

RESEARCH ARTICLE

Does human foot anthropometry relate to plantar flexor fascicle mechanics and metabolic energy cost across various walking speeds?

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ABSTRACT

Foot structures define the leverage in which the ankle muscles push off against the ground during locomotion. While prior studies have indicated that inter-individual variation in anthropometry (e.g. heel and hallux lengths) can directly affect force production of ankle plantar flexor muscles, its effect on the metabolic energy cost of locomotion has been inconclusive. Here, we tested the hypotheses that shorter heels and longer halluces are associated with slower plantar flexor (soleus) shortening velocity and greater ankle plantar flexion moment, indicating enhanced force potential as a result of the force–velocity relationship. We also hypothesized that such anthropometry profiles would reduce the metabolic energy cost of walking at faster walking speeds. Healthy young adults ($N=15$) walked at three speeds (1.25, 1.75 and 2.00 m s⁻¹), and we collected *in vivo* muscle mechanics (via ultrasound), activation (via electromyography) and whole-body metabolic energy cost of transport (via indirect calorimetry). Contrary to our hypotheses, shorter heels and longer halluces were not associated with slower soleus shortening velocity or greater plantar flexion moment. Additionally, longer heels were associated with reduced metabolic cost of transport, but only at the fastest speed (2.00 m s⁻¹, $R^2=0.305$, $P=0.033$). We also found that individuals with longer heels required less increase in plantar flexor (soleus and gastrocnemius) muscle activation to walk at faster speeds, potentially explaining the reduced metabolic cost.

KEY WORDS: Biomechanics, Locomotion, Muscle

INTRODUCTION

During the ground contact phase of locomotion, the foot and ankle structures function like a lever system (Carrier et al., 1994; Cunningham et al., 2010) to produce forces that keep the body upright and generate forward velocity (McGowan et al., 2008; McGowan et al., 2009; Neptune et al., 2001). As the foot makes ground contact from heel to toe, the ankle plantar flexor muscles produce forces to create a moment about the joint, directly influencing the magnitude and location of the ground reaction force (GRF). As such, the lever arm of the GRF (relative to the ankle) and the lever arm of the plantar flexor muscle dictate the

foot–ankle structures' capacity to produce force and thus affect the body's forward acceleration. The ratio of the GRF and plantar flexor muscle lever arms has been termed 'gear ratio' (Carrier et al., 1994) – the inverse is called 'effective mechanical advantage' (Biewener, 1989; Biewener et al., 2004) – and has been theorized to affect muscle function during locomotion. A high gear ratio, for example, requires a high force output from the plantar flexors, but the muscles will operate at a slower shortening velocity (Carrier et al., 1994), where they can generate more force, according to the force–velocity curve (Hill, 1938). These built-in mechanisms to adjust force output are thought to allow humans (Carrier et al., 1994; Ray and Takahashi, 2020; Takahashi et al., 2016) and other animals (Carrier et al., 1998; Gronenberg, 1996; Roberts and Marsh, 2003) to push off effectively during the late stance phase of locomotion when the force requirement is greatest. While the lever functions or gear ratio of the foot and ankle have advanced our understanding of how skeletal muscle functions during locomotion, there is a lack of consensus on how inter-individual variation in lever arms through foot anthropometry (e.g. heel and hallux lengths) affects locomotion outcomes.

Foot anthropometry can influence the gear ratio by either modifying the GRF lever arm or plantar flexor muscle lever arm, which in turn can affect the force-producing potential during locomotion. For example, 'heel length', defined as the horizontal distance between the malleolus and the most posterior point on the Achilles tendon (Scholz et al., 2008; van Werkhoven and Piazza, 2017a,b), is a surrogate measure for the plantar flexor lever arm. Similarly, 'hallux length', defined as the horizontal distance from the first metatarsal head to the most anterior aspect of the toe (Rolian et al., 2009; van Werkhoven and Piazza, 2017a), can modify the GRF lever arm relative to the ankle joint (Rolian et al., 2009). Theoretically, anatomical variation in the heel and hallux lengths can influence the muscle's capacity to produce force. For example, in an individual with a shorter heel (and hence a shorter plantar flexor moment arm), the muscle–tendon unit would shorten less under the same angular displacement, enhancing the force potential due to the force–velocity effect (Baxter et al., 2012). Likewise, in an individual with a longer hallux, the longer GRF lever arm will decrease the ankle angular displacement, allowing the muscle–tendon unit to contract slower (Rolian et al., 2009). Prior studies have suggested that these theoretical benefits of a higher gear ratio can yield tangible performance benefits – for example, in sprinters that have naturally shorter heels and longer halluces that favor high acceleration tasks (Baxter et al., 2012; Lee and Piazza, 2009).

While anatomical variation in foot anthropometry (e.g. heel and hallux lengths) can affect the gear ratio and plantar flexor force production, it is less clear how this translates to the metabolic energy cost of locomotion. The plantar flexors are the largest source of positive mechanical work among the lower extremity structures during level-ground walking (Farris and Sawicki, 2012a; Nuckolls

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et al., 2020). Various models estimate that these muscles can account for ~30–60% of the whole-body energy costs (Mohammadzadeh Gonabadi et al., 2020). The energy cost of a muscle is influenced by the active muscle volume (Beck et al., 2019; Beck et al., 2020; Kipp et al., 2018a), dictated by the force–length and force–velocity operating regions, and the activation required to produce a given force. While factors such as tendon compliance can affect the muscle force–length and force–velocity operating regions and metabolic energy cost (Lichtwark and Wilson, 2008; Orselli et al., 2017), variation in foot anthropometry is also likely to affect the muscle mechanics and metabolic energy cost. Although a high gear ratio, such as in individuals with shorter heels, can theoretically enhance muscle performance by maintaining the muscles in a beneficial portion of the force–velocity curve (Baxter et al., 2012; Lee and Piazza, 2009), a high gear ratio could also necessitate greater plantar flexion in order to generate a sufficient ankle moment and hence GRF – thus requiring higher active muscle volume that could incur greater energy cost (Biewener, 1989; Biewener et al., 2004; Griffin et al., 2003; Kipp et al., 2018a). As such, variation in gear ratios influenced by foot anthropometry may have competing effects on the energy cost of locomotion. Such competing effects may partially explain the inconclusive results regarding the influence of foot anthropometry on metabolic energy cost during locomotion. For example, studies by Scholz et al. (2008) and Raichlen et al. (2011) found that shorter heels were associated with reduced metabolic energy cost during running. However, van Werkhoven and Piazza (2017a) found no correlation between foot anthropometry and the metabolic cost of running, and Raichlen et al. (2011) found no correlation during walking at a preferred speed. Another recent study also found that longer Achilles tendon moment arms (measured via magnetic resonance imaging) correlated with reduced running metabolic cost (Kovács et al., 2021). The explanatory factors for the inconclusive (and sometimes conflicting) results among these studies are currently difficult to discern. One plausible explanation is that the effects of foot anthropometry on energetic cost may depend on the locomotion speed or mode.

