and (2) landing with a NHS foot posture at initial contact (see Fig. 2B; circles highlight estimated COP translation shortly after touchdown). Subjects were first instructed to walk (HS) at their self-selected, preferred walking speed for 5 trials ( $1.14 \pm 0.15$  m s<sup>-1</sup>). The same procedure was followed for a slow self-selected walking speed ( $0.78 \pm 0.18$  m s<sup>-1</sup>) and a fast self-selected walking speed ( $1.47 \pm 0.21$  m s<sup>-1</sup>). After the first three conditions were met, subjects were directed to walk with a NHS gait, contacting the ground with the distal metatarsal heads (balls of the foot) initially instead of the heel,

with heel contact occurring later in the step (see Fig. 2B). This foot posture was demonstrated to the subjects after a verbal explanation. Subjects performed practice trial walks to adjust to this change in gait before data collection began. As with the HS trials, subjects were instructed to walk at self-selected, preferred ( $1.01 \pm 0.20$  m s<sup>-1</sup>), slow ( $0.78 \pm 0.19$  m s<sup>-1</sup>) and fast ( $1.31 \pm 0.21$  m s<sup>-1</sup>) speeds.

Kinematic data were collected at 200 Hz using a Vicon high-speed, six-camera, motion capture system (Hauppauge, NY). Twenty-four reflective markers were affixed to the subjects at joint centers, limb segments, and foot landmarks including the first and fifth distal metatarsal heads, lateral ankle, and heel. An AMTI multi-axis force plate (Watertown, MA) embedded midway along the track collected kinetic data at 4 kHz. A successful trial required complete, single-foot contact with the force plate using the specified foot-strike. Trial data were averaged at each speed and foot-posture before data analysis.

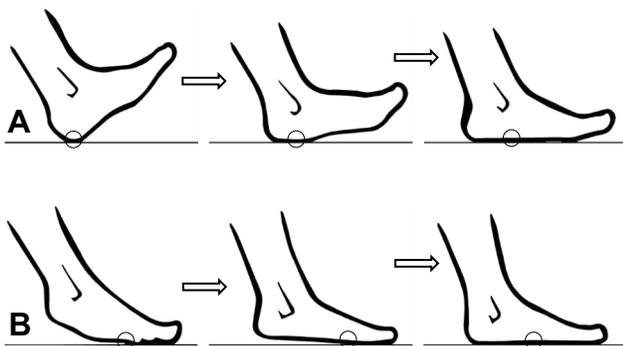
$L$  was calculated from the average hip height (m) throughout a step following Pontzer (2007b).  $L'$  was calculated two ways. First, following Pontzer (2007b),  $L'$  was calculated trigonometrically at touchdown and toe-off using the distance in meters the COP traveled in the sagittal plane (between touchdown and toe-off) and hip excursion angle (see Fig. 1C). The two limb lengths obtained from touchdown and toe-off were averaged to produce an  $L'$  during stance. Second,  $L'$  was calculated dynamically as the distance between the hip and the average intersection point for all hip-to-COP vectors for each motion analysis frame of the step. Dynamically calculated (DC)  $L'$  was calculated as the average intersection point between all hip-to-COP vectors throughout the step. Kinetic data at 4 kHz were resampled to match the kinematic data collected at 200 Hz. For every frame (200 frames s<sup>-1</sup>), a vector from the greater trochanter marker to the center of pressure was calculated in the sagittal plane. The intersections (pivot of the strut for the inverted pendulum between any two points) of all combinations of vectors were calculated and then averaged. Limb length was then calculated for each frame of the step from the hip joint marker to the average pivot point in the sagittal plane. While values were similar between subjects, dynamically calculated limb lengths were significantly longer than those calculated from touchdown and toe-off only ( $P < 0.001$ ). However, as noted below, results of locomotor comparisons between HS and NHS gaits do not change when using either the two-point method or the dynamic method. This method provided similar results to the method introduced by Pontzer (2007b; see Fig. S3 for results using the second, DC method).

