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SUMMARY

The phalangeal portion of the forefoot is extremely short relative to body mass in humans. This derived pedal proportion is thought to have evolved in the context of committed bipedalism, but the benefits of shorter toes for walking and/or running have not been tested previously. Here, we propose a biomechanical model of toe function in bipedal locomotion that suggests that shorter pedal phalanges improve locomotor performance by decreasing digital flexor force production and mechanical work, which might ultimately reduce the metabolic cost of flexor force production during bipedal locomotion. We tested this model using kinematic, force and plantar pressure data collected from a human sample representing normal variation in toe length (N=25). The effect of toe length on peak digital flexor forces, impulses and work outputs was evaluated during barefoot walking and running using partial correlations and multiple regression analysis, controlling for the effects of body mass, whole-foot and phalangeal contact times and toe-out angle. Our results suggest that there is no significant increase in digital flexor output associated with longer toes in walking. In running, however, multiple regression analyses based on the sample suggest that increasing average relative toe length by as little as 20% doubles peak digital flexor impulses and mechanical work, probably also increasing the metabolic cost of generating these forces. The increased mechanical cost associated with long toes in running suggests that modern human forefoot proportions might have been selected for in the context of the evolution of endurance running.

Key words: phalanges, gait, foot biomechanics, bipedalism, Australopithecus.

INTRODUCTION

Humans, as the only obligate bipedal primate, have a highly modified foot comprising not only skeletal apomorphies in the tarsals and metatarsals, but also uniquely derived phalangeal proportions (Schultz, 1963; Lewis, 1989; Aiello and Dean, 1990; Harcourt-Smith and Aiello, 2004). Compared with other extant hominoids and earlier hominins such as *Australopithecus*, human lateral pedal phalanges are straight and extremely short in relation to body size; and the hallux is adducted, more robust, and as long as the lateral digits (Table 1). Together, these apomorphies create a relatively and absolutely short phalangeal portion of the forefoot in which digital motion is limited to flexion and extension around a transverse metatarso–phalangeal axis (Lessertisseur and Jouffroy, 1978; Bojsen-Møller and Lamoreux, 1979; Susman, 1983).

This unique phalangeal morphology has long been assumed to be functionally adaptive for terrestrial bipedal locomotion, yet there have been few studies of toe function in human walking and running, and none has tested the extent to which shorter toes might benefit bipedal locomotion (Weidenreich, 1923; Morton, 1935; Elftman and Manter, 1935; Mann and Hagy, 1979; Hughes et al., 1990). In this study, we propose a simple biomechanical model of toe function in bipedal locomotion that suggests that shorter phalanges provide performance benefits during the stance phase of walking and, especially, during running. Specifically, we use forefoot kinematic and kinetic data collected from a sample of modern humans representing the normal variation in toe length to test the hypothesis that shorter phalanges improve locomotor performance by reducing the mechanical force and work output of the digital flexors required to maintain joint stability during stance.

Toe function during stance in bipedal locomotion

Stance in walking is divided into three periods: 'contact' (0–25% stance), when the plantar surface of the foot contacts the ground; 'midstance' (25–65% stance), when the body's center of mass (COM) vaults over the stance foot; and 'propulsion' (65–100% stance), in which the heel is first lifted off the ground, followed by the metatarsal heads and phalanges. During propulsion, the contralateral foot contacts the ground and initiates a phase of double support (Root et al., 1977). In running, stance is also divided into three periods: contact (0–20% stance), midstance (20–45% stance) and propulsion (45–100% stance), but there is no period when both feet are in contact with the ground (De Cock et al., 2005). During stance, variable ground reaction forces (GRFs) resulting from gravity and body segment accelerations are applied to the plantar surface of the foot and toes. The toes do not bear significant loads during contact and midstance; however, during propulsion, the metatarsal heads and distal phalanges are the only points of contact with the ground and hence become load bearing. In walking, the toes support between 30 and 40% of body mass, mostly under the first, second and third distal phalanges. In running, these loads range from 50 to 75% of body mass (Mann and Hagy, 1979; Hayafune et al., 1999; Wearing et al., 2001; Eils et al., 2004).

In addition to supporting the body and providing traction, the toes, specifically the digital flexors, help control the forward motion of the COM during propulsion. As propulsion begins, the ankle

Table 1. Absolute and relative lengths of lateral toes in male *Homo*, *Pan* and *Australopithecus*

	Third toe length (mm)	Fifth toe length (mm)	Body mass (kg)	Relative third toe length (mm/kg$^{1/3}$)	% Difference in relative third toe length *vs Homo*
H. sapiens (N=103)[1]	40.5	30.7	65[4]	10.1	0
P. troglodytes (N=37)[1]	65.4	48.8	50[4]	17.8	+76%
A. afarensis (N=1)[2]	49.4[3]	41.8	45[4]	13.9	+38%

Lateral toe lengths were obtained by adding the interarticular lengths of the proximal and intermediate phalanges. Relative toe length is length of third toe divided by the cube root of body mass.
[1]Extant data collected for an unrelated study (C.P.R., manuscript in preparation).
[2]AL333-115, a partial male *A. afarensis* forefoot from Hadar, Ethiopia. Data from Latimer and colleagues (Latimer et al., 1982).
[3]Only the intermediate phalanges of digits four and five are preserved in AL333-115. Third intermediate phalanx length was estimated using the scaling relationship between fifth toe phalanges in AL333-115.
[4]Extant estimates from Smith and Jungers (Smith and Jungers, 1997); *A. afarensis* estimate from McHenry (McHenry, 1992).

plantarflexes and the metatarsophalangeal (MTP) joints are passively dorsiflexed as the COM moves anterior to them. During this phase, the body has a tendency to pitch forward in the sagittal plane, such that propulsion can be viewed as a form of 'forward falling' (Mochon and McMahon, 1980). At the MTP joints, the combined effect of forward falling and GRF loads applied to the distal phalanges causes a tendency of these joints to collapse into dorsiflexion (hyperextension). However, electromyographic (EMG) studies indicate that the extrinsic and intrinsic digital flexors are active during propulsion, balancing the GRF dorsiflexion moments at the MTP joints and contributing to the control of the forward falling motion of the body (Mann and Inman, 1964; Reeser et al., 1983). Presumably, the digital flexors, contracting eccentrically, act as 'brakes' that control MTP dorsiflexion. At the end of stance, the digital flexors might also assist the more powerful ankle plantarflexors in generating lift, particularly in running and sprinting (Stefanyshyn and Nigg, 1997).

