

The influence of foot posture on the cost of transport in humans

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SUMMARY

Although humans appear to be specialized for endurance running, the plantigrade posture of our feet, in which the heel contacts the substrate at the beginning of a step, seems incompatible with economical running. In this study, we tested the hypothesis that plantigrade foot posture reduces the energetic cost of transport (COT) during walking in humans. When human subjects walked with their heels slightly elevated in a 'low-digitigrade' posture, COT increased by 53% above that of normal plantigrade walking. By contrast, there was no difference in COT when subjects ran with digitigrade *versus* plantigrade foot posture. Stride frequency increased and stride length decreased when subjects switched to digitigrade walking; however, this change did not influence the COT. Additionally, we found that possible reductions in postural stability appear not to have caused the elevated cost of digitigrade walking. Digitigrade walking, however, did (1) increase the external mechanical work performed by the limbs; (2) reduce the pendular exchange of kinetic and potential energy of the center of mass; (3) increase the average ground reaction force moment at the ankle joint; and (4) increase the recruitment of major extensor muscles of the ankle, knee, hip and back. These observations suggest that plantigrade foot posture improves the economy of walking. Relative to other mammals, humans are economical walkers, but not economical runners. Given the great distances hunter-gatherers travel, it is not surprising that humans retained a foot posture, inherited from our more arboreal great ape ancestors, that facilitates economical walking.

Key words: great ape, *Homo*, plantigrade, running, walking, foot strike type.

INTRODUCTION

Compared with other great apes, humans are hypothesized to be physiologically and anatomically specialized for endurance running (Carrier, 1984; Bramble and Lieberman, 2004). Although many species of mammals run faster over short distances, very few mammals have the aerobic, long-distance stamina of humans, particularly in warm or hot environments (Liebenberg, 2008; Liebenberg, 2006). Derived characters such as a relative lack of body hair, an exceptional ability to sweat (Carrier, 1984), a capacity to store elastic strain energy in extensor muscle-tendons of the ankle joint (Bramble and Lieberman, 2004), and short toes (Rolian et al., 2009) appear to be adaptations for endurance running.

Given this apparent specialization for endurance running, the anatomy of human feet presents a paradox. The heel-down (i.e. plantigrade) foot posture, that we share with the other great apes (Schmitt and Larson, 2005; Gebo, 1992), is both rare among mammals and inconsistent with adaptation for economical running (Fig. 1). Most mammalian species, including the fastest and most economical runners, have either digitigrade or unguligrade feet, in which the heel is held elevated above the ground so that the animal walks and runs on the balls of its feet or on its toes, respectively. Digitigrade and unguligrade postures are thought to improve locomotor economy by increasing step length (Hildebrand and Goslow, 1998). Additionally, plantigrade foot posture, in which the heel contacts the substrate and absorbs energy at the start of a running step, is expected to limit storage and recovery of elastic strain energy in the extensor muscles of the ankle joint (Ardigo et al., 1995). Furthermore, elite human sprinters, middle distance runners and some of the fastest marathon runners use digitigrade rather than

plantigrade posture (Ardigo et al., 1995; Nilsson and Thorstensson, 1989; Cavanagh and Lafortune, 1980). Thus, if humans are specialized for endurance running, why did our lineage retain plantigrade feet?

Plantigrade feet may confer an energetic advantage during walking. Relative to other species, humans appear to be economical walkers (Sockol et al., 2007; Steudel-Numbers, 2003). Humans also differ from other studied species in that it costs us substantially less to walk a given distance than to run the same distance (Rubenson et al., 2007; Farley and McMahon, 1992; McGeer, 1990; Margaria et al., 1963). This energetic advantage may be partially due to a reduction in the loss of mechanical energy associated with the directional change of the center of mass trajectory during a walking step (Ruina et al., 2005; McGeer, 1990). Large feet, in which the center of pressure translates from the rear of the foot to the tips of the toes, as occurs in plantigrade feet, appear to reduce these directional changes and therefore decrease the mechanical energy loss (Adamczyk et al., 2006). Additionally, humans are known to have greater mechanical advantage at their limb joints during walking than during running (Biewener et al., 2004) and plantigrade foot posture may be partially responsible for this difference. Thus, although the plantigrade structure of the human foot does not appear to be consistent with specialization for endurance running, it may help explain how humans are able to walk economically.

To determine if plantigrade foot posture influences the energetic cost of walking and running, we investigated the effect of different foot postures on the cost of walking and running in human subjects. Previously, Ardigo et al. (Ardigo et al., 1995) found that the cost of transport did not differ in human subjects running with forefoot

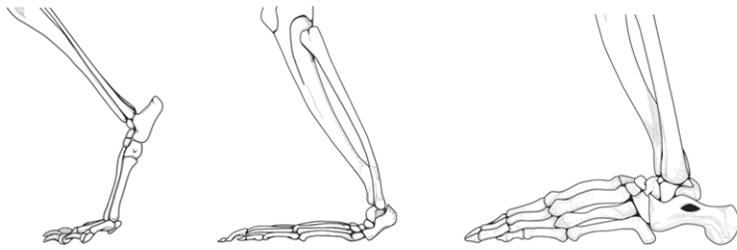


Fig. 1. Illustrations of the digitigrade locomotor foot posture that characterizes most therian mammals (e.g. dog; left), the semiplantigrade posture typical of most primates (e.g. gibbon; center) and the plantigrade posture characteristic of all great apes (e.g. gorilla; right). The illustration of the foot skeleton of the dog is modified from Hildebrand and Goslow (Hildebrand and Goslow, 1998) and the skeletons of the gibbon and the gorilla are modified from Gebo (Gebo, 1992).

(i.e. digitigrade) *versus* rearfoot (i.e. plantigrade) striking posture. To include walking in the analysis, we measured oxygen consumption and quantified several indices of locomotor mechanics as subjects walked and ran with their heels contacting the ground at the beginning of stance phase (i.e. plantigrade posture) or with their heels elevated so that they landed on the balls of their feet (i.e. digitigrade posture; Fig. 2). Although walking and running on the balls of one's feet are not typical for many of us, they are natural behaviors for humans. As mentioned above, many elite track athletes habitually run on the balls of their feet. Furthermore, during running unshod individuals avoid landing on their heels and instead land on the balls of their feet (Lieberman et al., 2010; Divert et al., 2005). Lieberman et al. (Lieberman et al., 2010) suggested that landing on the heels when running is a recent and artificial consequence of the thick-heel design of modern running shoes. Toe walking is common among young children and intermittent toe walking is considered normal up to the age of 7 years (Kelly et al., 1997; Kalen et al., 1986). It is also common for humans (and consequently, cartoon characters) to adopt a 'tiptoeing' foot posture when they wish to walk covertly and with stealth. Thus, the experiments of this study are based on a comparison of natural human movements.