### Active muscle volume and estimated cost of locomotion

The energy cost of activating muscle to support the body was used as an estimation of the metabolic cost of locomotion ( $\dot{E}_{COL}$ ) following validation by numerous studies across a range of species, including bipedal birds, quadrupedal mammals, and humans (Biewener et al., 2004; Foster et al., 2013; Griffin et al., 2004; Kram and Taylor, 1990; Pontzer, 2005, 2007b, 2009; Roberts et al., 1998a,b; Sockol et al., 2007; Taylor, 1994; Wright and Weyand, 2001). Inverse dynamics (performed in MATLAB, MathWorks) was used to estimate the change in muscle force production due to differences in foot-posture.  $\dot{E}_{COL}$  (J N s<sup>-1</sup>) is calculated as:

$$\dot{E}_{COL} = \frac{V_{\text{muscle}}}{t_c} k, \quad (2)$$

where  $V_{\text{muscle}}$  (cm<sup>3</sup> N<sup>-1</sup>) is active muscle volume,  $t_c$  (s<sup>-1</sup>) is the time the foot is in contact with the ground and  $k$  (J cm<sup>-3</sup>) is a constant that determines the rate at which a unit volume of muscle uses energy



**Fig. 2. HS and NHS plantigrady.** Differences in COP translation in HS (A) and NHS (B) plantigrady occurring after foot touchdown. Circled regions indicate the estimated COP.

(Roberts et al., 1998b). Since  $k$  is a constant at most walking speeds (Griffin et al., 2004; Roberts et al., 1998b), it was excluded from our calculation of  $\dot{E}_{COL}$ .

$V_{musc}$  is the product of muscle fascicle length ( $l_{fasc}$ , cm), and the cross sectional area ( $A$ , cm<sup>2</sup>) of activated muscle (Pontzer et al., 2009; Sockol et al., 2007). Here, average muscle group  $l_{fasc}$  was calculated following Biewener et al. (2004) and scaled to body mass for subjects in this study.  $A$  is proportional to the muscle force ( $F_{musc}$ ) produced during walking and is calculated as the muscle force (N) required to extend the limb in response to flexion moments ( $M$ ) at a specific joint, and the constant  $\sigma$  (where  $\sigma$  is muscle force per unit cross-sectional area, N cm<sup>-2</sup>) (Biewener et al., 2004). To estimate costs across experimental conditions, we assume  $\sigma$  remains constant despite differences in joint angles during stance phase when walking with an HS and NHS gaits. This assumption is supported by previous studies that have used this model to successfully predict energy costs in humans and other mammals walking and running with different limb joint postures (Foster et al., 2013; Ren et al., 2010; Sockol et al., 2007; Wright and Weyand, 2001).

$F_{musc}$  is determined by calculating external moments ( $M$ ) acting at each joint (Biewener et al., 2004). Moments were calculated using GRF vectors, limb segment accelerations, and flexion moments arising from two-joint muscles (Biewener et al., 2004; Winter, 2009). The finite differences method was used to calculate segmental acceleration (Winter, 2009), and limb segment inertial properties were estimated following Winter (2009). Net moments were calculated at each lower limb joint using the free-body method (Winter, 2009). The extensor muscle forces at each joint (hip, knee, and ankle) balancing these moments were calculated following equations in Biewener et al. (2004):

$$M_{ankle} = F_{ankle} r_{ankle}, \quad (3)$$

$$M_{knee} = F_{knee} r_{knee} - F_{(G)knee} r_{(G)knee} - F_{(H)knee} r_{(H)knee}, \quad (4)$$

$$M_{hip} = F_{hip} r_{hip} - F_{(RF)hip} r_{(RF)hip}, \quad (5)$$

where G (gastrocnemius), H (hamstrings) and RF (rectus femoris) are muscles acting on two joints and forces are calculated assuming the force produced by each is proportional to their physiological cross-sectional area (Biewener et al., 2004). Human anatomical moment arms were calculated from equations that relate moment arms to joint angles (Németh and Ohlsén, 1985; Rugg et al., 1990; Visser et al., 1990) and scaled to segment length. Relating moment arms to joint angles allows for an estimation of anatomical moments  $r_{musc}$ , while joint angles change during locomotion. Finally, following Biewener et al. (2004), muscle force impulses were divided by the GRF impulse to calculate the total volume of active muscle for use in Eqn 2:

$$V_{musc} = \frac{l_{fasc(hip)} \int F_{hip} + l_{fasc(knee)} \int F_{knee} + l_{fasc(ankle)} \int F_{ankle}}{\int GRF \sigma}. \quad (6)$$