One possible way to investigate the influence of foot anthropometry on metabolic energy cost is to study fast walking, a mode of locomotion that can amplify the importance of the force–velocity effect of muscles. During fast walking, less ground contact time is available to produce force, requiring a faster shortening speed that shifts the muscles into more unfavorable regions of the force–velocity relationship (Sasaki et al., 2009). Furthermore, at speeds near the walk-to-run transition, walking becomes more energetically costly than running (Neptune and Sasaki, 2005), and switching from walking to running shifts the plantar flexors to a more economical force–velocity operating region (Farris and Sawicki, 2012b). Thus, individuals with shorter heels and longer halluces (i.e. greater gear ratio) may show potential energetic benefits due to the heightened importance of maintaining the plantar flexors in economic operating portions of the force–velocity curve during fast walking. In fact, a recent study found that increasing gear ratio through stiff insole/shoes can reduce the energy cost of walking (Ray and Takahashi, 2020), but only at a fast speed (2.0 m s^{-1}) near the walk-to-run transition speed. Such a finding reinforces the theoretical benefits of high gear ratio, in particular, the speed-dependent effects on the energetic cost of walking, and provides a basis for studying the effect of foot anthropometry on the metabolic energy cost of walking at various speeds.

The purpose of this study was to investigate the associations between foot anthropometry (e.g. heel and hallux lengths), *in vivo*

muscle mechanics of the largest plantar flexor muscle (soleus) (Fukunaga et al., 1992), and whole-body metabolic cost across a range of walking speeds. We used a photograph-based method to quantify foot anthropometry – specifically, the heel and hallux lengths were extracted from lateral and medial images of the foot, respectively (Scholz et al., 2008; van Werkhoven and Piazza, 2017a,b). We chose to analyze the contractile behavior of the soleus muscle because of its large cross-sectional area (Fukunaga et al., 1992) and its role in the forward acceleration of the body (McGowan et al., 2009; Neptune et al., 2001). Given the influence of foot anthropometry on gear ratios (Baxter et al., 2012; Lee and Piazza, 2009), we hypothesized that shorter heel lengths and longer halluces are associated with slower soleus fascicle shortening velocity and greater ankle plantar flexion moment (i.e. a surrogate measure of force). We also hypothesized that shorter heels and longer halluces are associated with reduced metabolic energy cost at fast walking speeds.

MATERIALS AND METHODS

Participants

The data from 15 healthy young adults (3 females, 12 males; age 23 ± 2.1 years, height 176 ± 7.3 cm, mass 76.43 ± 12.43 kg, means \pm s.d.) were reanalyzed from a previous study (Ray and Takahashi, 2020). The sample size was based on a published study (Scholz et al., 2008) that found a significant correlation between heel length and metabolic cost of running (effect size of 0.75), although other similar studies in running had lower (0.21) (van Werkhoven and Piazza, 2017a) or larger effect sizes (0.89) (Raichlen et al., 2011). The power analysis indicated that 11 participants needed to provide 80% power to detect a similar correlation, with the α level set to 0.05.

Participants had to be able to walk at least 7 min on a treadmill continuously. Participants were free of cardiac and neurological pathologies such as arrhythmia, heart attack and stroke, and free of any musculoskeletal or pathological problems (osteoarthritis, bone fractures, etc.). These conditions were screened through a medical history form. The Institutional Review Board of the University of the Nebraska Medical Center approved all procedures. Each participant provided written informed consent before participating in the experiment.

Experimental protocol

Participants completed two visits: one visit to measure lower limb neuromechanics data (e.g. muscle activation, foot mechanics and soleus muscle fascicle behavior) and one visit to measure metabolic energy expenditure. On each visit, participants completed walking wearing standardized shoes (Reebok RealFlex Train) on an instrumented treadmill (Bertec, Columbus, OH, USA) at three different walking speeds (1.25 , 1.75 and 2.00 m s^{-1}). We selected these walking speeds because 1.25 m s^{-1} is close to the preferred walking speed in healthy adults, while 2.00 m s^{-1} is near the walk-to-run transition speed (Farris and Sawicki, 2012b); 1.75 m s^{-1} was selected to include speeds that were skewed towards faster than preferred walking.

The order of walking speeds and the two visits was randomized for each participant. The two visits were separated, by approximately 24 h (Fig. 1), because of the difficulty in obtaining all measurements simultaneously. During each visit, participants wore a tight-fitting ‘wrestling’ suit, which promoted accurate and consistent placement of retro-reflective markers. The retro-reflective markers were placed directly on the skin and the surface of the wrestling suit using double-sided tape at specific anatomical

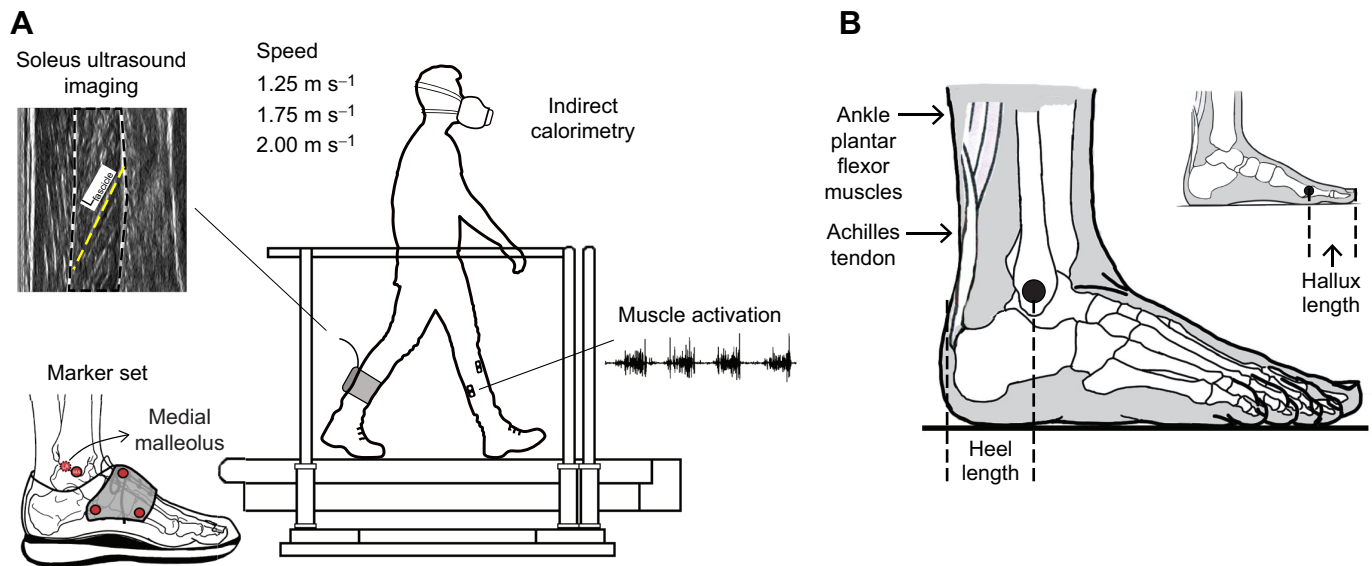


Fig. 1. Schematic diagram of the experimental apparatus, setup and procedure. Participants ($N=15$) completed shod walking on an instrumented treadmill at three different walking speeds (1.25 , 1.75 and 2.00 m s^{-1}). (A) In one visit, we collected kinematic, kinetic, muscle activation (left leg) and ultrasound muscle (soleus; right leg) imaging data. Metabolic measurements were collected during the other visit. The order of the visits was randomized. (B) Participants stood still on a wooden ruler block, and we obtained foot geometric data. Heel length was defined as the horizontal distance from the lateral malleolus to the line of action of the Achilles tendon (posterior aspect of the heel). Hallux length was measured as the horizontal distance from the metatarsophalangeal joint to the distal end of the great hallux.

locations on each participant. Marker clusters were used to track the movement of the foot, shank, thigh and pelvis (Holden et al., 1997). The foot model was a single-segment model with clusters of targets placed over the metatarsal region (Siegel et al., 1995). While more recent foot models allow for tri-planar analyses involving joints within the foot (Bruening and Takahashi, 2018; Bruening et al., 2012a,b; Leardini et al., 2019), we focused our analysis on sagittal plane ankle moment. A prior study has shown that the ankle moment estimates are relatively unaffected by degrees-of-freedom of the foot model (Dixon et al., 2012). Participants were not instructed to walk in any particular way, and data were excluded if subjects transitioned to a running gait (aerial phase) during a trial.

