

LEAKEY FOUNDATION RESEARCH GRANT – FINAL REPORT

"BIPEDALISM AND THE EVOLUTION OF SHORT LATERAL TOES IN HUMANS"

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SUMMARY

The lateral toes are extremely short relative to body mass in humans. This derived pedal length is thought to have evolved in the context of bipedalism, but the benefits of shorter toes for walking and/or running have not previously been tested. With the financial support of the Leakey Foundation, we tested 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. 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 increase in digital flexor output associated with longer toes in walking. In running, however, multiple our analyses suggest that increasing average relative toe length by as little as 20% doubles peak digital flexor impulses and mechanical work, in turn likely also increasing the metabolic cost of generating these forces. Based on these results, we suggest that modern human forefoot proportions may have been selected for in the context of the evolution of endurance running.

The following report is an abbreviated version of the published article. Reprints from the article can be obtained from Campbell Rolian (campbellrolian@gmail.com), or retrieved using the following reference:

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BACKGROUND AND HYPOTHESES

Humans have a highly modified foot comprising not only skeletal apomorphies in the tarsals and metatarsals, but also uniquely derived phalangeal proportions (Schultz 1963). Compared to other extant hominoids and *Australopithecus*, human lateral toes are straight and extremely short in relation to body size; and the hallux is adducted, more robust, and long. Together, these traits 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. This unique morphology has long been assumed to be functionally adaptive for terrestrial bipedal locomotion, yet to date no study has tested the extent to which shorter toes may benefit bipedal locomotion. In this study we tested a simple biomechanical model of toe function in bipedal locomotion that suggests that shorter phalanges provide performance benefits during the stance phase of walking, but especially running. We tested 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

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. In running, stance is also divided into three periods: contact (0-20% stance), midstance (20-45% stance) and propulsion (45-100% stance). 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. During propulsion, the metatarsal heads and distal phalanges become the only points of contact with the ground and hence become load-bearing. In walking, the toes support between 30 and 40% body weight, mostly under the first, second and third distal phalanges. In running, these loads range from 50 to 75% body weight.

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 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”. 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, 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 body’s forward falling motion (Reeser et al 1983). In other words, the digital flexors act as “brakes” that control MTP dorsiflexion.

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, while 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. The two individuals will have similar GRF profiles during propulsion. The individual with longer toes may not actually benefit from a greater load-bearing area, because in the foot’s normal position 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 net angular accelerations are negligible, 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. For roughly equal muscle moment arms, our model predicts that an individual with longer toes must thus generate larger plantarflexor forces, and do more mechanical work, to balance the larger dorsiflexion joint moments. All else being equal, greater force production and mechanical work will also likely increase the metabolic cost of generating digital flexor force in the long-toed individual.

Walking vs. Running: Our model predicts increased mechanical output in long-toed individuals relative to short-toed individuals. This difference in outputs may increase markedly in running, for two reasons. First, peak GRFs during propulsion are 2 to 4 times larger than walking at endurance running speeds. Accordingly, balancing digital flexor forces should also be substantially larger in running, with commensurate effects on muscular effort. Second, unlike walking, 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.

HYPOTHESES TESTED

We used kinematic, force and plantar pressure data from a sample of human subjects representing 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 were tested based on this hypothesis:

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

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 males, 13 females). Mean age of the sample was 22.8 years (SD 5.2, range 18-38 yrs), mean body mass 72.5 kg (SD 15, range 54-118kg) and mean stature 171.9 cm (SD 10.6, range 157-191cm). Subjects had no history of lower limb or foot pathology at the time of the study or in the previous six months. All experimental procedures were approved by the relevant Institutional Review Boards, and written informed consent was obtained from each subject prior to participation.

Experimental Protocol: 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 (RSScan International) flush and centered in a 25 meter long trackway. In the second set, subjects walked and ran across a force plate (AMTI) 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). 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 1st MTP joint, supero-lateral aspect of the fifth MTP joint, and the free margin of the nail plate on the first and 3rd 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). Kinematic data were used to

estimate hallux length, segment and joint angles and joint angular velocities at the first MTP joint during stance. 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 “toe length”). Force/pressure and kinematic data were combined to obtain external forces and moments acting on the toes and MTP joints, using a simplified inverse dynamics approach.

Calculation of MTP Joint Moments: In our analyses, we assumed that the GRF dorsiflexion moment was 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. The GRF dorsiflexion moment acting at the MTP joints was calculated using different methods in the force and pressure plates (see full article for details).