### Treadmill walk-to-run speed determination

Subjects were also asked to participate in two separate WTR speed determination procedures, which were modified from Farinatti and Monteiro (2010). Initially, subjects became accustomed to walking on a treadmill (SOLE Fitness, Salt Lake City, UT) with a 5 min warm up. The warm-up consisted of a non-recorded walk at a speed of 1.33 m s<sup>-1</sup>. Once subjects completed the warm up, a covering was placed over the treadmill display, blocking time and speed data from the subject. Subjects started the WTR protocol using a

programmed treadmill function, which began at a speed of 1.52 m s<sup>-1</sup> and increased by 0.089 m s<sup>-1</sup> every 30 s. The transition speed was recorded only when subjects ran a complete 30 s interval, giving them time to switch back to walking if running at the speed felt awkward to ensure a complete transition to running. The test was then stopped and the subjects went back to walking at 1.33 m s<sup>-1</sup> for a 5 min cool down. Subjects then repeated the WTR trial using an NHS gait. For the second WTR trial, subjects were asked to walk with the same forefoot gait used in the motion capture walkway trials.

### Data analysis

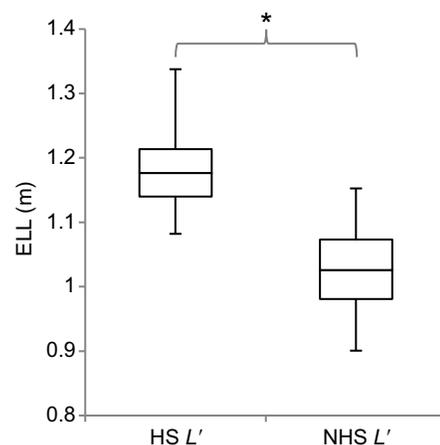
To determine whether the effects of HS on walking mechanics and energetics are due mainly to increased ELL (see Fig. 1), we compared locomotor variables at Froude numbers calculated with hip height ( $L$ ), and  $L'$ .  $Fr$  using  $L$ , and  $Fr'$  using  $L'$ , were calculated and compared for each motion capture trial between each self-selected speed category (slow, preferred and fast) for both foot postures to examine the role of ELL in determining the energy costs and speed of walking.

Between-subject and between-speed differences were tested for  $Fr$ ,  $Fr'$ ,  $L$ , and  $L'$  with a repeated-measures two-way analysis of variance (ANOVA) test, using foot-posture and self-selected speed category (as multiple conditions). The relationship between  $Fr$ ,  $Fr'$  and  $\dot{E}_{COL}$ , and  $Fr'$  and IT, were tested using linear mixed-effects analyses with  $Fr$  or  $Fr'$ , foot posture (HS versus NHS) and IT as fixed effects, and subject as a random effect having an interaction with foot posture. Associated  $P$ -values were found by likelihood ratio tests of the full model versus the model without the effects in question. The WTR transition speed was compared between HS and NHS trials with a Student's  $t$ -test. For all tests, level of significance was 0.05.

## RESULTS

### Effective limb length and dynamic similarity

We hypothesized that NHS walking would lead to a shorter  $L'$ , forcing subjects to walk at lower absolute speeds. Indeed,  $L'$  was significantly shorter in NHS trials (Fig. 3;  $-0.185 \pm 0.029$  m,  $F_{1,13} = 459.8$ ,  $P < 0.0001$ ). Additionally, human HS plantigrade gaits increased  $L'$  significantly more than adding the utilized length of the foot to the hindlimb, as in a digitigrade gait (the limb length gained by the translating pivot point was  $24.19 \pm 7.16\%$  higher than the sum of foot length and hip height,  $P < 0.0001$ ). This estimate is likely to be



**Fig. 3. Effective limb length in HS and NHS walking.** Effective limb length  $L'$  (m) is significantly longer during HS, heel-to-toe gait compared with NHS gaits ( $N=14$ ,  $F_{1,13} = 459.8$ ;  $*P < 0.0001$ ).

low considering the length of the entire foot (from heel to toe in the sagittal plane) would not simply be added to total limb length in a true digitigrade gait. DC  $L'$  was also significantly shorter in NHS trials (see Fig. S1;  $-0.247 \pm 0.109$  m,  $P < 0.0001$ ) when compared with HS trials at preferred walking speeds.