Analysis of metabolic energy expenditure using indirect calorimetry

A portable gas exchange system was used to measure rates of oxygen inhalation and carbon dioxide exhalation (TrueOne, ParvoMedics Inc., Salt Lake City, UT, USA). Before the first walking trial, participants stood quietly for 6 min, and we approximated the metabolic power (W kg^{-1}) of quiet standing. All walking trials lasted 6 min. We averaged only the last 2 min of calorimetry data, and we estimated rates of metabolic energy expenditure using the Peronnet and Massicotte (1991) equation (Kipp et al., 2018b). We calculated net normalized metabolic power by subtracting the metabolic power of quiet standing from walking trial data. Net metabolic cost of transport ($\text{J kg}^{-1} \text{m}^{-1}$) was then calculated by dividing net metabolic power by walking speed, giving a measure of whole-body metabolic energy expenditure per unit distance traveled. Metabolic data were collected early in the morning, before participants ate breakfast, to control for the effects of dietary intake on metabolic data.

Analysis of foot anthropometry (heel and hallux lengths)

The anthropometric characteristics of the foot (heel and hallux lengths) were measured by using the technique of previous studies

(Scholz et al., 2008; van Werkhoven and Piazza, 2017a,b). To estimate heel length (i.e. a surrogate measure for the plantar flexor lever arm), with the participant standing at a neutral ankle angle (with the foot flat and shank oriented vertically) on a reference block, we took photographs of each subject's right ankle from the lateral view. The lateral edge of the foot was aligned with the reference block. This block served as a calibration object to convert the pixel coordinates of the photograph to metric units. Then, using custom-written digitizing software (MathWorks, MA, USA), we digitized two anatomical landmarks: the lateral malleolus and the posterior aspect of the Achilles tendon (the line of action of the Achilles tendon) at the same height as the malleolus (van Werkhoven and Piazza, 2017a). In a prior study, heel length, also called 'lateral heel length' (van Werkhoven and Piazza, 2017b), was defined as the horizontal distance between these two landmarks, which served as a proxy for the plantar flexor lever arm at a neutral ankle angle (Fig. 1). As the center of rotation of the ankle is close to the midpoint between the medial and lateral malleoli (Lundberg et al., 1989), we also computed an 'average heel length' by computing the average between the heel lengths obtained from lateral and medial images (i.e. the distance between the medial malleolus and posterior aspect of the Achilles tendon). However, a previous study found that heel length estimated based on only the lateral image is a stronger predictor of locomotion performance than 'average heel length' (van Werkhoven and Piazza, 2017b). Thus, we focused our data analyses on the lateral heel length – however, the average heel length was also provided as supplementary data.

To quantify the hallux length, we collected a medial image of the foot and digitized the head of the first metatarsal and the distal end of the hallux. The hallux length was defined as the horizontal distance between these two landmarks. A prior study showed that similar photography-based techniques to estimate foot arch height index during standing, which would include digitization of similar anatomical landmarks (e.g. the head of the first metatarsal and the distal end of the hallux), produced excellent reliability with an intraclass correlation coefficient of 0.94 (Pohl and Farr, 2010).

Finally, to provide additional insight into the relationship among foot morphology, energy cost and muscle function, we quantified a few additional anthropometric variables (Tables S2 and S3). Specifically, we estimated the length of the ‘mid-foot’ as the horizontal distance between the medial malleolus and the first metatarsal head. We also computed the ratio of hallux and heel lengths and the ratio of mid-foot and heel lengths. Such measurements serve as surrogates of the lever arm of the GRF. Previous studies have highlighted its importance in mammals, including human locomotion (Biewener, 1989; Biewener et al., 2004; Carrier et al., 1994; Carrier et al., 1994; Kram and Taylor, 1990). However, we decided to center our study on the hallux length for two reasons. First, modern humans’ hallux length (i.e. length of the toes) has been treated as an adaptation for improving economy during faster locomotion modes, such as running (Rolian et al., 2009). Second, we expected that the halluces might affect the absolute length of the lever arm of the GRF during the latter part of the contact phase.

Analysis of lower limb mechanics

Three-dimensional limb kinematic data (100 Hz) were captured using an eight-camera motion-capture system (VICON Vero v2.2, Oxford, UK) with a resolution of 2.2 megapixels. An instrumented treadmill (Bertec, Columbus, OH, USA) was used to capture limb kinetic data (1000 Hz). A six degree-of-freedom (6 DOF) marker set was used (Holden et al., 1997) to track the motion of the lower extremities. This type of marker set has shown good-to-excellent reliability in joint angle and moment estimates, with an intraclass correlation coefficient greater than 0.75 (Wilken et al., 2012). Before all processing and analysis, raw data from marker trajectories and GRFs were filtered by applying a second-order dual-pass low-pass Butterworth filter of 6 Hz for kinematic data and 25 Hz for kinetic data. A 20 N threshold for the vertical GRF defined the start and the end time for each stance phase of walking. To compute the joint moment at the ankle joint, we applied the built-in function of the Visual 3D software (C-motion Inc., Germantown, MD, USA) using the shank segment as the resolution coordinate system. GRF lever arm relative to the ankle was estimated using a technique described in a prior study (van Werkhoven and Piazza, 2017a). Briefly, the GRF lever arm was calculated as the sagittal plane ankle moment component due to the GRF divided by the magnitude of the GRF.

Analysis of soleus muscle fascicle velocity using ultrasonography

A flat, linear ultrasound probe (Telemed, Vilnius, Lithuania) was secured to the subject’s lower leg, superficial to the ankle plantar flexor muscles, then rotated and translated until a clear image of a soleus fascicle from end to end was visible on the screen, corresponding to when the fascicle and probe were within the same plane. Soleus fascicle contractions were captured at approximately 78 Hz. This method for recording muscle fascicle behavior has been previously proven to be reliable and accurate (Aggeloussis et al., 2010; Reeves et al., 2004). We used a semi-automated tracking algorithm (Farris and Lichtwark, 2016) to quantify the length of fascicles over time. We differentiated the length of fascicles to achieve soleus fascicle velocity. The shortening velocity of soleus fascicles was analyzed as an average over the stance phase and as the instantaneous velocity at peak ankle plantar flexion moment.

Supplementary analysis

We collected electromyography (EMG) data (Delsys, MA, USA) on the tibialis anterior, medial gastrocnemius, lateral gastrocnemius and soleus on the leg without the ultrasound probe to record muscle activity ($N=14$, one subject EMG removed because of technical difficulties).