MATERIALS AND METHODS

We tested three foot postures during walking: plantigrade, low-digitigrade, in which the heel was held slightly elevated above the substrate during stance (approximately 1 cm; Fig. 2), and high-digitigrade, in which the heel was held elevated as much as possible above the substrate during the support phase of a step. To avoid injuries during running trials, we tested only plantigrade and low-digitigrade foot postures. Subjects gave informed consent. Procedures associated with the recording of the cost of transport and mechanics of digitigrade walking were approved by the University of Utah Internal Review Board and procedures associated with the recording of surface EMGs were approved by the Ethics Committee of the University of Jena (0558-11/00).

Analysis of the cost of transport

We measured the cost of transport (COT) as subjects walked and ran with plantigrade and digitigrade foot posture on a motorized treadmill. All 11 subjects (seven males, four females, body mass 70.2 ± 12.2 kg; age 33 ± 11.1 years; means \pm s.d.) were healthy, and seven were competitive runners, triathletes or soccer players.

Oxygen consumption was measured using open-circuit indirect calorimetry. The subjects wore a full-face mask (Hans Rudolph, Inc; Kansas City, MO, USA) through which air was drawn at a flow rate measured with a gravity flow meter (King Instrument Co., Garden Grove, CA, USA). A small fraction of the expired air was continuously monitored for oxygen content with an oxygen analyzer (S-3A/1, AEI Technologies, Naperville, IL, USA).

We asked the subject to pick their preferred walking speed by self-adjusting the speed of the treadmill (5.17 ± 0.25 km h⁻¹; mean \pm s.d.). Using this speed, we collected oxygen consumption data during three walking trials: with plantigrade, low-digitigrade and high-digitigrade foot postures. During each trial, we gave the subjects 4 min to reach metabolic steady state and then collected oxygen consumption data for the last minute of the 5-min trial. Subjects rested by standing quietly for 3 min between walking trials. The order of the walking trials was randomized among subjects. Each recording session began with a recording of oxygen consumption during quiet standing. We also collected data as the subjects ran using plantigrade and low-digitigrade foot posture at two to four running speeds: 7.2, 9.7, 12.1 and 13.7 km h⁻¹. Subjects rested for 5 min between each running trial. The order of the running speeds and foot posture was randomized among subjects. The rate of oxygen consumption during quiet standing was subtracted from the rates during walking and running to calculate the rate of oxygen consumed for locomotion. The mass-specific rate was divided by the speed of walking or running to yield the net COT (the oxygen consumed to move a kilogram of body mass one kilometer). Sample size varied at the different speeds because initially we did not collect running data at the low running speed and some of the subjects could not sustain the two highest running speeds: walking at preferred speed $N=11$; running at 7.2 km h⁻¹ $N=6$; 9.7 km h⁻¹ $N=10$; 12.1 km h⁻¹ $N=9$; 13.7 km h⁻¹ $N=6$.

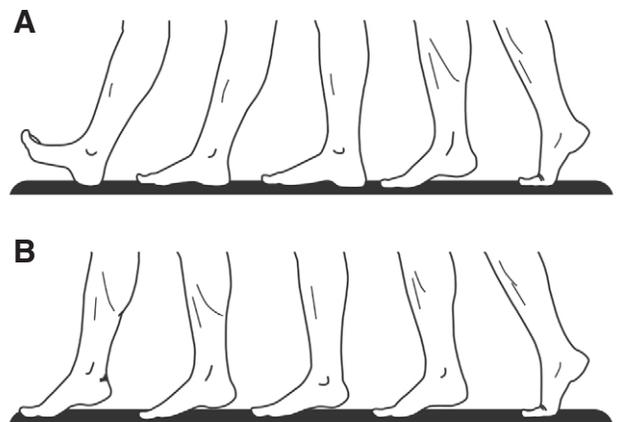


Fig. 2. Illustrations of the plantigrade (A) and low-digitigrade (B) foot postures investigated in this study. The heel of the foot is used to make contact with the substrate in a plantigrade step whereas the toes and ball of the foot contact the substrate in a digitigrade step. Also note that the heel is held elevated above the substrate throughout the step during a digitigrade step.

Analysis of recruitment of the extensor muscles of the limb and back

We monitored the activity of 13 muscles of the back and leg during plantigrade, low-digitigrade and high-digitigrade walking (Table 1). Subjects walked at their preferred speed for a 4-min warm-up period and then we recorded 20 steps for each of the three foot postures. Sixteen healthy men (body mass 73.6 ± 7.4 kg; age 32.1 ± 8.1 years, means \pm s.d.) participated in this study.

Methods followed those of Anders et al. (Anders et al., 2009). Briefly, bipolar surface electromyography (SEMG; 5–700 Hz, Biovision, Wehrheim, Germany) was recorded from each muscle simultaneously from both sides of the body. Electrode positions were chosen according to internationally established recommendations (Hermens et al., 1999; Ng et al., 1998). Disposable Ag–AgCl electrodes (H93SG, Arbo, Germany) with a circular, 1 cm diameter uptake area and an inter-electrode distance of 2.5 cm were used. The signal from an accelerometer attached to the left foot was used to identify contact of the foot with the substrate, i.e. the beginning of the stride cycle.

Twenty strides were analyzed for each of the walking postures. Raw SEMGs were centered and high-pass filtered (fourth order Butterworth filter; 20 Hz). Grand averaged SEMG curves were calculated for all walking postures. To do this, we calculated root mean square (RMS) values using a window of 15 ms. Data from both sides of the body were pooled by shifting the time normalized SEMG curves of all right side muscles by 50% of stride cycle. From these pooled grand averaged curves, mean integrated area ($\mu\text{V} \cdot \text{s}$) was calculated for each foot posture.