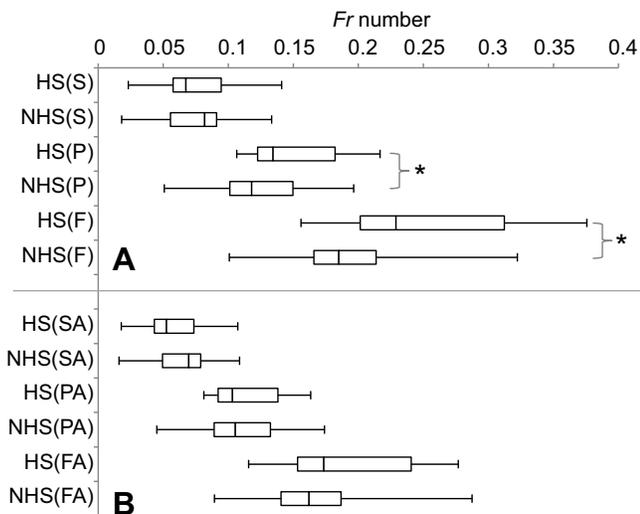
Absolute HS walking speeds were significantly faster compared with NHS walking across self-selected speed categories ( $F_{1,13} = 8.43$ ;  $P = 0.012$ ), however, *post hoc* tests showed that the slow walking speeds were not significantly different ( $P = 0.49$ ). HS  $Fr$  values (using hip height) were also significantly higher compared with NHS postures at any given self-selected speed (Fig. 4A;  $F_{1,13} = 8.78$ ;  $P = 0.011$ ), yet there was no significant difference between HS and NHS  $Fr'$  [calculated using plantigrade adjusted ELL ( $L'$ )] in self-selected speeds (Fig. 4B;  $F_{1,13} = 0.543$ ,  $P = 0.4744$ ). There was no significant difference between DC HS and NHS  $Fr'$  (see Fig. S2; slow,  $P = 0.10$ ; preferred,  $P = 0.48$ ; fast,  $P = 0.87$ ).

### Estimated cost of locomotion

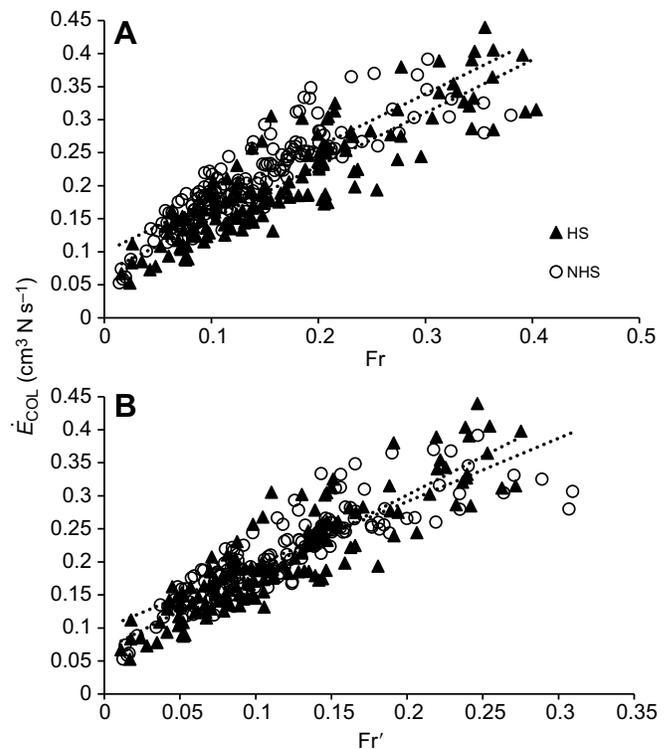
Estimated cost of locomotion ( $\dot{E}_{COL}$ ; see Eqn 2) was increased by an average of  $0.029 \pm 0.007$  cm<sup>3</sup> N s<sup>-1</sup> at all speeds by NHS walking [Fig. 5A;  $\chi^2(1) = 9.92$ ,  $P = 0.0016$ ] when using  $Fr$ . However, foot posture had no significant effect on  $\dot{E}_{COL}$  when  $Fr'$  was used to adjust for effective limb length [Fig. 5B;  $\chi^2(1) = 1.26$ ,  $P = 0.2614$ ]. These results suggest the effects of foot posture on the energetics of walking are due in some part to the increased ELL associated with a HS gait.  $\dot{E}_{COL}$  was not significantly different between HS and NHS footfalls after calculating limb length dynamically [see Fig. S3;  $\chi^2(1) = 0.19$ ,  $P = 0.6660$ ].