The effects of longer toes on propulsion in bipedal locomotion

The phalangeal musculoskeletal complex in humans serves two important functions during propulsion: the metatarsal heads and distal phalanges are load bearing and provide traction, whereas the digital flexors stabilize the MTP joints and control the forward motion of the COM. Given these functions, one expects toe length to affect locomotor performance. Consider two individuals identical in all respects but with differing toe lengths (Fig. 1). The two individuals will have similar GRF profiles during propulsion. The individual with longer toes might not actually benefit from a greater load-bearing area because, in the normal position of the foot on the ground, phalangeal GRF loads are applied only to the distal phalanges. At the same time, however, these loads will be applied further from the MTP joints in this individual, causing higher MTP dorsiflexion moments.

Assuming that the net angular acceleration of the toe segments is negligible during propulsion, the net joint moment at the MTP joints will be zero and the larger GRF dorsiflexion moments will be balanced by larger plantarflexion moments in the long-toed individual. These plantarflexion moments are produced by the digital flexors, flexor digitorum brevis and longus in the lateral toes, f. hallucis brevis and longus in the hallux, and the dorsal interossei and quadratus plantae. For roughly equal muscle moment arms, an individual with longer toes must thus generate larger plantarflexor forces to balance the larger dorsiflexion joint moments, leading to greater force impulses over stance. The flexors will also do more mechanical work, both per unit time (instantaneous power) and over stance (Winter, 1990). Note that joint power and mechanical work

are expected to be mostly negative during propulsion as the MTP joints are dorsiflexing despite the plantarflexing action of the digital flexors.

The model in Fig. 1 thus predicts that the long-toed individual will produce larger digital flexor forces and do more mechanical work to prevent the MTP joints from collapsing into hyperextension during propulsion. All else being equal, greater force production and mechanical work will also probably increase the metabolic cost of generating digital flexor force in the long-toed individual, even though these muscles are contracting eccentrically (e.g. Ryschon et al., 1997). In other words, the model predicts that short toes improve locomotor performance
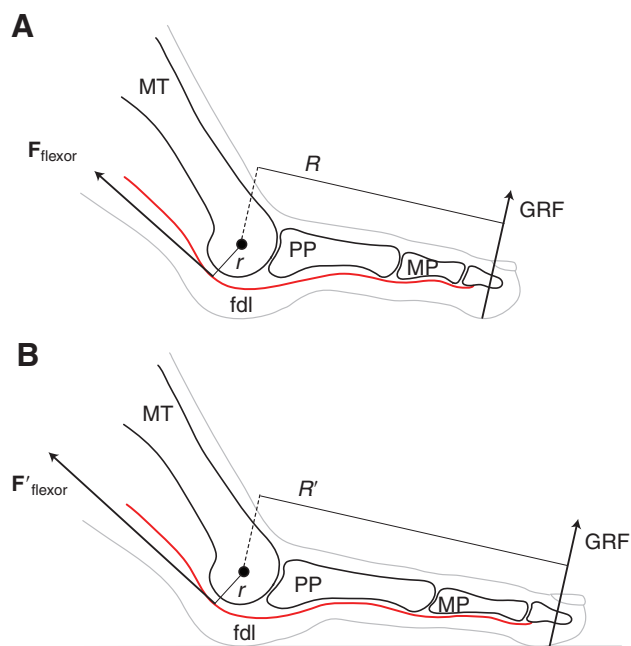

Fig. 1. Schematic model of musculoskeletal function in the second toe during propulsion. For simplicity, only the action of the flexor digitorum longus is depicted. (A) During propulsion, the component of the ground reaction force (GRF) acts on the distal toe pad at a distance *R* from the MTP joint center of rotation (black circle) to create a dorsiflexion moment at this joint. This moment is balanced by a plantarflexion moment produced by the digital flexors, which exert a force (F_{flexor}) acting at a distance *r* (lever arm) from the joint center of rotation. (B) Longer segments are hypothesized to increase the external moment arm (*R'*), increasing the dorsiflexion moment and digital flexor forces required to stabilize the joints (F'_{flexor}). Other abbreviations: fdl, flexor digitorum longus tendon; MP, middle phalanx; MT, metatarsal; PP, proximal phalanx.

proximately by reducing the mechanical cost of stabilizing the MTP joints and, ultimately, by reducing the metabolic cost of digital flexor force production.

Walking *versus* running

Differences in digital flexor output suggest that long-toed individuals are at a disadvantage during bipedal locomotion, in terms of increased mechanical output, and probably also with respect to the metabolic cost associated with this mechanical output. This disadvantage might increase markedly in running, for two reasons. First, peak GRFs during propulsion are two to four times larger than walking at endurance running speeds (Keller et al., 1996). Accordingly, balancing digital flexor forces should also be substantially larger in running, with commensurate effects on muscular effort. Second, whereas in walking some of the load is transferred to the contralateral foot, the stance forefoot in running is the only contact point with the substrate during propulsion. Accordingly, digital flexor muscle output must be maintained throughout propulsion in running, and these muscles might even assist the ankle plantarflexors in overcoming the larger GRFs and generating the lift necessary to initiate the aerial phase of running.

Hypothesis to be tested

We used kinematic, force and plantar pressure data from a sample of human subjects representing the normal variation in toe length to test the general hypothesis that short phalanges in humans reduce digital flexor mechanical output during stance in bipedal locomotion. Two specific predictions are tested based on this hypothesis.

Prediction 1. Phalangeal length will be significantly correlated with digital flexor output during stance. Specifically, peak flexor forces, digital flexor impulses and the total mechanical work delivered are predicted to be greater in magnitude in individuals with relatively longer toes, both in walking and running.