Muscle activation is associated with the metabolic cost of walking (Franz and Kram, 2012; Hortobágyi et al., 2011; Lay et al., 2007), and changes at the moment arm of the ankle plantar flexor muscles could affect their activation level (Nourbakhsh and Kukulka, 2004). Thus, we included the EMG measurements as a supplementary analysis to provide potential explanations for the study’s primary hypotheses (i.e. a link between foot morphology, muscle mechanics and energetic cost).

EMG data were high-pass filtered at 20 Hz, rectified and then low-pass filtered at 10 Hz with second-order Butterworth filters to achieve a linear envelope. EMG data were then time integrated from heel strike to toe-off to quantify the amount of muscle activation over stance. A variety of methods have been proposed for the normalization of EMG data (Burden, 2010; Sinclair et al., 2015). In our study, we were not able to measure maximum voluntary muscle activity. For this reason, we used the average time-integrated activation level of each muscle during the slowest walking speed (1.25 m s^{-1}) as the reference value for the normalization. While this normalization can limit comparisons between muscles or individuals relative to their maximal physiological capacity, this analysis can assess the relative changes in muscle activation to walk at faster speeds (1.75 and 2.00 m s^{-1}). Thus, we aimed to assess whether foot anthropometry relates to how much additional muscle activation is required to walk at faster speeds relative to the slowest speed.

Statistical analyses

We used Pearson correlation analyses to determine whether foot anthropometric variables (hallux and heel lengths) were associated with: (a) GRF lever arm relative to the ankle joint at the time of peak plantar flexion moment, (b) average soleus fascicle shortening velocity during stance, and instantaneous shortening velocity at the time of peak ankle plantar flexion moment, (c) peak ankle plantar flexion moment, (d) metabolic cost of transport, and (e) EMG. To account for the potential confounding factor in anthropometry differences among individuals of varying stature, we performed the correlations with anthropometric variables normalized to body height. For completeness, we also report the correlation results with unnormalized anthropometric variables (see Tables S2–S5). The significance threshold was set to $P \leq 0.05$. Our supplementary correlational analyses were conducted to gain additional mechanistic insights regarding the effects of foot anthropometry variations. As we did not apply any corrections for multiple comparisons, we report all P -values and R^2 for full transparency of the results.

The homoscedasticity of our data was tested using a scatterplot that plotted the standardized values our model would predict against the standardized residuals that were obtained. We tested whether our model is biased by any influential cases using Cook’s distance values. Any values above one were identified as significant outliers. We used SPSS (IBM SPSS Statistics 24, SPSS Inc., Chicago, IL, USA) for all assumptions and statistical methods.

RESULTS

The demographic data and anthropometric measurements are given in Table 1. No significant association was found between anthropometric measurements (body mass and height, heel and hallux lengths) (Table S1). The time-series data of soleus muscle fascicle mechanics and ankle moment data are given in Fig. 2.

Foot anthropometry affects the GRF lever arm

Hallux length (cm) and height (cm) were positively associated with the ground reaction lever arm at the time of peak ankle plantar flexion moment for all walking speeds (hallux: 1.25 m s^{-1} ;

Table 1. Participant characteristics (N=15)

Participant	Sex	Age (years)	Height (cm)	Mass (kg)	Heel length (cm)	Hallux length (cm)
1	F	23	166	73.74	4.16	6.46
2	M	24	178	69.00	5.29	7.32
3	M	21	179	64.18	3.81	6.80
4	M	26	170	85.00	3.72	6.97
5	F	23	171	75.94	4.12	6.90
6	M	23	175	87.70	3.13	6.14
7	F	22	173	58.10	3.87	5.98
8	M	22	184	88.90	4.98	7.06
9	M	19	174	101.6	3.70	6.13
10	M	23	168	68.50	3.73	5.91
11	M	28	165	59.90	3.01	4.92
12	M	23	190	81.20	4.13	6.87
13	M	22	186	84.80	4.16	6.09
14	M	22	179	83.50	4.32	6.09
15	M	22	175	64.40	4.92	5.35
Mean±s.d.	F:3; M:12	23±2.1	176±7.3	76.43±12.43	4.07±0.63	6.34±0.67

$R^2=0.303$, $P=0.033$; 1.75 m s^{-1} : $R^2=0.300$, $P=0.035$; 2.00 m s^{-1} : $R^2=0.448$, $P=0.006$; height: 1.25 m s^{-1} : $R^2=0.480$, $P=0.004$; 1.75 m s^{-1} : $R^2=0.453$, $P=0.006$; 2.00 m s^{-1} : $R^2=0.466$, $P=0.005$). Additionally, heel length was positively associated with the ground reaction lever arm at the time of peak ankle plantar flexion moment only for the fast walking speed (2.00 m s^{-1} : $R^2=0.342$, $P=0.022$; 1.25 m s^{-1} : $P=0.062$; 1.75 m s^{-1} : $P=0.068$).

Foot anthropometry (normalized to body height) does not affect ankle mechanics

A significant negative association was found only between heel length and soleus fascicle shortening velocity at peak ankle plantar flexion moment during walking at 1.75 m s^{-1} ($R^2=0.320$, $P=0.028$), but not for the other two speeds (1.25 m s^{-1} : $P=0.183$; 2.00 m s^{-1} : $P=0.858$) (Fig. 3B). Cook's distance values indicated a possible outlier. When we removed the outlier and re-ran the analysis ($N=14$), there was no significant association between heel length and soleus fascicle shortening velocity at peak ankle plantar flexion moment during walking at 1.75 m s^{-1} ($P=0.166$). Hallux length was not associated with soleus fascicle shortening velocity at the time of peak ankle plantar flexion moment (1.25 m s^{-1} : $P=0.377$; 1.75 m s^{-1} : $P=0.515$; 2.00 m s^{-1} : $P=0.276$) (Fig. 3B). Neither of the anthropometrical measurements was significantly associated with the average soleus fascicle shortening velocity (heel length: 1.25 m s^{-1} : $P=0.846$; 1.75 m s^{-1} : $P=0.961$; and 2.00 m s^{-1} : $P=0.925$; hallux length: 1.25 m s^{-1} : $P=0.952$; 1.75 m s^{-1} : $P=0.728$; and 2.00 m s^{-1} : $P=0.948$) (Fig. 3A).

No significant association was found between the foot anthropometrical measurements and peak ankle plantar flexion moment (heel length: 1.25 m s^{-1} : $P=0.234$; 1.75 m s^{-1} : $P=0.454$; 2.00 m s^{-1} : $P=0.397$; hallux length: 1.25 m s^{-1} : $P=0.185$; 1.75 m s^{-1} : $P=0.307$; 2.00 m s^{-1} : $P=0.217$) (Fig. 3C).

Foot anthropometry (normalized to body height) affects whole-body metabolic energy cost of transport only at the fastest speed

A significant negative association was found between heel length and cost of transport during fast walking (2.00 m s^{-1} : $R^2=0.305$, $P=0.033$). However, the association between hallux length and cost of transport was not significant ($P=0.432$) (Fig. 3D). The equation that predicted the cost of transport from the heel length was:

$$\text{Cost of transport} = 5.52 - 0.98\text{heel}(\% \text{ height}).$$

On average, every unit increase in heel length (% height) was associated with $0.98 \text{ J kg}^{-1} \text{ m}^{-1}$ decrease in the metabolic cost of transport. No statistically significant associations were found between the other two walking speeds and the foot's anthropometric measurements (heel length: 1.25 m s^{-1} : $P=0.701$; and 1.75 m s^{-1} : $P=0.126$; hallux length: 1.25 m s^{-1} : $P=0.487$; and 1.75 m s^{-1} : $P=0.798$).