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:

$$M_{\text{muscle}} = F_{\text{muscle}} \times r \quad \text{Eq. 1}$$

Where M_{muscle} is the net muscle moment at the MTP joints (equal to the GRF dorsiflexion moment), 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. 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. Digital flexor forces were then used to calculate a flexor impulse, given by the integral of the digital flexor force over contact time:

$$\text{Impulse} = \int F_{\text{muscle}} dt \quad \text{Eq. 2}$$

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

$$P_{\text{musc}} = M_{\text{muscle}} \times \omega \quad \text{Eq. 3}$$

Where M_{muscle} is the plantarflexion muscle moment and ω is the joint’s angular velocity. The net work done by the digital flexors (W_{musc}), in Joules, is the integral of instantaneous power over stance time:

$$W_{\text{musc}} = \int P_{\text{musc}} dt \quad \text{Eq. 4}$$

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 style. 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 by calculating partial correlations between toe length and the biomechanical variables, while controlling for the effects of body mass, contact time, toe contact time and toe-out angle (see full article for details and justification).

Predicting the effects of toe length on flexor output. As a complement to partial correlations, 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 constant. In short, 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, to predict the effect of varying only toe length on digital flexor force production and work.

RESULTS

Dependent Variables: Flexor mechanical variables were found to be highly variable in this sample. As expected, negative work was significantly larger than positive work in all trials and gaits, reflecting the braking role of the digital flexors during propulsion. There was 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, likely because the flexor force is integrated over a much shorter contact time despite being significantly larger in runs. Variability in mechanical output for the lateral toes was also high in both walks and runs.

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. Results from the partial correlations analysis showed that at preferred walking speeds, increasing relative toe length had no effect on any of the mechanical output variables. In running, however, partial correlations between toe length and mechanical output based on force plate data were all highly significant. These data show that toe length has a direct effect on the magnitude of digital flexor mechanical output 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. Pressure plate data were more variable but consistent with the force plate data.

Predicting the effects of Toe Length on Flexor Output. The partial correlation data support the prediction that longer toes increase flexor mechanical output. The effect of toe length on flexor mechanical output was further quantified using multiple regression analysis. Only running data were evaluated. Predicted estimates for the dependent variables 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 mechanical work to stabilize the MTP joints during stance. Estimates for the pressure plate trials indicate that in the hypothetical long-toed individual, hallux flexor output variables are 2-3 times greater than 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 to 6 times larger in magnitude in the long-toed individual.

DISCUSSION

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. Pressure plate running data are consistent with the force plate data. 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 the lack of significant correlations in the lateral toes is due in part to small sample size: observed correlations suggest that 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.

Gait variability was a significant issue for this study. 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. 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 may align the COM closer to the MTP joints, placing relatively more weight on the metatarsal heads and relieving loads on the lateral toes. 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.

The multiple regression data show that when factors such as body mass and contact times are held constant, individuals with relatively long toes require 2 to 4 times greater digital flexor force and mechanical work than short-toed individuals. Under these conditions, it is likely that such an increase in flexor output would lead to at least a small increase in the metabolic cost of digital flexor force generation. Long toes may have an even greater impact on mechanical work and metabolic expenditure when considered over an individual's running range. For example, at a speed of 3.8 m/s, the average stride length among trained runners is ~1.3 meters, or approximately 385 steps per foot per kilometer. At this step frequency, the effects of phalangeal length on the metabolic cost of flexor force production are likely compounded by the distance travelled.

Larger flexor forces and impulses in long-toed individuals may also increase wear and tear damage to the digital flexor tendons. *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. The larger flexor tendon forces observed in long-toed individuals may 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*.

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 may contribute to an increased risk of overuse injury during running. These effects may have been significant enough to impose the kind of selective pressures that lead to 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 *Pan*, but approximately 40% longer and more curved than in modern humans. This intermediate phalangeal morphology is thought to reflect a mixed behavioral repertoire comprising substantial arboreality and facultative terrestrial bipedalism (Jungers and Stern 1983).

Long lateral toes may 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. The multiple regression analysis shows that modern toes that are only 20% longer than average (84 vs. 69 mm hallux length) require peak forces and impulses that are nearly twice as large. 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 3 times larger than average.

Even though *A. afarensis* was smaller in stature and may 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 may have required these hominins to be more terrestrial, and potentially to run, in order to cover larger distances between food patches. Individuals with shorter lateral toes may 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.

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 have been 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). The results of this study are consistent with this hypothesis, suggesting that short toes may be part of a suite of adaptations for endurance running that evolved in the genus *Homo* around 2 million years ago.

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