Prediction 2. As a corollary to Prediction 1, if the disadvantages of longer toes are greatest in running, then the effect of phalangeal length on mechanical output is predicted to be greater in running than walking.

MATERIALS AND METHODS
Sample

The study included 25 human volunteers (12 male, 13 female). The mean age of the sample was 22.8 years (s.d. 5.2, range 18–38 years), mean body mass 72.5 kg (s.d. 15, range 54–118 kg) and mean stature 171.9 cm (s.d. 10.6, range 157–191 cm). The subjects had no history of lower limb or foot pathology at the time of the study or in the previous 6 months. All experimental procedures were approved by the Institutional Review Boards at Harvard University and at the University of Massachusetts Amherst, and written informed consent was obtained from each subject before participation.

Experimental protocol

The subjects completed two sets of trials in which they walked and ran barefoot at their self-selected preferred speeds. In one set, subjects walked and ran across a plantar pressure plate sampling at 100 Hz (walking) and 400 Hz (running) (RSScan International, Olen, Belgium, 2 m×0.4 m×0.02 m, 4 sensors cm^{-2}) flush and centered in a trackway of length 25 m. In the second set, subjects walked and ran across a force plate sampling at 1000 Hz (AMTI, 1.2 m×0.6 m) flush with the ground. The order in which pressure and force plate trials were performed was randomized. A minimum of three stance events in each gait were averaged and used for analysis in the force and pressure plate sets.

Kinematic data were collected during both sets using a high-speed infrared camera system (Qualisys Motion Capture Systems, Gothenburg, Sweden) sampling at a frequency of 200 Hz. Kinematic and force/pressure data were collected synchronously using a software-based voltage trigger. The kinematic system was re-calibrated between force and pressure trials, so that the origin of the coordinate system was located either on the posterior left corner of the force plate or on the left-most pressure cell in the posterior-most row of sensors on the pressure plate. Reflective markers were adhered to the skin overlying the following landmarks of the left limb: greater trochanter, fibular head, medial and lateral malleoli, superior calcaneal tuberosity, medial aspect of the first MTP joint, supero-lateral aspect of the fifth MTP joint and the free margin of the nail plate on the first and third toes.

Data analysis

Raw force, pressure and kinematic data were processed and analyzed using semi-automated routines in MatLab (v7.1, the MathWorks, Natick, MA, USA). Force and kinematic data were filtered using a low-pass fourth-order Butterworth filter with cutoff frequencies of 100 Hz and 10 Hz, respectively. Kinematic data were used to estimate hallux length, segment and joint angles and joint angular velocities at the first MTP joint during stance. Hallux lengths derived from kinematic data were in agreement with length data collected directly using digital calipers (R=0.84). In this study, we used hallux length as a global length measurement for all toes, under the assumption that lateral toe length scales isometrically with hallux length (hereafter referred to as 'toe length'). In the force plate trials, stance was derived by finding data points where the value of the vertical component of the GRF exceeded 5 N. In the pressure plate trials, stance included all frames where at least one pressure sensor was activated. Force/pressure and kinematic data were then combined to obtain external forces and moments acting on the toes and MTP joints, using a simplified inverse dynamics approach (Winter, 1990).

Calculation of MTP joint moments

In our analyses, we assumed that the net angular and linear accelerations of the toe segments during stance were negligible. In other words, the GRF dorsiflexion moment was assumed to be entirely balanced by a plantarflexion moment resulting from contractions of the digital flexor muscles. Similarly, the net force resulting from external forces acting on the toe segments (e.g. GRF, flexor tendon forces) was assumed to be dissipated as internal phalangeal force and stress (Fig. 1; $\mathbf{F}_{res}$). The GRF dorsiflexion moment acting at the MTP joints was calculated using slightly different methods in the force and pressure plates.

Force plate data

Force plates provide a three-dimensional GRF over stance, but it is a resultant force with a single point of application known as the center of pressure (COP). Accordingly, in these trials, the phalanges were modeled as a single anatomical unit (the 'forefoot') comprising a polygon delimited by the kinematic markers on the first and fifth MTP joints and on the distal phalanges of the first and third toes (Fig. 2A). The transverse axis running between the first and fifth MTP markers was treated as a single, hinge-like MTP axis. The COP was translated into the kinematics coordinate system, and the perpendicular line from the transverse MTP axis to the COP was used to estimate the moment arms and moment acting at the MTP axis. This method takes into account inter-subject variability in toe-out angle, defined as the angle between the long axis of the foot at midstance and the line of progression of the body (Chang et al., 2007).
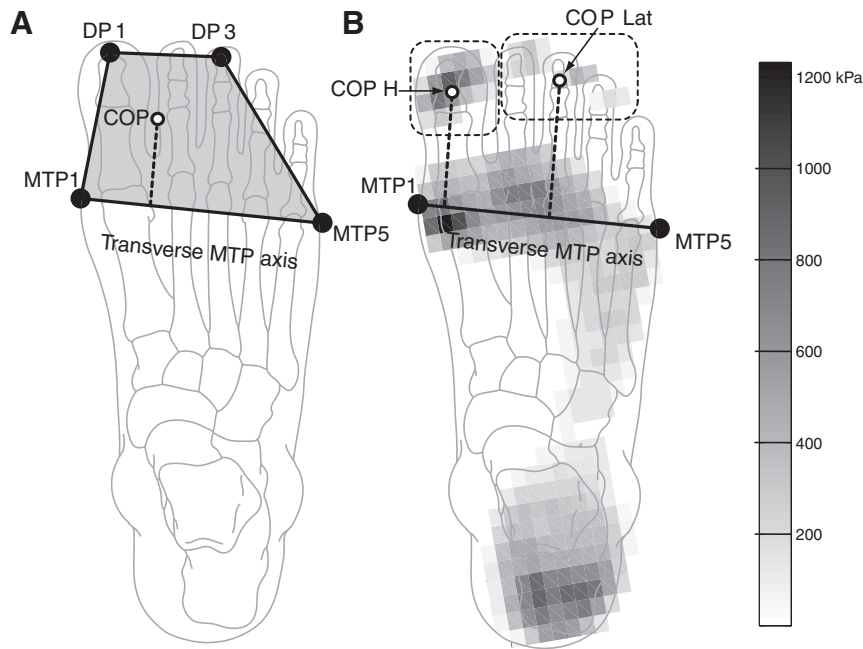
Fig. 2. Method for calculating external moments acting on the MTP joints in the force plate (A) and pressure plate trials (B). Black dots represent kinematic markers on the first (MTP1) and fifth (MTP5) metatarsophalangeal joints and distal phalanges of the first (DP1) and third toes (DP3). The image in B shows the peak pressure, in kPa, recorded from each sensor cell over the entire stance event. This composite image is used to determine the outlines of the hallux and lateral toe pressure zones. Note that, in this individual, there was little pressure detected under the fourth toe, and none under the fifth toe. COP, center of pressure; COP H, hallux center of pressure; COP Lat, center of pressure for the lateral toes as a group.