The rest of the associations between foot anthropometric measurements (normalized by body height) and dependent variables can be found in the Table S2. The associations between unnormalized foot anthropometric measurements and dependent variables can be found in Table S3.

Foot anthropometry (normalized to body height) affects EMG magnitude (normalized to activation at 1.25 m s^{-1})

A significant negative association was found between heel length and stance-integrated EMG activation of the soleus (relative to the magnitude at 1.25 m s^{-1}) during walking at 1.75 m s^{-1} ($R^2=0.306$, $P=0.040$), but not at 2.0 m s^{-1} ($P=0.061$) (Fig. 4). In addition, a significant negative association was found between heel length and stance-integrated EMG activation (relative to the magnitude at 1.25 m s^{-1}) of the medial gastrocnemius during walking at 1.75 m s^{-1} ($R^2=0.676$, $P<0.001$) and 2.00 m s^{-1} ($R^2=0.376$, $P=0.020$) walking speed. No other stance-integrated muscle EMG signals were associated with heel length (lateral gastrocnemius; 1.75 m s^{-1} : $P=0.122$; 2.00 m s^{-1} : $P=0.104$; tibialis anterior; 1.75 m s^{-1} : $P=0.498$; 2.00 m s^{-1} : $P=0.503$).

Hallux length was not significantly associated with any of the stance-integrated muscle EMG signals. Table S4 contains the statistics for normalized foot anthropometrics. The associations between unnormalized foot anthropometric measurements and stance-integrated muscle activation can be found in Table S5.

DISCUSSION

While the foot structures provide a mechanical advantage to the ankle plantar flexors (Carrier et al., 1994; Lee and Piazza, 2009), the effects of foot anthropometry (heel and hallux length) on the metabolic cost of locomotion have been inconclusive (Karamanidis et al., 2011; Raichlen et al., 2011; Scholz et al., 2008; van Werkhoven and Piazza, 2017a). In this study, we examined walking at various speeds along with *in vivo* muscle mechanics to investigate the effects of foot anthropometry on metabolic energy cost. We hypothesized that shorter heels and longer halluces would be

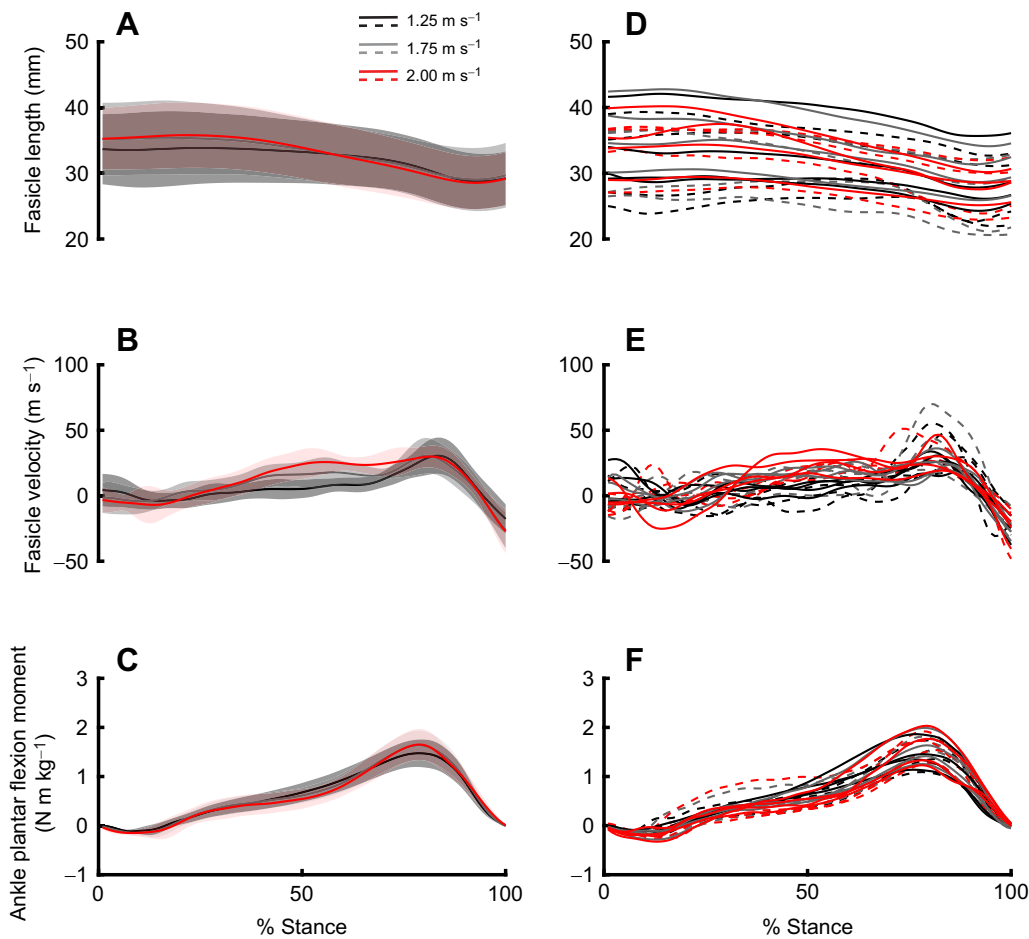


Fig. 2. Time-series soleus fascicle mechanics and ankle moment data. (A–C) Average soleus fascicle length (A), velocity (B) and ankle plantar flexion moment (C) time-series data (grand mean \pm s.d.) during the stance phase of different walking speeds (1.25, 1.75 and 2.00 m s $^{-1}$) of all participants ($N=15$). We analyzed the shortening velocity of soleus fascicles both as an average over the stance phase and as the instantaneous velocity at the peak ankle plantar flexion moment. (D–F) Average soleus fascicle length (D), velocity (E) and ankle plantar flexion moment (F) time-series data during the stance phase of different walking speeds of participants in the 1st quartile (dashed lines) and 3rd quartile (solid lines) for heel lengths.

associated with slower soleus fascicle shortening velocity and higher ankle moment production (i.e. more favorable force–velocity operation), leading to lower metabolic cost, at the faster walking speeds. Our hypotheses were not supported in that shorter heels or longer halluces were not associated with slower shortening velocity or enhanced plantar flexion moment, effectively not revealing a force–velocity benefit. Additionally, contrary to our hypothesis, longer heels were associated with reduced metabolic cost of walking, but only at the fastest speed of 2.0 m s $^{-1}$ ($P=0.033$). At this fast walking speed, every unit increase in heel length (% height) was associated with 0.98 J kg $^{-1}$ m $^{-1}$ decrease in the metabolic cost of transport.