Analysis of the effect of change in stride frequency on cost of transport

Stride frequency increased by 7.6% when subjects switched to digitigrade walking (see Results). An increase in stride frequency might contribute to an elevated COT by increasing the frequency of muscle recruitment and/or by increasing accelerations required to swing the limbs back and forth during each stride. To address these possibilities, we measured the energetic cost of walking with plantigrade posture at both a subject's preferred stride frequency and at a stride frequency that was 10% greater than the subject's preferred frequency. Ten healthy subjects participated in this

experiment (six males, four females, body mass 70.6 ± 13.0 kg; age 29.2 ± 11.3 years; means \pm s.d.). We recorded oxygen consumption as subjects walked with plantigrade foot posture at both frequencies on a treadmill. They synchronized the heel strike of one of their feet with a metronome set at their measured preferred stride frequency (control) and at the frequency that was 10% greater than their preferred frequency (experiment). During each trial we gave the subjects 4 min to reach metabolic steady state and then measured their oxygen consumption for the last minute of the 5-min trial. Each recording session began with a recording of oxygen consumption during quiet standing.

Analysis of the effect of decreased stability on metabolism

We hypothesized that a loss of stability due to supporting the body's weight on the balls of the feet might contribute to the increase in metabolism observed during digitigrade walking. To test the effect of reduced stability resulting from digitigrade posture on energetic cost, we compared the oxygen consumption of nine subjects (six males, three females, body mass 71.5 ± 13.5 kg; age 29.0 ± 12.0 years; means \pm s.d.) standing with low-digitigrade posture while contacting a handrail of the treadmill with one hand, to provide stability, to when they stood with low-digitigrade posture without holding the handrail. We calculated the difference in oxygen consumption between standing with support *versus* standing without support. During each trial, we gave the subjects 4 min to reach metabolic steady state and then measured their oxygen consumption for the last minute of the 5-min trial. Each recording session began with a recording of oxygen consumption during quiet standing in plantigrade posture (without contacting the handrail).

Interpretation of this analysis is limited by the fact that the measurements are of static stability rather than the dynamic stability that occurs during walking. Nevertheless, we suspect that maintenance of static stability while standing in digitigrade posture, as tested here, is actually more expensive energetically than maintenance of dynamic stability during digitigrade walking.

Analysis of the external mechanical work

Plantigrade foot posture has been suggested to increase the energetic economy of walking by reducing the work that the limb muscles must do in the transition from one step to the next (Rolian et al.,

Table 1. Mean of the integrated area (μVs) of the activity of muscles of the back and leg during walking with plantigrade, low-digitigrade and high-digitigrade foot posture

Muscle	Function	Plantigrade (μVs ; mean \pm s.d.)	Low digitigrade (μVs ; mean \pm s.d.)	High digitigrade (μVs ; mean \pm s.d.)	Change P to LD (%)	Change P to HD (%)	Change LD to HD (%)
Erector spinae	Extensor of back	4.141 \pm 1.548	4.806 \pm 2.100	5.570 \pm 1.604	16*	42**	25
Multifidus	Extensor of back	4.400 \pm 1.236	5.616 \pm 1.944	6.610 \pm 2.672	28**	49***	17*
Gluteus maximus	Extensor of hip	2.243 \pm 0.900	2.488 \pm 1.016	2.906 \pm 1.072	11**	32***	19*
Gluteus medius	Stabilizer of hip	6.411 \pm 2.424	6.343 \pm 2.876	9.240 \pm 4.700	–2	43***	49***
Semitendinosus	Extensor of hip and flexor of knee	5.235 \pm 1.888	7.569 \pm 3.332	9.355 \pm 3.968	44***	79***	27**
Biceps femoris	Extensor of hip and flexor of knee	5.085 \pm 1.768	8.728 \pm 3.796	11.409 \pm 4.472	74***	140***	37***
Tensor fascia latae	Extensor of knee	4.364 \pm 1.628	5.732 \pm 1.688	10.860 \pm 4.260	39**	188***	106***
Vastus lateralis	Extensor of knee	5.181 \pm 1.648	6.391 \pm 1.900	11.214 \pm 3.700	28*	133***	81***
Rectus femoris	Extensor of knee	2.465 \pm 1.372	4.366 \pm 2.120	10.434 \pm 5.508	93***	381***	154***
Vastus medialis	Extensor of knee	4.060 \pm 1.300	6.302 \pm 3.424	12.556 \pm 6.024	55***	215***	110***
Gastrocnemius lat.	Extensor of ankle	9.898 \pm 4.008	21.741 \pm 7.928	26.213 \pm 6.996	128***	182***	26***
Soleus	Extensor of ankle	12.459 \pm 5.024	26.238 \pm 13.236	28.947 \pm 13.312	107***	142***	17
Tibialis anterior	Flexor of ankle	14.439 \pm 4.268	9.513 \pm 2.928	9.998 \pm 3.320	–32***	–28**	7

P, plantigrade; LD, low-digitigrade; HD, high-digitigrade.

* $P < 0.017$; ** $P < 0.0017$; *** $P < 0.00017$; $N = 16$.

2009; McGeer, 1990). During walking, muscular work is required in the step-to-step transition to redirect the trajectory of the center of mass of the body from a forward and downward direction to a forward and upward direction (McGeer, 1990). Plantigrade feet, in which the center of pressure exerted on the ground progresses forward from heel to toe, are thought to produce an energetic savings, compared with smaller digitigrade or unguligrade feet, by reducing the magnitude of the directional change the center of mass velocity must undergo (Adamczyk et al., 2006; Ruina et al., 2005; McGeer, 1990).

To test this, we measured the positive and negative external work performed by each limb as subjects (six males, two females, body mass 73.8 ± 14.2 kg; age 31.1 ± 11.6 years, means \pm s.d.) walked with plantigrade and digitigrade foot posture at their preferred walking speeds. Subjects walked at their preferred speed on an 18-m track and we recorded ground reaction forces with a force plate (Kistler, 9281B SB, Amherst, NY, USA) mounted in the center of the track. Subjects maintained constant walking speed by matching their velocity to markers on a rope-pulley system driven by an adjustable-speed electric motor. To calculate external work, we used the individual limb method (Donelan et al., 2002). Because we recorded forces from only one limb (i.e. from a single force plate), it was necessary to generate composite ground forces to estimate the total force applied to the center of mass. This was done by assuming symmetrical force production from the right and left limbs, adding the vertical and horizontal ground forces recorded during the first period of double limb support to the end of the step, and adding the forces recorded during the second period of double limb support to the beginning of the step. These composite ground forces allowed calculation of the instantaneous velocity of the center of mass (Cavagna, 1975). We then determined the external mechanical power generated by a limb during a step from the dot product of the ground reaction force of the limb and the velocity of the center of mass. We calculated the magnitudes of the positive and negative external mechanical work per step from the time-integrals of the positive and negative portions of the external mechanical power generated by the limb (Donelan et al., 2002).