The GRF moment was obtained by summing the products of the horizontal component of the GRF and vertical component of the load arm (elevation of the transverse MTP axis at the point where it intersects the COP load arm), and the vertical component of the GRF and horizontal component of the load arm. We excluded external moments when the COP is proximal to the transverse MTP axis. Such moments technically 'plantarflex' the MTP joints, but there is no real plantarflexion motion at that joint because the plantar surface of the foot and toes is supported against the ground.

Plantar pressure data

Pressure plates provide only the vertical component of the GRF, but this force can be divided into multiple anatomical regions, allowing a more precise measurement of load distribution and moments acting on individual zones of the foot. Here, the phalangeal portion of the forefoot was divided into two zones, based on the maximal plantar pressure profile provided by the custom MatLab routine (Fig. 2B): the first includes only the hallux and the second encompasses the four lateral toes. The lateral toes were grouped because of the greater variability in load distribution under toes two through five (Hayafune et al., 1999; Wearing et al., 2001). The total pressure plate force profile was calibrated using the average vertical component of the GRF from the force plate trials. The resultant force in each forefoot zone was then obtained by summing the calibrated force output per unit time from each activated pressure sensor within a zone.

The COP in each zone was obtained as follows: based on the known location of each pressure sensor, the force output can be used to calculate two moments for each sensor, acting at a known distance from the left [moment around the anteroposterior (AP) axis] and bottom borders of the pressure plate [moment around the mediolateral (ML) axis]. Both moments for each sensor in a given zone are added, producing total AP and ML moments for that zone. The total AP and ML moments are then divided by the total force of the zone to find an ML and AP coordinate, respectively, for the COP in that zone. The load arms of the GRF components acting at the MTP joints in the hallux and lateral toe zones were calculated as the perpendicular distance between the COPs and the transverse

MTP axis. GRF dorsiflexion moments were calculated as above, based only on the vertical GRF.

Flexor force and work output

The digital flexor force required to balance the observed dorsiflexion moment at the MTP joints was obtained using the following equation:

$$\mathbf{M}_{muscle} = \mathbf{F}_{muscle} \times r , \qquad (1)$$

where $\mathbf{M}_{muscle}$ is the net muscle moment at the MTP joints (equal to the GRF dorsiflexion moment), $\mathbf{F}_{muscle}$ is the digital flexor force, and r is the muscle lever arm, the perpendicular distance between the center of rotation of the MTP joint and the line of action of the digital flexors. For the force plate trials, the lever arm of the 'forefoot' digital flexors was taken as half the height of the hallucial metatarsal head, measured with spreading calipers (Stefanyshyn and Nigg, 1997). This measurement was taken five times and averaged, before the experiment, with the foot at rest. The same lever arm was used for the hallucial flexors in the pressure plate trials. The lever arm for the lateral flexors was obtained by scaling the hallucial lever arm by a factor of 0.77, corresponding to the ratio of third to first metatarsal head heights measured in a sample of 206 humans collected for an unrelated study (C.R., manuscript in preparation). Although the true muscle lever arms probably vary over stance, they should vary in a similar way across individuals. Accordingly, the use of average lever arms in each individual should not significantly affect the study of the relationship between variation in flexor output and variation in phalangeal length. Digital flexor forces were then used to calculate a flexor impulse, given by the integral of the digital flexor force over contact time:

$$\text{Impulse} = \int \mathbf{F}_{muscle} dt . \qquad (2)$$

Instantaneous joint power delivered by the digital flexors (P_{musc}), in watts, was obtained using the following equation:

$$P_{musc} = \mathbf{M}_{muscle} \times \omega , \qquad (3)$$

where $\mathbf{M}_{muscle}$ is the plantarflexion muscle moment and ω is the angular velocity of the joint. The net work done by the digital flexors

Table 2. Means, standard deviations and ranges of the five independent variables and speed and in walking and running

	Body mass (kg)	Toe length (mm)	Speed (m s^{-1})	Contact time (s)	Toe contact time (s)	Toe-out angle (deg.)
Walks (W)	72.5±15 (49–112)	69±6.3 (58–84)	1.56±0.22 (1.07–1.96)	0.61±0.06 (0.51–0.78)	0.34±0.05 (0.25–0.42)	12.3±5.8 (4.5–25.8)
Runs (R)			3.69±0.57 (2.46–4.68)	0.23±0.03 (0.17–0.29)	0.16±0.04 (0.10–0.28)	10.6±4.9 (1.1–19.3)

Speed was estimated by the horizontal distance travelled by the hip marker over stance. Data derived from force plate trials (means ± s.d.).