Because of the purported benefit of a higher gear ratio (Baxter et al., 2012; Carrier et al., 1994; Ray and Takahashi, 2020), we had initially hypothesized that individuals with shorter heels and longer halluces would have reduced metabolic energy cost, at fast walking speeds. However, this hypothesis was largely unsupported. While there was a speed-dependent effect of heel length on energetic metabolic cost, longer heels showed an energetic benefit at the fastest walking speed (2.0 m s $^{-1}$), contrary to our hypothesis. Such a finding, combined with the non-significant association between heel length and ankle moment, may potentially indicate that longer heels permit energy savings as a result of reduced force production or active muscle volume at the fast walking speed. A longer heel (and assuming a longer lever arm), for example, would require a smaller plantar flexor force to produce a given ankle moment (Baxter and Piazza, 2014) – which may require less active muscle volume and may reduce metabolic energy cost (Beck et al., 2019,

2020; Kipp et al., 2018a). As such, our finding regarding the negative association between heel length and metabolic energy cost (at the fastest walking speed) may indicate that longer heels require less plantar flexor force and hence less active muscle volume. While active muscle volume was not directly quantified in this study, such an idea is supported by EMG data. Individuals with longer heels required a lower increase in plantar flexor muscle activation (including soleus and gastrocnemius) to walk at faster speeds (1.75 and 2.00 m s $^{-1}$). This finding also corroborates prior studies suggesting that individuals with shorter heel lengths have greater medial gastrocnemius activation (Ahn et al., 2011), and muscle activation is associated with the metabolic cost of walking (Franz and Kram, 2012; Hortobágyi et al., 2011; Lay et al., 2007). More recently, a study involving competitive marathon runners found that longer Achilles tendon moment arms (estimated via magnetic resonance imaging) were associated with a reduced metabolic cost of running (Kovács et al., 2021), in line with our observations during fast walking. However, our results are inconsistent with other published running studies, which warrants further investigation. As a speed-dependent effect of heel length on metabolic cost was observed in our study, it is possible that differences in locomotion speed or task could explain the inconsistent findings.

There are, however, other possible mechanisms besides foot anthropometry that may be responsible for the observed reduction in metabolic cost with longer heels during fast walking. For example, the elastic Achilles tendon can reduce the work output of the plantar flexor muscle fascicles (Farris and Sawicki, 2012b; Ishikawa et al., 2005; Lichtwark and Wilson, 2008) and alterations in Achilles

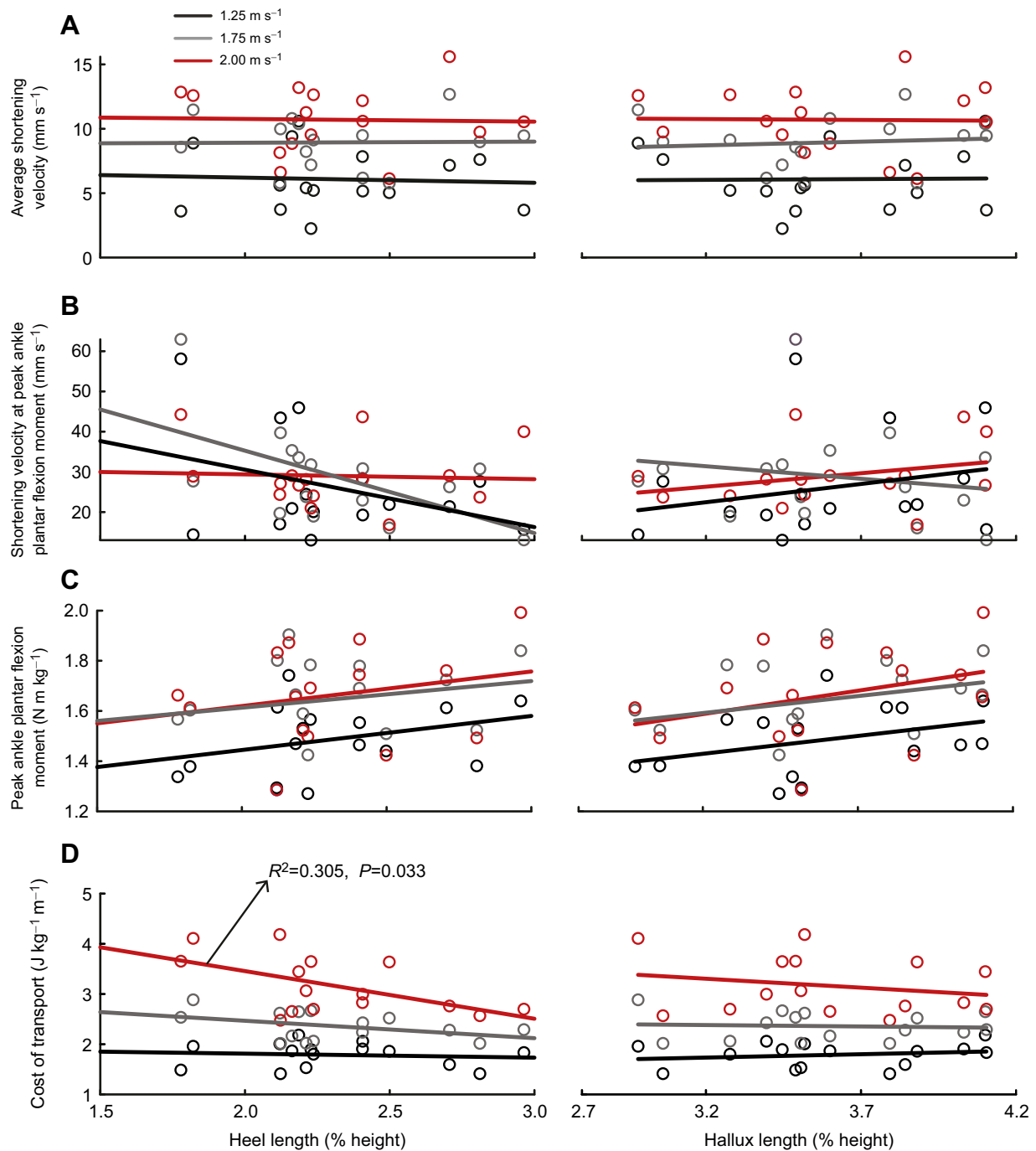


Fig. 3. Regressions between normalized foot anthropometric measurements and dependent variables. (A) Average shortening velocity, (B) shortening velocity at peak ankle plantar flexion moment, (C) peak ankle plantar flexion moment and (D) cost of transport against heel and hallux length (normalized to height) for each participant ($N=15$). The soleus shortening velocity at peak ankle plantar flexion moment was negatively associated with heel length, but only for 1.75 m s^{-1} walking speed ($P=0.028$); however, when a detected outlier was removed, the correlation was non-significant ($P=0.166$). Additionally, heel length was significantly associated with the cost of transport only for the fastest walking speed ($P=0.033$). No other associations were statistically significant.

tendon stiffness can directly affect muscle mechanics and metabolic energy costs (Lichtwark and Wilson, 2008; Orsell et al., 2017). Thus, it is possible that tendon stiffness, which was not quantified in this study, could confound the results of our study. However, based on data from our study and findings from prior studies, it is unlikely that longer-heeled individuals had greater tendon energy storage and return to produce a metabolic benefit. First, we found no significant correlation between heel length and plantar flexion

moment. Assuming that heel lengths are surrogates for muscle lever arm, such data may indicate that the in-series tendon of a longer heel experienced less force, reducing the energy storage for a given tendon stiffness. While greater energy storage may be possible if longer-heeled individuals have more compliant tendons, this idea seems unlikely given that a prior running study revealed that shorter heels are associated with greater tendon energy storage and return (Scholz et al., 2008). The same study also found that variation in