Walking is distinguished from running by a pendular exchange of gravitational potential and forward kinetic energy during each step (Cavagna et al., 1977). This transfer of energy can result in a 70% reduction in the work required of the locomotor muscles. We suspected that walking digitigrade might in some way decrease the transfer of kinetic and potential energy. To calculate the pendular exchange of potential and kinetic energy during each step (i.e. percentage recover), we used the composite ground forces to calculate the positive external mechanical work done on the center of mass with the combined limb method of Cavagna (Cavagna, 1975). We then subtracted the external work done on the center of mass from the sum of the vertical and forward work done on the center of mass and divided by the sum of the vertical and forward work (Willems et al., 1995; Cavagna et al., 1977).

Analysis of ground reaction force moments at the limb joints

To determine the effect foot posture has on the ground reaction force (GRF) moments at the limb joints, we recorded the force exerted on the ground with a force plate and the kinematics of the ankle, knee and hip joints with high speed video ($250 \text{ images s}^{-1}$) as subjects walked at their preferred speed with plantigrade and low-digitigrade foot posture. We restricted our analysis of joint moments to the components due to the ground reaction forces, and did not quantify contributions to joint moments due to segment mass and inertia, for two reasons. First, it has previously

been shown that the mechanical advantage at the joints differs between walking and running (Biewener et al., 2004) and differences in foot posture and the location of the center of pressure under the foot may be partially responsible. Second, our analysis demonstrated that the COT was not affected by an observed increase in stride frequency associated with digitigrade walking (see below). This implies that digitigrade walking did not influence the net internal work of walking, and, therefore, the internal contributions to joint moments.

We measured the ground reaction force moments at the ankle, knee and hip joints in six subjects (four males, two females, body mass 75.1 ± 14.2 kg; age 30.2 ± 11.4 years, means \pm s.d.) as they walked with plantigrade and low-digitigrade foot postures at their preferred speeds. Ground reaction forces were recorded as described above. Video recordings at 250 Hz were taken of the subjects as they stepped on the force plate, using a NAC HSV 500 camera (Simi Valley, CA, USA). The camera was positioned 6 m from the track to minimize parallax. Markers were placed on the skin over the shoulder (lateral acromion), hip (proximal greater trochanter), knee (lateral condyle), ankle (lateral malleolus), and metatarsophalangeal (base of the fifth proximal phalanx) joints.

Twelve recordings were made of each subject for both plantigrade and low-digitigrade foot postures. From these 12, the three recordings in which the impulses of the fore and aft horizontal forces differed the least (usually less than 10% difference) were selected for analysis. Two-dimensional coordinate data for the joints were obtained by digitizing the video recordings and transforming them into the reference coordinate frame of the digitized ground reaction force data. The length of the ground reaction force moment arms at the ankle, knee and hip joints were determined by calculating the orthogonal distance from the vector of the ground reaction force to the joint marker (Biewener et al., 1992). Ground reaction force moment was calculated by multiplying the magnitude of the ground force by the moment arm.

Statistical analysis

We used non-parametric, Wilcoxon signed-rank tests throughout the analysis. In cases in which the analysis compared plantigrade with low-digitigrade foot posture, we assumed the results were significantly different when the P -value was less than 0.05. In analyses, in which we compared all three foot postures (i.e. plantigrade, low-digitigrade and high-digitigrade), we adopted a simple Bonferroni correction and assumed the results were significantly different when the P -value was less than 0.017. Unless noted otherwise, tests are two-tailed.

RESULTS

Cost of transport

When the subjects walked at their preferred speed with their heels slightly elevated above the surface of the treadmill (i.e. low-digitigrade) the average oxygen consumed to walk a kilometer (COT) increased by $53 \pm 20\%$ (mean \pm s.d.) above that of walking with plantigrade foot posture ($P=0.001$; Fig. 3). When the subjects walked with a high-digitigrade foot posture, the COT increased by $83 \pm 33\%$ above normal plantigrade walking and $21 \pm 23\%$ above low-digitigrade walking ($P=0.001$ and 0.0014 , respectively). By contrast, there was not a significant difference in the COT when subjects ran with low-digitigrade *versus* plantigrade foot posture at four different speeds: 7.2 km h^{-1} ($P=0.156$); 9.7 km h^{-1} ($P=0.846$); 12.1 km h^{-1} ($P=0.496$); and 13.7 km h^{-1} ($P=0.156$). These observations suggest that plantigrade posture bestows a biomechanical advantage during walking but not running.

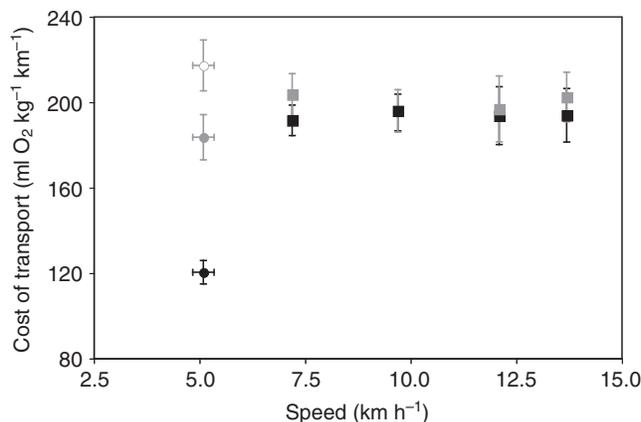


Fig. 3. Cost of transport (mean \pm s.e.m.) versus locomotor speed for human subjects walking (circles) and running (squares) with plantigrade (black), low-digitigrade (gray), and high-digitigrade (white) foot posture. The horizontal error bars on the circles represent the standard error of the subject's preferred walking speeds. Sample size varied at the different speeds: walking at preferred speed $N=11$; running at 7.2 km h^{-1} $N=6$; 9.7 km h^{-1} $N=10$; 12.1 km h^{-1} $N=9$; 13.7 km h^{-1} $N=6$.