### Walk-to-run transition

NHS gait WTR transition speeds (m s<sup>-1</sup>) were significantly lower than HS gaits ( $P = 0.0025$ ), and therefore subjects transitioned to running at a significantly higher  $Fr$  during HS walking (HS =  $0.426 \pm 0.055$ , NHS =  $0.365 \pm 0.045$ ,  $P = 0.0025$ ). However, when taking into account  $L'$ , there were no significant differences in  $Fr'$  at



**Fig. 4. The effect of  $L'$  on Froude number.** (A)  $Fr$  numbers differed significantly between preferred and fast trials ( $N = 14$ ,  $F_{1,13} = 8.78$ ,  $*P = 0.011$ ). (B) After adjustment using  $L'$ , there was no significant difference between HS and NHS trials ( $N = 14$ ,  $F_{1,13} = 0.543$ ,  $P = 0.4744$ ). HS, heel-strike; NHS, non-heel-strike; S, slow; P, preferred; F, fast; SA, slow adjusted; PA, preferred adjusted; FA, fast adjusted.

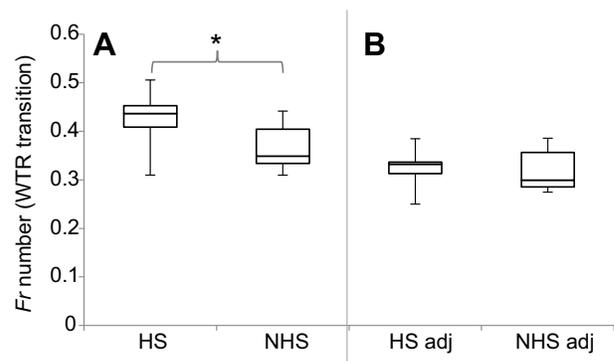


**Fig. 5. Estimated cost of locomotion ( $\dot{E}_{COL}$ ) before and after accounting for the effects of HS on  $L$ .** (A)  $\dot{E}_{COL}$  [ $V_{mus}/t_c$  (cm<sup>3</sup> N s<sup>-1</sup>)] differed significantly before limb length was adjusted for a heel-striking gait ( $N = 12$ ,  $\chi^2(1) = 20.56$ ,  $P < 0.0001$ ). (B) The estimated COL was not significantly different between foot postures ( $N = 12$ ,  $\chi^2(1) = 2.23$ ,  $P = 0.1353$ ) when using  $Fr'$ .

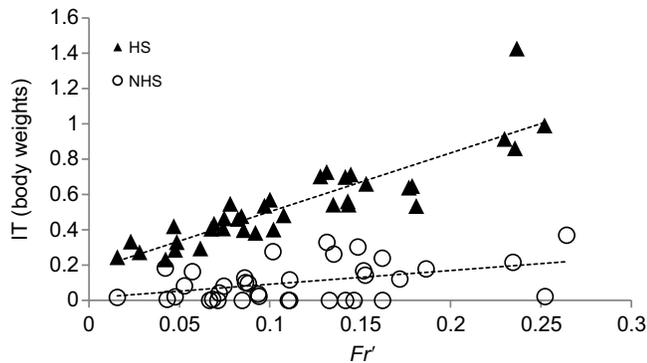
the WTR transition (Fig. 6; HS =  $0.322 \pm 0.038$ , NHS =  $0.319 \pm 0.041$ ,  $P = 0.43$ ). Thus, the differences in WTR transition speed between HS and NHS walking appear to be due to the effects of foot posture on ELL. DC dimensionless  $Fr'$  WTR transition speeds were not statistically different between HS and NHS (see Fig. S4;  $P = 0.34$ ).

### Impact transient

NHS walking reduced impact transients by an average of  $0.447 \pm 0.031$  bodyweights compared with HS walking (Fig. 7;  $\chi_1^2 = 98.79$ ,  $P < 0.0001$ ). Similar to running (Lieberman et al., 2010), subjects displayed minimal IT values (Fig. 7) during NHS walking



**Fig. 6. The effect of foot posture on walk-to-run (WTR) speed.** (A) Froude number for hip height ( $L$ ) WTR transition speed was significantly different between HS and NHS trials ( $N = 14$ ,  $*P = 0.0025$ ). (B) However,  $L'$  adjusted WTR  $Fr'$  transition speeds were not significantly different ( $N = 14$ ,  $P = 0.43$ ).