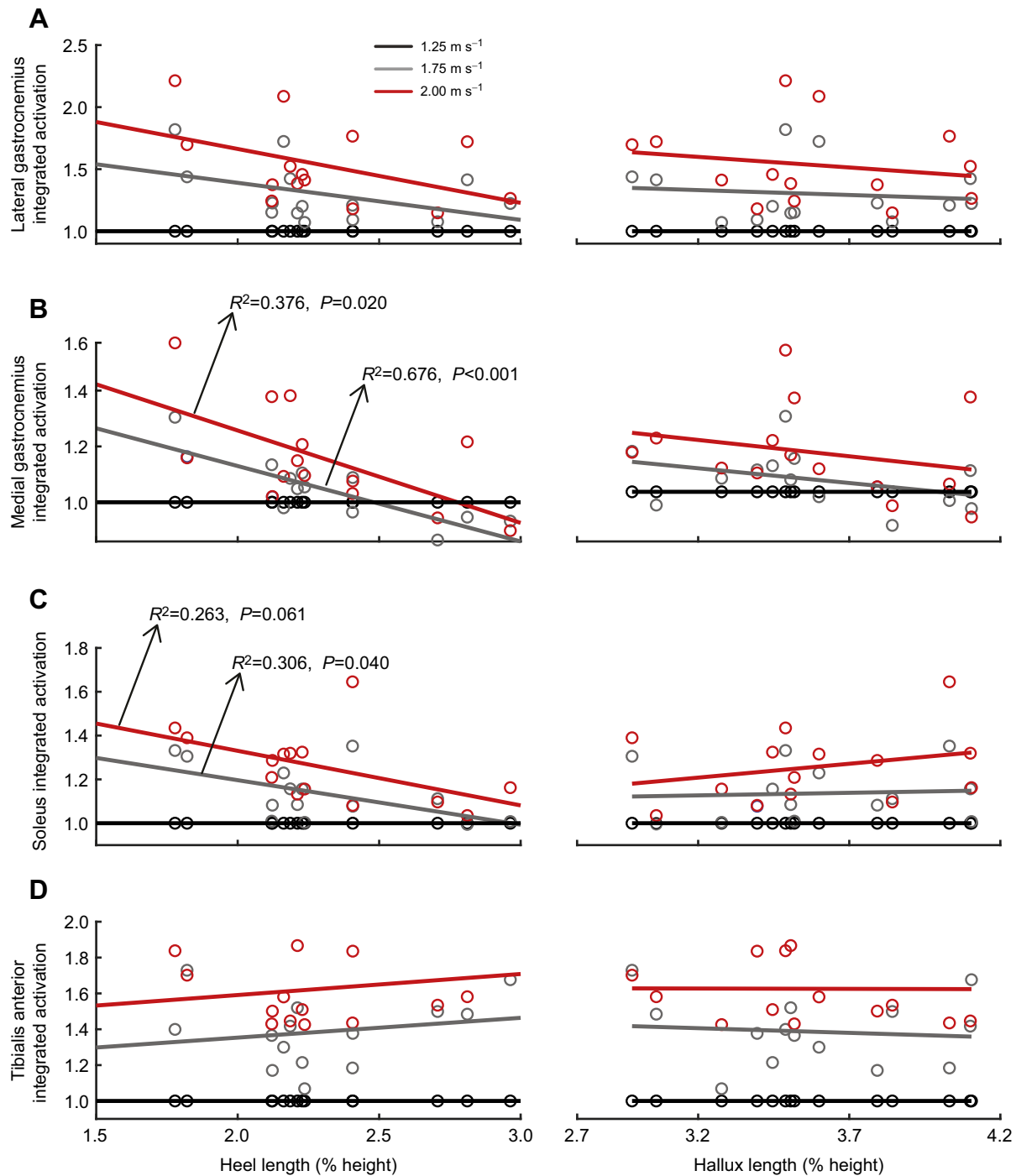


Fig. 4. Stance-integrated muscle activation of four left-leg muscles. (A) Lateral gastrocnemius, (B) medial gastrocnemius, (C) soleus and (D) tibialis anterior integrated activation against heel and hallux length (normalized to height) for each participant ($N=14$). Heel length was statistically significantly associated with soleus and medial gastrocnemius activation (medial gastrocnemius: 1.75 m s^{-1} : $R^2=0.676$, $P<0.001$; 2.00 m s^{-1} : $R^2=0.376$, $P=0.020$; soleus: 1.75 m s^{-1} : $R^2=0.306$, $P=0.040$; 2.00 m s^{-1} : $R^2=0.263$, $P=0.061$). None of the other stance-integrated muscle activations was statistically significantly associated with anthropometric measurements.

stiffness has less of an effect on tendon energy storage than variation in lever arm. Therefore, while we cannot definitively rule out the possibility, it seems unlikely that longer heels had reduced metabolic energy cost due to greater contributions of elastic tendons.

Our study has certain limitations worth noting. First, the EMG results, presented as secondary analyses, need to be interpreted cautiously because of the normalization technique of using data

from 1.25 m s^{-1} as the reference value. With such a normalization technique, we cannot infer the EMG results relative to a muscle's maximum voluntary contraction capacity. Instead, we can only infer that longer heels required less additional muscle activation to achieve faster walking. Further, our findings may be limited by the fact that the participants wore shoes. Previous studies have shown that the stiffness of shoes can influence the metabolic energy cost of walking (Ray and Takahashi, 2020) and running (Day and Hahn,

2020; Hoogkamer et al., 2018; Ortega et al., 2021). However, the participants all wore standardized shoes, and thus it is unlikely that variations in shoe stiffness among individuals created large variations in the metabolic energy cost. We also acknowledge that the knee and hip joints could contribute to metabolic cost variation as previous studies have shown that their activation and energy consumption depend on the locomotion speed (den Otter et al., 2004; Margaria, 1968; Weyand et al., 2013). However, our study did not examine the influence of foot anthropometry on the mechanics of the knee and hip joints, and future studies should study the propagating effects of foot anthropometry variation on proximal joints. Additionally, the foot model used in this study was a single-segment foot model, and our kinetics analysis involved only the sagittal ankle moments. Recent *in vivo* studies have suggested that the structures within the foot, such as the arch, can function like a spring (Kelly et al., 2019; Stearne et al., 2016; Wager and Challis, 2016; Welte et al., 2018) – which may be important to address in future studies to examine the spring-like function in the context of metabolic energy cost. Our sample size was based on a prior study examining the linear correlation between heel length and the metabolic cost of running (Scholz et al., 2008); however, our study was not adequately powered to study interactions among other variables that may affect metabolic cost. Furthermore, our study included additional dependent variables to gain mechanistic insight at the muscle and joint levels, which comes at the expense of increasing the chances of a false-positive result. While we did not adjust for multiple comparisons, we reported all *P*-values and *R*² values for full transparency.