Recruitment of limb and back muscles

Eleven of the 13 muscles we studied function to extend the back, hip, knee, or ankle (Table 1). All 11 muscles exhibited significant increases in activity when the subjects switched from plantigrade to low-digitigrade walking. With the exception of the soleus muscle, the extensor muscles also experienced significant increases in activity when the subjects switched from low- to high-digitigrade walking. These increases in activity were most dramatic in the distal muscles. Fig. 4 illustrates the average activity of four extensor muscles. The increase in activity of the extensor muscles of the limb joints suggests that the moment and/or the mechanical work done at each of the joints increased when the subjects switched from plantigrade to digitigrade posture. The elevated activity in the back muscles is consistent with increased stabilization of the trunk associated with increased mechanical work by the limbs.

Effect of stride frequency

On average, stride frequency during low-digitigrade walking was 7.6% ($P<0.0001$) higher than that during plantigrade walking. An increase in stride frequency might contribute to an elevated COT by increasing the frequency of muscle recruitment and/or by increasing accelerations required to swing the limbs back and forth during each stride. Nevertheless, the increase in stride frequency appears to have had little or no effect on the COT. We found that COT did not differ between plantigrade trials at the preferred stride frequency and plantigrade trials at 110% of the preferred stride frequency: $149 \pm 43 \text{ ml O}_2 \text{ kg}^{-1} \text{ km}^{-1}$ (mean \pm s.d.) versus $150 \pm 40 \text{ ml O}_2 \text{ kg}^{-1} \text{ km}^{-1}$ ($P=0.423$). Based on this result, we assumed that the increase in stride frequency did not significantly change the internal work of the limb and for this reason we did not quantify internal work.

Potential effect of reduced stability

We hypothesized that a loss of stability when subjects walked with digitigrade posture might contribute to the increase in metabolism observed during digitigrade walking. To test this, we compared the oxygen consumption of subjects standing with low-digitigrade posture stabilized versus non-stabilized. On average, instability from low-digitigrade standing was associated with an $8.8 \pm 5.4\%$

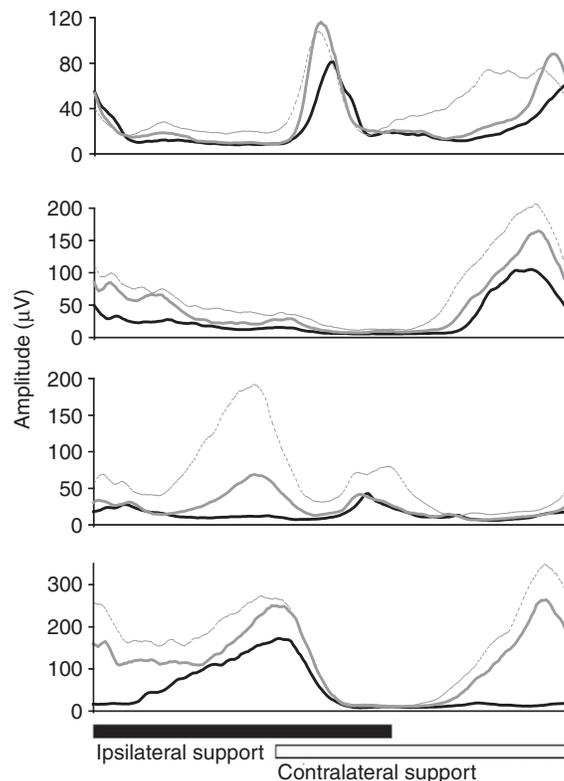


Fig. 4. Grand averaged SEMG curves of the multifidus, biceps femoris, rectus femoris and lateral gastrocnemius muscles from 16 subjects as they walked at their preferred speed with plantigrade (black), low-digitigrade (gray) and high-digitigrade (dashed) foot posture. The stride period starts at the time of ground contact of the ipsilateral foot and is indicated by bars at the bottom of the figure. Stance duration was 63% of the stride cycle for all three foot postures. Data from the two legs were pooled.

(mean \pm s.d.) increase in oxygen consumption (increase of $0.03 \text{ ml O}_2 \text{ kg}^{-1} \text{ min}^{-1}$). This represents 1.9% of the cost to walk with a low-digitigrade posture. Thus, this measure of the metabolic cost of low-digitigrade instability suggests that increased instability is not a significant contributor to the 53% increase in metabolism.

Additionally, activity of two muscles that are expected to be associated with postural stability did not increase when subjects walked with low-digitigrade posture. The gluteus medius muscle abducts the leg and is generally thought to help provide lateral stability during walking. Its activity did not change when subjects switched from plantigrade to low-digitigrade walking (Table 1). However, activity of this muscle increased by 76% when the subjects used a high-digitigrade posture, indicating that reduced stability may explain part of the elevated cost of high-digitigrade walking. The tibialis anterior muscle is a flexor of the ankle joint. Increased co-activation of this muscle with the extensors to stabilize the ankle joint is expected in situations in which postural control is reduced. Relative to plantigrade walking, activity of the tibialis anterior muscle decreased when the subjects switched to both low- and high-digitigrade walking; suggesting that postural stability was not greatly impaired by the digitigrade postures.

External mechanical work performed by the limbs

Plantigrade foot posture has been suggested to increase the energetic economy of walking by reducing the work that the limb muscles must do in the transition from one step to the next (Ruina et al., 2005; McGeer, 1990). We found that the rate of both positive and

negative mechanical work performed by the limbs during a walking stride was higher when subjects walked with low-digitigrade than when they walked with plantigrade posture. Average positive power was $1.015 \pm 0.465 \text{ W kg}^{-1}$ (mean \pm s.d.) during plantigrade walking and $1.157 \pm 0.459 \text{ W kg}^{-1}$ during low-digitigrade walking ($P=0.011$, one-tailed). Average negative power was $-0.975 \pm 0.174 \text{ W kg}^{-1}$ during plantigrade walking and $-1.136 \pm 0.207 \text{ W kg}^{-1}$ during low-digitigrade walking ($P=0.004$, one-tailed). These numbers represent a 16–17% increase in the rate of external mechanical work when subjects switched to low-digitigrade walking. Thus, it appears that one of the ways in which plantigrade foot posture increases walking economy is by reducing the mechanical work required to redirect the trajectory of the body center of mass from a forward and downward direction to a forward and upward direction.