Table 3. Normal correlation coefficients between the independent variables in the force plate trials

	Body mass	Toe length	Contact time	Toe contact time	Toe-out angle
Body mass	–	R=0.35 (P=0.08)	R=–0.13 (P=0.54)	R=0.03 (P=0.87)	R=–0.02 (P=0.93)
Toe length	R=0.35 (P=0.08)	–	R=0.02 (P=0.94)	R=0.26 (P=0.21)	R=–0.09 (P=0.67)
Contact time	R=–0.06 (P=0.77)	R=0.18 (P=0.38)	–	**R=0.49** (P=0.01)	R=–0.05 (P=0.80)
Toe contact time	R=0.30 (P=0.15)	**R=0.48** (P=0.02)	R=0.26 (P=0.21)	–	R=0.23 (P=0.27)
Toe-out angle	R=0.18 (P=0.37)	R=0.01 (P=0.96)	R=–0.26 (P=0.21)	R=–0.10 (P=0.63)	–

Values below the diagonal are correlation coefficients for walks and above the diagonal are for runs. Correlation coefficients in bold are significant at the P=0.05 level.

(W_{musc}), in joules, is the integral of instantaneous power over stance time:

$$W_{musc} = \int P_{musc}\, \mathrm{d}t . \qquad (4)$$

Negative and positive work delivered at the MTP joints was obtained by integrating the negative and positive portions of the power curve separately. Finally, all data were made comparable between individuals and across gaits by standardizing the stance event from 0% to 100% contact time.

Statistical design

In locomotor biomechanics, mechanical output variables are often influenced by factors unique to each individual, including morphological variables such as body mass, leg length or foot length, and variables related to gait, such as preferred running speed or running style [e.g. midfoot *vs* forefoot strikers (Kerr et al., 1983)]. These factors can confound the effects of toe length on selected mechanical performance criteria. In this study, we used partial correlations to measure the strength of the linear association between forefoot length and the flexor output variables, controlling for the potential effects of morphological and gait confounders.

Prediction 1 was tested separately in walking and running by calculating partial correlations between toe length and the biomechanical variables, while controlling for the effects of four covariates: body mass, contact time, toe contact time and toe-out angle. Body mass is included because it is strongly correlated with GRFs (Valiant, 1990), thus influencing phalangeal loading. We used contact time as a proxy for travelling speed, which also influences GRF magnitude. Contact time is highly correlated with travelling speed (in this sample, R^2=0.67 in walking, 0.74 in running). More importantly, however, it might be better correlated with variables that are integrated over time, such as impulse and work, unlike other measures of speed such as Froude number or duty factor. Toe contact time measures the time that the whole-body COP is anterior to the MTP joints, accounting for individual differences in footstrike patterns: if two individuals have similar contact times, but one is a toe striker, then he/she will spend virtually 100% of stance loading the phalanges. Finally, toe-out angle measured at midstance is included because it can influence the trajectory of the COP, placing loads more medially with increasing rotation (Chang et al., 2007). Prediction 2 was assessed qualitatively by comparing the strength of the partial correlations between forefoot length and the mechanical variables in walking and in running.

Predicting the effects of toe length on flexor output

As a complement to partial correlations, we used multiple regression analysis to predict the effect of varying a single independent variable on a dependent variable. Specifically, we regressed the flexor output variables against the five independent variables and then used the regression equations to predict the effect of different toe lengths on flexor mechanical output, while holding the other four covariates (body mass, etc.) constant. Put differently, we created hypothetical individuals with sample average values for body mass, contact times and toe-out angles, and toe lengths ranging from one end of the sample to the other (Table 2), to predict the effect of varying only toe length on digital flexor force production and work. This analysis was performed separately for walking and running in the force and pressure plate trials. All statistical analyses were performed in Statistica v. 6.1 (Statsoft).

RESULTS
Independent variables

Mean values, standard deviations and ranges for the five independent variables and the velocity of the COM (given by the horizontal distance travelled by the hip marker over stance) are given in Table 2. The values reported were obtained from the force plate trials only, as there was no significant difference between force and pressure plate trials. Differences in velocity and contact times between walking and running were significant (ANOVAs, P<0.05, numerator d.f.=1, denominator d.f.=48), but the difference in toe-out angle was not. Only two pairs of independent variables are significantly correlated (Table 3). In both cases, the correlation coefficients are generally low and explain approximately 25% of variation, indicating an overall low level of colinearity between independent variables.

Dependent variables

Sample means, standard deviations and ranges for the dependent variables in force and pressure plate trials are reported in Table 4. Standard deviations and ranges suggest that the flexor mechanical variables are highly variable in this sample. As expected, negative work is significantly larger than positive work in all trials and gaits, reflecting the braking role of the digital flexors during propulsion.

There is a significant increase in the magnitude of peak flexor forces and negative work between walking and running in the force plate trials but not in flexor impulse and positive work. Digital flexor impulses actually decreased in the walk–run transition, probably

Table 4. Raw means, standard deviations and ranges of the five mechanical output variables in walking and running

	Peak flexor force (N)	Flexor impulse (Ns)	Negative work (J)	Positive work (J)
Force plate trials (single forefoot model)				
Walks	1227±577 (473–2977)	209±91 (58–366)	–10.7±4.82 (–22.3– –0.54)	0.70±0.49 (0.09–1.57)
Runs	1982±552 (850–3176)	166±86 (62–519)	–14.6±5.15 (–23.6– –6.6)	0.87±1.32 (0.01–6.5)
Difference	**755±541** (–34–2042	–43.3±99.5 (–216–180)	**–3.9±6.33** (–22.12–5.44)	+0.16±1.29 (–1.3–5.16)
Pressure plate trials – hallux data				
Walks	362±318 (0–1334)	53.7±81.4 (0–363.5)	–2.44±2.97 (–13.5– –0.00)	0.04±0.12 (0.00–0.58)
Runs	449±169 (140–742)	46.2±22.2 (15.7–108.9)	–3.65±1.82 (–7.98– –1.13)	0.23±0.30 (0.00–1.34)
Difference	+87±312.6 (–858–653)	–7.5±80.5 (–312.8–100.6)	–1.24±2.97 (–7.7–8.32)	**+0.19±0.32** (–0.41–1.34)
Pressure plate trials – lateral toe data				
Walks	48±94 (0–315)	4.5±9.0 (0–28.1)	–0.20±0.42 (–1.42–0.42)	0.007±0.03 (0.00–0.16)
Runs	162±151 (0–532.3)	16.0±16.5 (0–56.6)	–0.80±0.81 (–2.51–0.00)	0.04±0.07 (0.00–0.26)
Difference	**+113±129** (–73–469)	**+11.5±14.2** (–4.5–52.0)	**–0.60±0.66** (–2.31–0.05)	**+0.037±0.07** (–0.12–0.25)

Data are means ± s.d. Data for force and pressure plate trials are presented separately. Significant differences in the biomechanical variables between walks and runs are highlighted in bold.

because the flexor force is integrated over a much shorter contact time despite being significantly larger in runs. In the pressure trials, walk–run differences in the dependent variables parallel those reported for the force plate trials. However, in the hallux, only the increase in positive work between walks and runs was significant, probably because of a greater variability in hallucial flexor output during walks (Table 4). Variability in mechanical output for the lateral toes was also high in both walks and runs, but, for these toes, all increases in the magnitude of the mechanical variables associated with the walk–run transition were significant.