**Fig. 7. Impact transients (ITs) in HS and NHS gaits.** HS ITs (in multiples of body weight) were significantly higher at all speeds compared with NHS ITs ( $N=12$ ,  $\chi^2=98.79$ ,  $P<0.0001$ ).

throughout the self-selected speeds (range, 0.00–0.37 bodyweights). IT values in HS trials, however, displayed much greater variation and increased with speed (Fig. 7; range, 0.23–1.43 bodyweights).

## DISCUSSION

This study examined the effects of both plantigrady and HS on the human walking gait. By experimentally altering foot posture during walking, we measured the effects of intra-individual limb length changes on walking mechanics (i.e.  $L$  versus  $L'$  under different conditions). A plantigrade foot and HS ground contact lengthens the effective limb ( $21.9\pm 3.9\%$  compared with NHS  $L'$ ) by shifting the COP anteriorly across the entire length of the foot throughout stance. Our results suggest that HS walking plays an important role in minimizing energetic costs during walking, which is aided by lengthening ELL ( $L'$ ). As hypothesized, energy and speed differences between HS and NHS walking lose significance once  $L'$  is used to calculate  $Fr'$ . Thus, if human HS and NHS walkers were two different organisms with limb lengths adjusted for COP translation, we would conclude that their locomotor costs scale appropriately with limb length regardless of foot morphology or speed. Additionally calculating  $L'$  using data from across the step, both dynamically and using a two-point, touchdown and toe-off method, shows that translation of the COP effectively lengthens the inverted pendulum strut. While both methods are valid, we suggest that for ease of use by future researchers, the two-point method of calculating  $L'$  is appropriate for most studies.

Our data also support the importance of ELL (and therefore foot-posture) in determining WTR transition speed. The reduction in transition speed during NHS walking is well explained by the increased  $L'$  in HS compared with NHS walking. Using  $L'$ ,  $Fr'$  at the WTR transition does not differ significantly between HS and NHS walking, even though absolute transition speeds are statistically different. Not surprisingly, because of the importance of limb length in calculation of  $Fr$ , the  $Fr'$  at which subjects transitioned from walking to running calculated using  $L'$  was lower than values from previous research (Hreljac et al., 2008; Kram et al., 1997; Thorstensson and Roberthson, 1987). Increased ELL due to HS gaits reduced  $Fr'$  at the WTR transition to  $0.322\pm 0.038$ , which is close to values found for the walk-to-trot transition for horses across a broad size range ( $Fr\approx 0.30$ – $0.37$ ) (Griffin et al., 2004). These results raise an intriguing suggestion that one advantage of HS foot-posture is an increase in range of available walking speeds, delaying the transition to a running gait.

While there are important benefits to using an HS gait, we also found that NHS postures effectively reduce ITs during walking, similar to results of studies examining ITs in NHS running gaits (Lieberman et al., 2010). These results suggest that the evolution of consistent HS walking in our hominin ancestors came with trade-offs and that foot anatomy specific to our lineage (e.g. a robust calcaneal tuberosity) may reflect the tolerance of consistently high ITs (see Gebo, 1992; Latimer and Lovejoy, 1989).

## Study limitations

While our results support the notion that there are trade-offs between energy cost and impact forces in HS and NHS walking, the estimation of energy costs from the inverse dynamics analysis relies on key assumptions that require further testing. As noted by Roberts et al. (1998b) when developing this method, the link between active muscle volume and the metabolic costs of locomotion relies on the assumption that muscle force produced per unit of cross-sectional area ( $\sigma$ ) remains constant across experimental conditions. Within an individual, this assumption is upheld across experimental conditions if muscles operate with similar relative shortening velocities ( $v/v_{\max}$ ) and in similar regions of the muscle force-length curve. If these assumptions are violated, the same muscle might activate different amounts of volume to generate a given force under different experimental conditions. In our study, it is possible that changes in ankle and knee kinematics lead to muscle activation at different shortening velocities or different portions of the force-length curve, which would limit our ability to estimate the energy costs of walking between gaits with very different limb postures.