Recovery of potential and kinetic energy

Walking is characterized by a pendular exchange of gravitational potential and forward kinetic energy during each step (Cavagna et al., 1977). We suspected that walking digitigrade might in some way decrease the transfer of kinetic and potential energy. We found that the mean percentage recovery was $70.8 \pm 6.1\%$ (mean \pm s.d.) when the subjects walked with plantigrade posture and $64.8 \pm 6.4\%$ when they walked with low-digitigrade posture. The mean difference in percentage recovery for the eight subjects was $6.0 \pm 5.8\%$ ($P=0.025$, one-tailed). Thus, walking with low-digitigrade posture appears to reduce the pendular transfer of kinetic and potential energy.

Ground reaction force moments at the limb joints

Postural changes in the moments at the joints might also increase the COT because an increase in a joint moment requires greater recruitment of the muscles acting at that joint. At the ankle joint, the GRF vector was in front of the joint for the entire duration of stance so that the moment was always positive (i.e. extensor moment) for both postures (Fig. 5). The average moment arm at the ankle was 40% larger and the average moment impulse was 44% larger during low-digitigrade steps than during plantigrade steps (Tables 2 and 3). By contrast, at the knee and hip joints, the GRF vector was in front of both joints at the beginning of stance but behind the joints by the end of stance, such that both positive and negative moments were observed at both joints. Relative to the ankle joint, the moments at the knee and hip were of small magnitude and, for the most part, not different between plantigrade and low-digitigrade walking (Tables 2 and 3). Thus, plantigrade foot posture reduces the GRF moment at the ankle because the center of pressure resides under the heel of the foot during the first half of stance and this reduces the length of the GRF moment arm.

Table 2. Average ground reaction force moment arms (m) at the limb joints

Joint	Plantigrade (m; mean \pm s.d.)	Low-digitigrade (m; mean \pm s.d.)	P-value
Ankle positive	0.090 \pm 0.017	0.124 \pm 0.012	0.015*
Ankle negative	None	None	–
Knee positive	0.054 \pm 0.007	0.056 \pm 0.017	1.000
Knee negative	-0.038 \pm 0.005	-0.050 \pm 0.012	0.313
Hip positive	0.079 \pm 0.024	0.091 \pm 0.032	0.563
Hip negative	-0.036 \pm 0.020	-0.052 \pm 0.012	0.094

*Statistically significant.

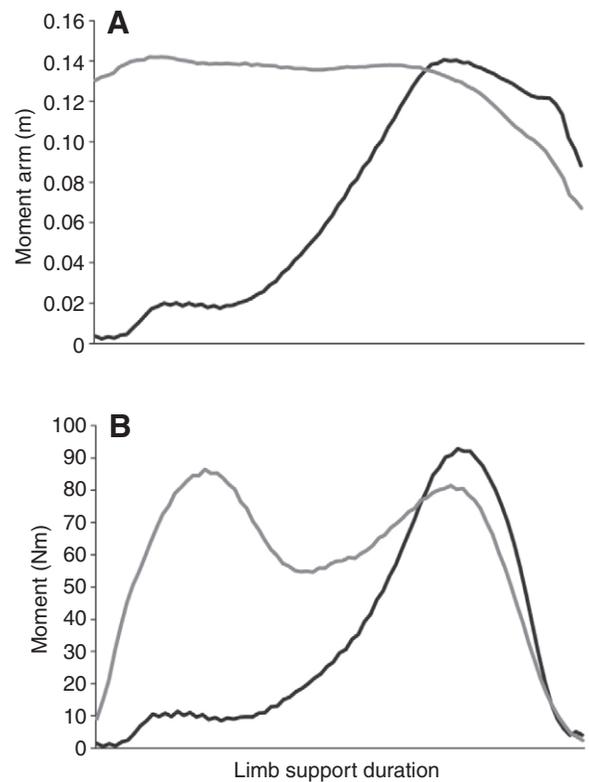


Fig. 5. (A) Sample recording of change in ground force moment arm of the ankle joint as the subject walked with plantigrade (black) and low-digitigrade (gray) foot posture. (B) Sample recording of change in ground force moment of the ankle joint from the same step as shown in (A). The x-axis represents the period of stance phase.

DISCUSSION

When the subjects walked with their heels slightly elevated above the surface of the treadmill (i.e. low-digitigrade) the oxygen consumed to walk a kilometer (COT) increased by 53% above that of walking with plantigrade foot posture. When the subjects walked with a high-digitigrade foot posture, the COT increased further. By contrast, there was no difference in the COT when subjects ran with low-digitigrade *versus* plantigrade foot posture, as has been reported previously (Ardigo et al., 1995). These results indicate that plantigrade foot posture substantially improves locomotor economy during walking but does not influence the economy of running in humans. Our analysis of the activity of the extensor muscles of the

Table 3. Average ground reaction force moment impulses (Nm) at the limb joints

Joint	Plantigrade (Nm; mean \pm s.d.)	Low-Digitigrade (Nm; mean \pm s.d.)	P-value
Ankle positive	34.25 \pm 10.19	48.02 \pm 10.75	0.015*
Ankle negative	None	None	–
Knee positive	8.47 \pm 6.42	4.00 \pm 5.36	0.156
Knee negative	-6.83 \pm 3.04	-10.54 \pm 6.22	0.094
Hip positive	5.97 \pm 6.47	8.64 \pm 7.01	0.094
Hip negative	-7.92 \pm 5.39	-9.85 \pm 4.26	0.156

*Statistically significant.

ankle, knee, hip and back indicates that the moment and/or the mechanical work done at each of the limb joints increased when the subjects switched from plantigrade to digitigrade postures during walking. Our analysis of the mechanics of plantigrade *versus* low-digitigrade walking suggests that the greater economy associated with plantigrade foot posture is *not* related to the observed lower stride frequency or to a potential increase in postural stability. Instead, the improved economy of plantigrade foot posture appears to result from (1) lower collisional losses of the body as a whole, (2) increased recovery of kinetic and potential energy, and (3) lower ground reaction force moments specifically at the ankle joint. Although this study was done on humans, the results probably apply to other mammalian species with plantigrade foot posture and may also be relevant to any walking and running biped, such as many species of terrestrial birds.