Relationship between toe length and the dependent variables

Our predictions state that toe length will account for a significant portion of the observed variation in mechanical output variables across individuals (Table 4), after controlling for the effect of body mass, contact times and toe-out angle. Results from the partial correlations analysis are presented in Table 5. At preferred walking speeds, partial correlations data show that increasing relative toe length has no effect on any of the mechanical output variables. In running, however, the partial correlations between toe length and mechanical output based on force plate data are all highly significant. In other words, in running, flexor force, impulse and mechanical work increase in magnitude as toe length increases, even after removing the effects of body mass, contact times and toe-out angles. These data show that toe length has a direct effect on the magnitude of digital flexor mechanical output in running. Moreover, as partial correlations between toe length and mechanical output are only significant in running, the data indirectly support our prediction that the effect of long toes on flexor mechanical output would be greater in running than in walking.

The pressure plate data are consistent with the force plate data. In the hallux, the partial correlations between toe length and flexor impulse, negative and positive work are significant in running, indicating that hallucial flexor output increases as toe length increases. In the lateral toes, there is no significant relationship between toe length and any dependent variable in walking. In running, however, statistically non-significant trends are present between toe length and mechanical output variables for the lateral toe group, with several leaning towards significance (e.g. impulses, peak forces and negative work; see Table 5). The absence of statistically significant correlations with toe length might be due to the much higher variance in flexor output and internal forces in both gaits.

Predicting the effects of toe length on flexor output

The partial correlation data support the prediction that longer toes increase flexor mechanical output (Table 5). However, the actual increase in mechanical cost cannot be predicted directly using partial correlations because the latter are correlations of residuals after removing the effects of the covariates. Instead, the effect of toe length on flexor mechanical output was further quantified using multiple regression analysis, as described in the Materials and Methods. Only running data are reported, as none of the biomechanical variables was significantly correlated in walking (Table 5). Predicted values for the dependent variables derived from force plate data are presented in Table 6. The estimates show that, all else being equal, the hypothetical long-toed individual – in which relative toe length is approximately 40% longer than the shortest toes in the sample – has flexor impulses that are 2.5 times greater than the short-toed individual, while also doing nearly twice as much

Table 5. Partial correlation coefficients between toe length and flexor mechanical variables in walks and runs, controlling for the effects of body mass, contact time, toe contact time and toe-out angle

	Peak flexor force (N)	Flexor impulse (Ns)	Negative work (J)	Positive work (J)
Force plate trials (single forefoot model)				
Walks	0.40 (*P*=0.08)	0.16 (*P*=0.50)	–0.28 (*P*=0.22)	0.26 (*P*=0.25)
Runs	**0.61** (*P*=0.004)	**0.71** (*P*<0.001)	**–0.59** (*P*=0.005)	**0.57** (*P*=0.007)
Pressure plate trials – hallux data				
Walks	–0.18 (*P*=0.43)	–0.23 (*P*=0.32)	0.15 (*P*=0.51)	–0.10 (*P*=0.67)
Runs	0.37 (*P*=0.10)	**0.51** (*P*=0.02)	**–0.52** (*P*=0.02)	**0.44** (*P*=0.05)
Pressure plate trials – lateral toe data				
Walks	–0.0007 (*P*=0.99)	0.04 (*P*=0.86)	–0.03 (*P*=0.89)	–0.08 (*P*=0.73)
Runs	0.36 (*P*=0.11)	0.37 (*P*=0.10)	–0.40 (*P*=0.07)	0.33 (*P*=0.14)

Data are means ± s.d. Data for force and pressure plate trials are presented separately. Partial correlation coefficients in bold are significant at the *P*=0.05 level.

Table 6. Estimated flexor output variables and 95% confidence limits for average and extreme toe lengths, predicted using the multiple regression equations derived from the force plate running trials

Average individual with:	Peak flexor force (N)	Flexor impulse (Ns)	Negative work (J)	Positive work (J)
Shortest toes (58 mm)	1579 (1273–1884)	108 (73–140)	−10.7 (−13.8– −7.6)	0.0 (−0.9–0.7)
Average toes (69 mm)	2002 (1866–2139)	170 (155–185)	−14.9 (−16.3– −13.5)	0.9 (0.6–1.3)
Longest toes (84 mm)	2580 (2197–2963)	256 (213–299)	−20.6 (−24.5– −16.7)	2.3 (1.3–3.3)
Longest–shortest difference	**+1001 N (924–1079)**	**+148 Ns (140–159)**	**−9.9 J (−10.7– −9.1)**	**+2.3 (2.1–2.6)**

Average values for body mass, contact time, toe contact time and toe-out angle are as in Table 2.