Previous work has shown that comparisons between humans and other mammals walking and running with different joint postures do not violate these assumptions. As described earlier, estimates of active muscle volume seem to reflect the energy costs of both walking and running in the same individuals (see Biewener et al., 2004; Ren et al., 2010). Thus, differences in joint angles during stance across speeds do not significantly affect the use of this model. This method also accounts for energy cost differences within individuals using fundamentally different gaits. For example, despite key difference in joint posture (Pontzer et al., 2014), between-gait differences in active muscle volume in chimpanzees walking bipedally and quadrupedally explain differences in metabolic cost measured through oxygen consumption (Sokol et al., 2007). Similarly, metabolic costs and active muscle volumes increased proportionally in humans walking with a flexed-knee and hip gait compared with humans walking with normal extended-limb bipedalism (Carey and Crompton, 2005; Foster et al., 2013). This 'groucho' gait is an entirely novel gait pattern with limb joints acting at different levels of flexion during stance phase. Finally, Wright and Weyand (2001) compared active muscle volume and metabolic costs in forwards and backwards running. The heel touches down after the toes in backwards running, making it a novel gait, and yet the increased metabolic costs were matched by the same percentage increase in active muscle volume (Wright and Weyand, 2001). Therefore, while we did not test the assumptions of the active muscle volume model using direct measures of metabolic cost, we believe there is strong support for its use here, and this method provides an important perspective on the potential energetic advantages of walking with a consistent HS.

## Evolutionary implications of HS walking

Our results have important implications for the reconstruction of morphology and locomotor performance in the fossil record. Since apes use a variety of footfall patterns in both quadrupedal and

bipedal gaits, we believe it is likely that our pre-bipedal ancestors also experienced variation in foot postures at touchdown, including both human-like HS, initial contact with the heel and midfoot simultaneously, and NHS walking, as examined here. If true, the evolution of consistent HS walking occurred some time within the hominin lineage, either with the earliest bipeds, or later in human evolution. By focusing on the two extreme foot postures described for nonhuman apes (HS and NHS), we have highlighted the effects of COP translation during the stance phase on locomotor biomechanics. In doing so, we have shown that a shift to a consistent HS, as we suspect occurred during early human evolution, has advantages over plantigrade species that use gaits with more minimal COP translations.

Foot anatomy in early hominins suggests that the use of a consistent HS may have been beneficial across much of human evolutionary history. While the feet of early bipeds lack derived features seen in the genus *Homo* that allow for effective endurance running, they may have been well adapted to HS walking (Bramble and Lieberman, 2004; Spoor et al., 1994). For example, the relatively short toes, and therefore shorter feet, seen in modern humans are advantageous to endurance running because they reduce plantar–flexor moments at the metatarso–phalangeal joints (Rolian et al., 2009) and probably evolved with the origins of the *Homo* genus. *Australopithecus*, a hominin genus that preceded *Homo*, had relatively long feet, which Rolian et al. (2009) hypothesize would have detracted from running performance. Our results suggest that relatively long feet in australopithecines may have led to improved walking performance through increased translation of the COP, and therefore increased ELL. Thus, foot proportions in fossil hominins may reflect competing selection pressures for walking and endurance running.

This hypothesis requires a walking gait with consistent human-like HS in species with relatively long feet. The Laetoli footprints (fossilized footprints found in volcanic ash at Laetoli, Tanzania) are perhaps the best indicator that, by at least 3.6 million years ago, ancient hominins walked with an HS (Leakey, 1981; Leakey and Hay, 1979; Raichlen et al., 2010). Most researchers believe these footprints were made by *Australopithecus afarensis*, and while complete fossil feet are rare in the early hominin fossil record, estimated foot lengths suggest that these early bipeds had relatively long feet compared with modern humans (Sellers et al., 2005). By combining estimated foot lengths with COP<sub>c</sub> (see Fig. 1) and hip excursion data collected here, it is possible to predict how increased foot length would have altered  $L'$  in these early bipeds. Based on fossil limb lengths and estimates of foot length (Jungers, 1988; Sellers et al., 2005; Wang et al., 2004), *A. afarensis* (AL 288-1) had an  $L'$  of  $\approx 0.725$  m when using HS gaits, an increase of  $\approx 40.4\%$  from  $L$  for this species ( $\approx 0.516$  m). In our sample of modern humans, calculations of  $L'$  increased effective limb length by  $32.6 \pm 3.3\%$  compared with  $L$ . Thus, the relatively long feet of *A. afarensis* led to a greater increase in  $L'$  compared with modern humans.