Among mammals, walking is generally more economical than running and this pattern is particularly pronounced in humans (Rubenson et al., 2007; Farley and McMahon, 1992; Margaria et al., 1963). A recent analysis of published data indicates that for a mammal the size of humans (70 kg) the COT of running is expected to be 16% greater than the COT of walking (Rubenson et al., 2007). The meta-analysis, however, indicates that the metabolic cost for humans to run a given distance is 72% greater than the cost of walking (Rubenson et al., 2007). (Note that the subjects in our study exhibited a 61% difference.) Remarkably, the economic advantage of human walking over running disappears if humans walk without a heel plant (Fig. 3). Thus our ability to walk economically may largely be the result of the plantigrade posture of our feet; a design that characterized great apes long before the evolution of the terrestrial bipeds that gave rise to humans.

Humans (genus *Homo*) are thought to have evolved from australopith ancestors approximately 2.5 million years ago (Wolpoff, 1998). For more than 99% of this period, humans made their living as hunter-gatherers, acquiring edible plants and animals from the environment. This lifestyle is associated with large daily travel distances and home ranges. Among modern hunter-gatherers, distances traveled per day average 9.5 km for females and 14.1 km for males (Marlowe, 2005). By contrast, daily distances traveled by orangutans, chimpanzees, bonobos and gorillas are 0.5–0.8 km (Bean, 1999), 3–10 km (Williams et al., 2002; Bean, 1999), 2.4 km (Williams et al., 2002; Bean, 1999) and 0.5–2.6 km (Doran and McNeilage, 2001; Bean, 1999), respectively. The average home ranges of human hunter-gatherers also greatly exceed those of the other species of great apes: human, 175 km² (Marlowe, 2005); orangutan, 1.5–30 km² (Singleton and van Schaik, 2001; Delgado and van Schaik, 2000; Bean, 1999); chimpanzee, 4–32 km² (Bean, 1999); bonobo, 22–58 km² (Bean, 1999); gorilla, 4–23 km² (Williams et al., 2002; Bean, 1999). Given the great distances hunter-gatherers travel, it is not surprising that humans are economical walkers or that we retained a foot posture, inherited from our more arboreal ancestors, that facilitates economical walking.

But did plantigrade foot posture evolve in great apes to improve the economy of walking? Although this is a possibility (see Gebo, 1998; Gebo, 1992), great apes are thought to be anatomically specialized for climbing and below branch, suspensory locomotion (Ward, 2007). Additionally, an analysis of heel contact and heel strike in a variety of arboreal primates suggests that the plantigrade foot posture of great apes may not have evolved in a terrestrial habitat (Schmitt and Larson, 2005). We suspect that the heel down posture of great apes evolved for reasons other than economical arboreal or terrestrial transport. First, as reviewed above, most species of extant apes travel relatively short distances. Second, compared to

the bipedal gait of humans, the quadrupedal gait of great apes approximately halves collisional energy losses that occur in a walking stride (Bertram and Gutmann, 2008; Ruina et al., 2005), further reducing the significance of any energetic savings that plantigrade feet provide. Thus, we believe that the adaptive significance of plantigrade feet in great apes remains an open question.

Our finding that plantigrade foot posture improves the economy of walking in humans does not indicate that humans are more specialized for walking than for endurance running. Humans have a suite of characters that are consistent with specialization for both economical walking and endurance running. Some characteristics of *Homo*, such as long legs (Studel-Numbers and Tilkens, 2004; Studel-Numbers, 2003; Pontzer, 1998; Kram and Taylor, 1990) and reduced upper body mass, increase the economy of both walking and running. Other characters such as a relative lack of body hair, a great capacity for sweating (Carrier, 1984), long Achilles tendons (Bramble and Lieberman, 2004), and short toes (Rolian et al., 2009) are more likely adaptations for endurance running than for economical walking. By contrast, plantigrade foot posture appears to be advantageous for walking but not running.

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REFERENCES

- Adamczyk, P. G., Collins, S. H. and Kuo, A. D. (2006). The advantages of a rolling foot in human walking. *J. Exp. Biol.* **209**, 3953–3963.
- Anders, C., Wagner, H., Puta, C., Grassme, R. and Scholle, H. C. (2009). Healthy humans use sex-specific co-ordination patterns of trunk muscles during gait. *Eur. J. Appl. Physiol.* **105**, 585–594.
- Ardigo, L. P., LaFortuna, C., Minetti, A. E., Mognoni, P. and Saibene, F. (1995). Metabolic and mechanical aspects of foot landing type, forefoot and rearfoot strike, in human running. *Acta Physiol. Scand.* **155**, 17–22.
- Bean, A. (1999). Ecology of sex differences in great ape foraging. In *Comparative Primate Socioecology* (ed. P. C. Lee), pp. 339–362. Cambridge: Cambridge University Press.
- Bertram, J. E. and Gutmann, A. (2008). Motions of the running horse and cheetah revisited: fundamental mechanics of the transverse and rotary gallop. *J. Roy. Soc. Inter.* **6**, 549–559.
- Biewener, A. A., Farley, C. T., Roberts, T. J. and Tomaner, M. (2004). Muscle mechanical advantage of human walking and running: implications for energy cost. *J. Appl. Physiol.* **97**, 2266–2274.
- Bramble, D. M. and Lieberman, D. E. (2004). Endurance running and the evolution of *Homo*. *Nature* **432**, 345–352.
- Carrier, D. R. (1984). The energetic paradox of human running and hominid evolution. *Cur. Anthro.* **25**, 483–495.
- Cavagna, G. A. (1975). Force platforms as ergometers. *J. Appl. Physiol.* **39**, 174–179.
- Cavagna, G. A., Heglund, N. C. and Taylor, C. R. (1977). Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. *Am. J. Physiol.* **233**, R243–R261.
- Cavanagh, P. R. and LaFortune, M. A. (1980). Ground reaction forces in distance running. *J. Biomech.* **13**, 397–406.
- Delgado, R. A. J. and van Schaik, C. P. (2000). The behavioral ecology and conservation of the Orangutan (*Pongo pygmaeus*): A tale of two islands. *Evol. Anthropol.* **9**, 201–218.
- Divert, C., Mornieux, G., Baur, H., Mayer, F. and Belli, A. (2005). Mechanical comparison of barefoot and shod running. *Inter. J. Sports Med.* **26**, 593–598.
- Donelan, J. M., Kram, R. and Kuo, A. D. (2002). Simultaneous positive and negative external mechanical work in human walking. *J. Biomech.* **35**, 117–124.
- Doran, D. M. and McNeilage, A. (2001). Subspecific variation in gorilla behavior: the influence of ecological and social factors. In *Mountain Gorillas: Three Decades of Research at Karisoke* (ed. M. M. Robbins, P. Sicoite and K. J. Stewart). Cambridge: Cambridge University Press.
- Farley, C. T. and McMahon, T. A. (1992). Energetics of walking and running: insights from simulated reduced-gravity experiments. *J. Appl. Physiol.* **73**, 2709–2712.
- Gebo, D. L. (1992). Plantigrady and foot adaptation in African apes: Implications for hominid origins. **89**, 29–58.