Table 7. Estimated hallux and lateral toe biomechanical variables and 95% confidence limits for average and extreme toe lengths, predicted using the multiple regression equations derived from the pressure plate running trials

Average individual with:	Peak flexor force (N)	Flexor impulse (Ns)	Negative work (J)	Positive work (J)
Hallux				
Shortest toes (58 mm)	328 (167–488)	24.4 (4.8–44.1)	−1.8 (−3.4– −0.3)	0.001 (0–0.27)
Average toes (69 mm)	442 (372–516)	45.6 (36.7–54.4)	−3.6 (−4.2– −2.9)	0.24 (0.12–0.36)
Longest toes (84 mm)	602 (400–805)	74.4 (49.6–99.2)	−6.0 (−7.9– −4.0)	0.57 (0.23–0.91)
Lateral toes				
Shortest toes (58 mm)	67 (0–200)	4.9 (0–19.7)	−0.2 (−0.9–0)	0.001 (0–0.06)
Average toes (69 mm)	160 (101–221)	15.7 (9.0–22.4)	−0.8 (−1.1– −0.5)	0.04 (0.01–0.07)
Longest toes (84 mm)	289 (129–457)	30.5 (11.8–49.2)	−1.5 (−2.4– −0.7)	0.1 (0.02–0.18)

Average values for body mass, contact time, forefoot contact time and toe-out angle are as in Table 2.

mechanical work to stabilize the MTP joints during stance. Estimates for the pressure plate trials divided into hallux and lateral toes are presented in Table 7. Note that the confidence limits are much greater in these trials, particularly in the lateral toes, owing to lower correlation magnitudes (Table 5). Nonetheless, the estimates indicate that, in the hypothetical long-toed individual, hallux flexor output variables are 2–3 times greater than those of the short-toed individual. In the lateral toes, the difference in predicted flexor output between short- and long-toed individuals is even greater, being 4–6 times larger in magnitude in the long-toed individual (Table 7).

DISCUSSION

This study tested the general hypothesis that shorter toes in humans contribute to improving locomotor performance by reducing digital flexor force and mechanical work during stance. We predicted that, after controlling for the effects of body mass, contact times and toe-out angle, individuals with relatively longer toes would show greater digital flexor output and internal phalangeal forces (Prediction 1). We also predicted that the increased digital flexor output associated with long toes would be relatively greater in running (Prediction 2).

The results from the running trials support Prediction 1. In the force plate trials – in which the toes were grouped as a single 'forefoot' unit – flexor output variables were significantly correlated with phalangeal length, suggesting that long-toed individuals do more mechanical work to stabilize the MTP joints and control the forward motion of the COM. The pressure plate running data are consistent with the force plate data and also provide support for Prediction 1. In the hallux, toe length was significantly correlated with flexor impulse and mechanical work. In the lateral toes, flexor output variables showed similar trends to the hallux, but were generally lower and less strongly correlated with toe length in running. A *post hoc* power analysis suggests that the lack of significant correlations in the lateral toes is due in part to the small sample size: based on the observed correlations (Table 5), sample sizes ranging from 35 to 55 would have provided adequate power (0.8). Prediction 2 was indirectly supported, as the effects of toe length on flexor output were only significant in running, both in the force and pressure plate trials.

Although most partial correlations data were significant in running, the effects of phalangeal length on flexor mechanics are still modest. The overall variance in flexor output accounted for by variation in toe length, holding the effects of the other covariates fixed, is given by the squared semi-partial correlation between forefoot length and the residuals of the dependent variables. In the force plate trials, these values range from 13.5% (flexor impulse) to 17% (negative work), leaving a significant portion of the variance in flexor output to be explained by other factors, such as body mass or forefoot contact time, measurement error and additional factors that were not measured in this study, including variations in gait kinematics that influence load distribution under the foot.

Gait variability is a significant issue for this study. The flexor output data from the pressure plate trials were highly variable, with minimum values of zero for both hallux and lateral toes in walking, and for the lateral toes in running (Table 4). In other words, several individuals, both short- and long-toed, did not load their lateral phalanges during stance in either gait. This variability in phalangeal loading could relate to kinematic differences between subjects. For example, running with a more extended limb or a more vertical trunk might align the COM closer to the MTP joints, placing relatively more weight on the metatarsal heads and relieving loads on the lateral toes. More data on whole-body kinematics will be necessary to clarify the relationship between gait and phalangeal loading. The variability in flexor output could also be related to the use of only habitually shod subjects who are accustomed to walking and running on hard, level surfaces. Future studies on phalangeal biomechanics should use larger samples drawn from traditionally unshod populations who might load their toes more uniformly.

These limitations notwithstanding, the data suggest that shorter toes reduce digital flexor force production and mechanical work during running. In our model of toe function (Fig. 1), we further suggested that this proximate benefit of short toes would ultimately reduce the metabolic cost of generating digital flexor force during bipedal locomotion. The relationship between mechanical work and the metabolic cost of force generation in muscles is complex and depends on factors such as muscle/tendon architecture as well as the type and velocity of contraction (e.g. Cavagna et al., 1977; Taylor et al., 1980). As such, we cannot rule out the possibility that a likely increase in metabolic cost associated with increases in flexor output in the long-toed individuals of the sample is to some extent offset by differences in muscle/tendon architecture, in the capacity for

elastic energy storage or in the velocity of contraction between individuals.

Even so, the multiple regression data show that, when factors such as body mass and contact times are held constant, individuals with relatively long toes require two to four times greater digital flexor force and mechanical work than short-toed individuals (Tables 6 and 7). Under these conditions, it is unlikely that such an increase in flexor output would not lead to at least a small increase in the metabolic cost of digital flexor force generation. It is important to remember also that we estimated the effect of toe length on flexor output over a single stance event. Accordingly, long toes might have an even greater impact on mechanical work and metabolic expenditure – even if the increase in the latter is relatively small – when considered over an individual's running range. For example, at a speed of $3.8\,\mathrm{m\,s^{-1}}$, the average stride length of trained runners is ~1.3 meters, or approximately 385 steps per foot per kilometer (Cavanagh and Williams, 1982). At this step frequency, the effects of phalangeal length on the metabolic cost of flexor force production are probably compounded by the distance travelled, potentially contributing to reducing the total metabolic cost of locomotion.

Finally, our analyses suggest that reduced mechanical and metabolic costs might not be the only benefits of shorter toes. Specifically, the flexor force and work data suggest that short toes might also contribute to reducing the risk of trauma and injury – especially overuse injuries – to the feet and digital flexors during running. For example, in situations where the toes are cyclically loaded for long periods of time (e.g. during marathons), two to four times greater musculotendinous forces associated with longer toes might accelerate the onset of muscle fatigue. Digital flexor fatigue in particular has been associated with a load-bearing shift under the metatarsal heads, which is a known risk factor for metatarsal stress fractures (Donahue and Sharkey, 1999; Arndt et al., 2002; Nagel et al., 2008).