While long feet may have improved walking performance for *A. afarensis*, other early bipeds may have walked without using an HS. For example, *Australopithecus sediba*, a South African hominin living approximately 2 million years ago (Dirks et al., 2010), exhibits foot and ankle morphology suggestive of more ape-like foot postures (Desilva et al., 2012; Zipfel et al., 2011). These features include gracile calcaneal tubers, increased mid-foot mobility, medial plantar processes indicative of pedal grasping ability, and an ability to invert the foot similar to extant great apes during vertical climbing (Desilva et al., 2012; Zipfel et al., 2011). These

traits may improve climbing performance while putting less stable foot and ankle joints at a higher risk of injury in the presence of large impact forces during HS walking. Our results suggest that retaining NHS postures as part of their footstrike repertoire may have allowed *A. sediba* to maintain climbing ability by reducing impact transients.

Although reductions in foot length occurred with the evolution of the genus *Homo*, possibly to improve endurance running performance (Rolian et al., 2009), variation in foot length suggests the advantages of a long  $L'$  may have persisted in some species until relatively recently. For example, *Homo floresiensis*, a small-bodied hominin living on the island of Flores (Morwood et al., 2004), possessed relatively long feet compared with other members of the genus *Homo* (Jungers et al., 2009a). The foot of *H. floresiensis* (LB1) is roughly 70% of the length of its femur (Jungers et al., 2009a), which is exceptional compared with modern human foot lengths (54% of femur length) (White and Suwa, 1987). The long foot of *H. floresiensis* (Jungers et al., 2009b) would increase  $L'$  to  $\approx 0.797$  m, a  $\approx 43.6\%$  increase from hip height ( $L \approx 0.555$  m). Our sample of modern humans produced an average  $L'$  of  $1.18 \pm 0.06$  m ( $L = 0.90 \pm 0.05$  m) for comparison.

Finally, *Homo neanderthalensis* feet display a unique mix of short toes (Trinkaus and Hilton, 1996) and long calcaneal tubers (Miller and Gross, 1998; Raichlen et al., 2011; Schmitt, 1998; Trinkaus, 1975, 1983). The inclusion of short, robust limbs (Holliday, 1997; Trinkaus, 1981) suggests that Neanderthals were lackluster runners compared with modern humans, raising future research questions about Neanderthal  $L'$  and the selective pressures on walking/running. Thus, our results provide a novel view of foot length in the evolution of human walking and allow us to generate new, testable hypotheses for inter-specific variation in energy costs of walking throughout the human lineage.

## Conclusions

This study shows that human NHS walking decreases the anterior translation of the COP along the foot, shortening ELL ( $L'$ ). Adopting a plantarflexed foot posture at touchdown forced subjects to walk at a slower absolute speed, yet did not change the dynamically similar foot posture adjusted  $Fr'$  or estimated COL. Additionally, NHS gaits reduced absolute WTR transition speeds but not WTR  $Fr'$  compared with HS walking.

A long rigid foot may have been important to early bipeds by increasing walking speed in species that lack adaptations for endurance running. Our results suggest that both HS gaits and a relatively long rigid foot may have lengthened  $L'$  in early bipeds, thereby increasing maximum walking speed without affecting locomotor costs. While this was likely true for striding taxa like *A. afarensis*, other early bipeds, such as *A. sediba* may have retained NHS gaits as part of their variation in foot-landing postures to preserve an arboreal lifestyle, with reduced impact transients allowing for skeletal features of the feet best suited for climbing. Future work should focus on additional advantages NHS walking confers in specific ecological conditions inhabited by species with more mosaic foot morphology, such as *A. sediba*.

Interestingly, as endurance running entered the repertoire of early *Homo* species, toes shortened to reduce large digit flexor forces (Rolian et al., 2009). The relationship between toe length (and thus foot length) and absolute walking speed may have been mitigated by the acquisition of an efficient running gait, reducing the pressure of maintaining fast absolute walking speeds. Foot length, therefore, may be seen as an indicator of selection pressures on walking or running in the fossil record, and foot length and posture play an integral role in the evolution of bipedal locomotion. Thus, changes

in hominin foot length may directly reflect selection pressures on locomotor speed and energy costs.

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#### Competing interests

The authors declare no competing or financial interests.

#### Author contributions

Conceptualization, J.T.W. and D.A.R.; Methodology, J.T.W. and D.A.R.; Investigation, J.T.W.; Writing – Original Draft, J.T.W. and D.A.R.; Writing – Review & Editing, J.T.W. and D.A.R.; Funding Acquisition, D.A.R.; Resources, D.A.R.; Software, J.T.W.

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#### Supplementary information

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