- Gebo, D. L.** (1998). Climbing, brachiation, and terrestrial quadrupedalism: historical precursors of hominid bipedalism. *Am. J. Phys. Anthro.* **101**, 55-92.
- Hermens, H. J., Freriks, B., Merlietti, R., Stegeman, D. F., Blok, J., Rau, G. et al.** (1999). *European Recommendations for Surface ElectroMyoGraphy: Results of the SENIAM Project*. Roessingh Research and Development. ISBN: 90-75452-14-4 (CD-rom).
- Hildebrand, M. and Goslow, G.** (1998). *Analysis of Vertebrate Structure*. New York: John Wiley & Sons, Inc.
- Kalen, V., Adler, N., Bleck, M. A. and Bleck, E. E.** (1986). Electromyography of idiopathic toe walking. *J. Ped. Ortho.* **6**, 31-33.
- Kelly, I. P., Jenkinson, A. M., Stephens, M. and O'Brien, T.** (1997). The kinematic pattern of toe-walkers. *J. Ped. Ortho.* **17**, 478-480.
- Kram, R. and Taylor, C. R.** (1990). Energetics of running: a new perspective. *Nature* **346**, 265-267.
- Liebenberg, L.** (2006). Persistence hunting by modern hunter-gatherers. *Curr. Anthro.* **47**, 1017-1025.
- Liebenberg, L.** (2008). The relevance of persistence hunting to human evolution. *J. Hum. Evol.* **55**, 1156-1159.
- Lieberman, D. E., Werbel, W. A., Daoud, A. I., Venkadesan, M., D'Andrea, S., Mang'Eni, R. and Pitsiladis, Y.** (2010). Foot strike patterns and impact transient forces in habitually barefoot versus shod runners *Nature* **463** (in press).
- Margaria, R., Cerretelli, P., Aghemo, P. and Sassi, G.** (1963). Energy cost of running. *J. Appl. Physiol.* **18**, 367-370.
- Marlowe, F. W.** (2005). Hunter-gatherers and human evolution. *Evol. Anthro.* **14**, 54-67.
- McGeer, T.** (1990). Passive dynamic walking. *Inter. J. Robot. Res.* **9**, 62-82.
- Ng, J. K., Kippers, V. and Richardson, C. A.** (1998). Muscle fibre orientation of abdominal muscles and suggested surface EMG electrode positions. *Elec. Clin. Neurophysiol.* **38**, 51-58.
- Nilsson, J. and Thorstensson, A.** (1989). Ground reaction forces at different speeds of human walking and running. *Acta Physiol. Scan.* **136**, 217-227.
- Pontzer, H.** (1998). Predicting the cost of locomotion in terrestrial animals: a test of the limb model in humans and quadrupeds. *J. Exp. Biol.* **210**, 484-494.
- Rolian, C., Lieberman, D. E., Hamill, J., Scott, J. W. and Werbel, W.** (2009). Walking, running and the evolution of short toes in humans. *J. Exp. Biol.* **212**, 713-721.
- Rubenson, J., Heliams, D. B., Maloney, S. K., Withers, P. C., Lloyd, D. G. and Fournier, P. A.** (2007). Reappraisal of the comparative cost of human locomotion using gait-specific allometric analyses. *J. Exp. Biol.* **210**, 3513-3524.
- Ruina, A., Bertram, J. E. and Srinivasan, M.** (2005). A collisional model of the energetic cost of support work qualitatively explains leg sequencing in walking and galloping, pseudo-elastic leg behavior in running and the walk-to-run transition. *J. Theo. Biol.* **237**, 170-192.
- Schmitt, D. and Larson, S. G.** (2005). Heel contact as a function of substrate type and speed in primates. *Am. J. Phys. Anthro.* **96**, 39-50.
- Singleton, I. and van Schaik, C. P.** (2001). Orangutan home range size and its determinants in a Sumatran swamp forest. *Inter. J. Primatol.* **22**, 877-911.
- Sockol, M. D., Raichlen, D. A. and Pontzer, H.** (2007). Chimpanzee locomotor energetics and the origin of human bipedalism. *Proc. Nat. Acad. Sci. USA* **104**, 12265-12269.
- Studel-Numbers, K. L.** (2003). The energetic cost of locomotion: humans and primates compared to generalized endotherms. *J. Hum. Evol.* **44**, 255-262.
- Studel-Numbers, K. and Tilkens, M.** (2004). The effect of lower limb length on the energetic cost of locomotion: Implications for fossil hominids. *J. Hum. Evol.* **47**, 95-109.
- Ward, C. V.** (2007). Postural and locomotor adaptations of nonhuman hominoids. In *Handbook of Paleoanthropology Volume II: Primate Evolution and Human Origins*, vol. II (ed. W. Henke, R. Rothe and I. Tattersall). Berlin: Springer-Verlag.
- Willems, P., Cavagna, G. and Heglund, N.** (1995). External, internal and total work in human locomotion. *J. Exp. Biol.* **198**, 379-393.
- Williams, J. M., Liu, H. Y. and Pusey, A. E.** (2002). Costs and benefits of grouping for female chimpanzees at Gombe. In *Behavioural Diversity in Chimpanzees and Bonobos* (ed. C. Boesch, H. Gottfried and L. F. Marchant), pp. 192-203. Cambridge: Cambridge University Press.
- Wolpoff, M. H.** (1998). *Paleoanthropology*. McGraw-Hill Humanities/Social Sciences/Languages.