Larger flexor forces and impulses in long-toed individuals might also increase wear and tear damage to the digital flexor tendons. Although peak stresses in the digital flexor tendons during stance are probably below the ultimate tensile stress that causes tendon failure, *in vitro* experiments have shown that microtrauma from repetitive loading ultimately causes tendons to fail and that the fatigue life of tendons (the number of loading cycles until failure) decreases as a function of the magnitude of the stress applied (Schechtman and Bader, 1997; Schechtman and Bader, 2002; Ker, 2007). The larger flexor tendon forces observed in long-toed individuals might be associated with larger tendon stresses. At best, such stresses will require more frequent repair. At worst, the hypothesized increase in tendon stress could shorten flexor fatigue life and increase the risk of failure, particularly if the frequency and duration of loading exceeds the capacity of these tendons to repair *in vivo*. In this context, it is interesting to note that most reported cases of flexor avulsion fracture and/or tendon failure in humans were sustained during prolonged walking and running, such as military marches and marathons (e.g. Coghlan and Clarke, 1993; Romash, 1994).

Implications for human evolution

The data suggest that having longer pedal phalanges, in the hallux and to some extent in the lateral toes, increases digital flexor force and work and might contribute to an increased risk of overuse injury during running. Although these effects presumably have negligible fitness consequences for habitually shod recent-modern humans who do not run long distances daily, they might have been significant
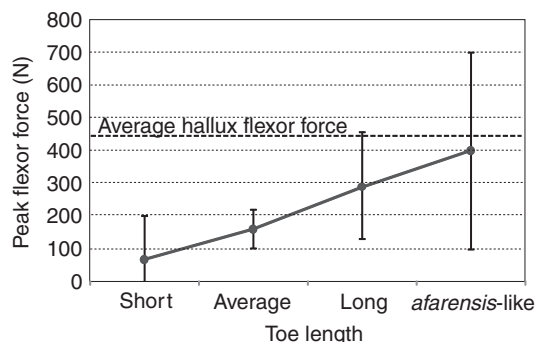

Fig. 3. Effect of increasing toe length on peak digital flexor force in the lateral toes, estimated using multiple regression equations derived from the study sample (see text and Table 7). Dots and vertical bars represent the predicted peak forces and their 95% confidence intervals, respectively, for four hypothetical individuals having the same body mass, contact times and toe-out angle, but with toe lengths ranging between the sample extremes (Short, Average and Long), and scaled to *A. afarensis* lateral toe length (*afarensis*-like). The *afarensis*-like individual was obtained by increasing the average hallux length by 40%, although it should be noted that the hallux of *A. afarensis* probably was not that long. The dotted line represents the average digital flexor force in the hallux (Table 2).

enough to impose the kind of selective pressures that led to the observed changes in phalangeal size and shape during human evolution. For example, partial foot remains recovered at Hadar, Ethiopia, suggest that, by 3.6 million years ago, the lateral phalanges of *A. afarensis* were shorter than in the African great apes, but approximately 40% longer and more curved than in modern humans (Latimer et al., 1982; Susman et al., 1984) (Table 1). This intermediate phalangeal morphology is thought to reflect a mixed behavioral repertoire comprising substantial arboreality and facultative terrestrial bipedalism (Stern and Susman, 1983; Stern, 2000). It has been suggested that this pedal morphology would have compromised efficient bipedal walking in *Australopithecus*, requiring an energetically costly 'high-stepping' gait to clear the toes from the ground at the end of stance (Jungers and Stern, 1983; Stern and Susman, 1983).

Long lateral toes might have affected walking kinematics in these early hominins, but our modern human data indicate that their long lateral toes would have had little or no effect on flexor output during walking. However, the data do suggest that the long lateral toes of *Australopithecus* could have adversely affected running performance. Although correlations between toe length and flexor biomechanics in running were only marginally significant in the lateral toes, the multiple regression analysis shows that modern toes that are only 20% longer than average (84 *vs* 69 mm hallux length; Table 2) require peak forces and impulses that are nearly twice as large (Table 7). By extrapolation, a modern human with *afarensis*-like lateral toes that are ~40% longer requires lateral digital flexor force, impulse and work outputs that are almost three times larger than average and comparable to the hallucial output of average modern humans (Fig. 3).

Even though *A. afarensis* was smaller in stature and might not have run like modern humans, the multiple regression data suggest that the long lateral toes of *A. afarensis* required significantly greater flexor force production during stance in running. The increased metabolic cost likely associated with producing greater forces could have had an impact on the fitness of australopithecines, particularly in the context of increasingly fragmented Pliocene habitats that might

have required these hominins to be more terrestrial, and potentially to run, in order to cover larger distances between food patches (Trauth et al., 2005). Individuals with shorter lateral toes might have been better able to reduce metabolic cost or delay pedal muscle fatigue, allowing them to forage farther and longer, with obvious positive fitness consequences. Thus, natural selection might already have favored reduced lateral toe length in Pliocene australopithecines.

Unfortunately, as there are no fossil pedal phalanges for early *Homo*, it is unclear when toe morphology changed from the longer, curved phalanges of australopithecines to the uniquely short lateral phalanges of modern humans. However, many other postcranial skeletal adaptations that first appear in *Homo* around 2 million years ago were recently suggested to have evolved in the context of an evolutionary transition from a semi-arboreal, ape-like species to a fully committed terrestrial biped that regularly engaged in endurance running (Bramble and Lieberman, 2004; Lieberman et al., 2006). The results of this study are consistent with this hypothesis, suggesting that short toes might be part of a suite of morphological and behavioral adaptations for endurance running that evolved in the genus *Homo* around 2 million years ago.

LIST OF ABBREVIATIONS

AP	anteroposterior
COM	center of mass
COP	center of pressure
GRF	ground reaction force
ML	mediolateral
MTP	metatarsophalangeal

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