Another limitation of our study is that our anthropometric variables (heel and hallux lengths) were static values. Therefore, we measured heel length as a surrogate estimate of the lever arm of the plantar flexor muscle. While our heel length measurements (4.07±0.63 cm) are in good agreement with prior studies that used the same photography-based method (4.4±0.6 cm: van Werkhoven and Piazza, 2017a; 4.85±0.36 cm: Scholz et al., 2008), these static heel measurements would not account for any changes in the lever arm due to ankle angular displacement (Leardini and O'Connor, 2002; Maganaris et al., 2000) or due to loading of the muscle (Franz et al., 2019). For example, the Achilles tendon lever arm can vary by ~3.8 mm during the stance phase of walking within an individual (Rasske et al., 2017), which is ~0.6 standard deviations of the inter-individual variability in heel lengths reported in our study. In addition, our heel length estimates were based on the lateral foot image (i.e. the distance between the lateral malleolus and the posterior aspect of the Achilles tendon), which was based on findings from a prior study involving jumping performance in an ankle-dominated task (van Werkhoven and Piazza, 2017b). Similar to the prior study (van Werkhoven and Piazza, 2017b), we also found that the heel length estimated based on the lateral image was the strongest predictor of locomotor performance, specifically the metabolic cost of walking (see Table S2). However, it is currently unclear why the lateral heel lengths are most strongly related to the movement performance. Future studies are needed to compare these heel length measurements with Achilles tendon moment arms using ultrasound or magnetic resonance imaging. Additionally, there was an over-representation of males in this study (12 males versus 3 females), and it is currently unclear how the findings generalize across male and female morphology.

In conclusion, we found that neither shorter heels nor longer halluces reduced the shortening velocity of the soleus muscle. Contrary to our hypotheses, longer heels were associated with reduced metabolic cost of transport, but only at a fast walking speed

of 2.00 m s⁻¹. A likely explanation is that longer heels required less of an increase in muscle activation to reach faster speeds. Future studies should aim to understand how the ankle plantar flexor lever arm determines the muscle activity level during dynamic tasks.

Acknowledgements

The authors would like to thank Drs Stephen J. Piazza and Herman van Werkhoven for their insights on foot anthropometry measurements and Drs Jonas Rubenson, Nathaniel Hunt and Philippe Malcolm for their valuable comments.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: N.P., S.F.R., K.Z.T.; Methodology: N.P., S.F.R.; Validation: N.P., S.F.R.; Formal analysis: N.P., S.F.R.; Investigation: N.P., S.F.R., K.Z.T.; Resources: K.Z.T.; Data curation: N.P., S.F.R.; Writing - original draft: N.P.; Writing - review & editing: N.P., S.F.R., K.Z.T.; Visualization: N.P., S.F.R.; Supervision: K.Z.T.; Project administration: K.Z.T.; Funding acquisition: N.P., K.Z.T.

Funding

This research project was supported by two Graduate Research and Creative Activity Awards from the University of Nebraska at Omaha, awarded to N.P. and S.F.R., a NASA Nebraska Space Grant Fellowship, awarded to S.F.R., the Center for Research in Human Movement Variability of University of Nebraska at Omaha, the National Institutes of Health (P20GM109090) and Research Development Program from the Office of Research and Creative Activity from University of Nebraska at Omaha awarded to K.Z.T. The funders had no role in study design, data collection and analysis, decision to publish, or manuscript preparation. Deposited in PMC for release after 12 months.

Data availability

All relevant data can be found within the article and its supplementary information.

ECR Spotlight

This article has an associated ECR Spotlight interview with Nikolaos Papachatzis.

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Table S1. Means, standard deviation (SD), and Pearson correlation matrix for anthropometric variables (N=15).

	Mean±SD	Heel (cm)	Hallux (cm)	Height (cm)	Mass (kg)
Heel (cm)	4.07±0.63	1.00			
Hallux (cm)	6.34±0.67	0.45	1.00		
Height (cm)	176±7.3	0.42	0.40	1.00	
Mass (kg)	76.43±12.43	-0.06	0.31	0.35	1.00

*. Correlation is significant at the 0.05 level (2-tailed).

Table S2. Regressions between normalized foot anthropometric measurements (% height) and dependent variables (N=15).

Definitions:

- **Heel:** The horizontal distance between the lateral malleolus and the most posterior point of the Achilles tendon.
- **Hallux:** The horizontal distance from the first metatarsal head to the most anterior aspect of the toe.
- **Heel_{Average}:** The average of 1) horizontal distance between the lateral malleolus and posterior point of the Achilles tendon and 2) horizontal distance between the medial malleolus and the most posterior point of the Achilles tendon.
- **Mid-foot:** The horizontal distance between the medial malleolus and the first metatarsal head.

A Soleus average shortening velocity (mms⁻¹)

Speed	1.25 ms ⁻¹			1.75 ms ⁻¹			2.00 ms ⁻¹		
	R ²	Slope	P-value	R ²	Slope	P-value	R ²	Slope	P-value
Heel	0.003	0.398	0.846	<0.001	-0.086	0.961	0.001	0.209	0.925
Hallux	<0.001	-0.117	0.952	0.010	-0.570	0.728	<0.001	0.135	0.948
Heel _{Average}	0.017	1.561	0.642	0.084	2.936	0.294	<0.001	0.174	0.962
Mid-foot	0.037	-0.817	0.492	0.011	0.382	0.707	0.005	0.335	0.795

*. Correlation is significant at the 0.05 level (2-tailed).

B Soleus shortening velocity at peak/maximum ankle plantar flexion moment (mms⁻¹)

Speed	1.25 ms ⁻¹			1.75 ms ⁻¹			2.00 ms ⁻¹		
	R ²	Slope	P-value	R ²	Slope	P-value	R ²	Slope	P-value
Heel	0.132	14.273	0.183	0.320	20.493	0.028*†	0.003	1.193	0.858
Hallux	0.060	-9.094	0.377	0.033	6.228	0.515	0.090	-6.710	0.276
Heel _{Average}	0.080	18.198	0.308	0.271	30.682	0.046*	<0.001	-0.442	0.968
Mid-foot	0.096	7.104	0.261	0.095	6.508	0.265	0.015	1.703	0.662

*. Correlation is significant at the 0.05 level (2-tailed).

†. Cook's distance values indicated a possible significant outlier. We removed the outlier, and we rerun the analysis (N=14). The output was: R² = 0.153, Slope = 9.831 and P-value = 0.166.

C Peak/maximum ankle plantar flexion (Nmkg⁻¹)

Speed	1.25 ms ⁻¹			1.75 ms ⁻¹			2.00 ms ⁻¹		
	R ²	Slope	P-value	R ²	Slope	P-value	R ²	Slope	P-value
Heel	0.107	0.136	0.234	0.044	0.106	0.454	0.056	0.138	0.397
Hallux	0.131	0.142	0.185	0.080	0.135	0.307	0.115	0.186	0.217
Heel _{Average}	0.001	0.019	0.923	0.015	-0.102	0.664	0.001	-0.033	0.902
Mid-foot	0.204	-0.109	0.091	0.091	-0.089	0.274	0.095	-0.105	0.263

*. Correlation is significant at the 0.05 level (2-tailed).

D Cost of transport (Jkg⁻¹m⁻¹)

Speed	1.25 ms ⁻¹			1.75 ms ⁻¹			2.00 ms ⁻¹		
	R ²	Slope	P-value	R ²	Slope	P-value	R ²	Slope	P-value
Heel	0.012	-0.081	0.701	0.171	-0.357	0.126	0.305	-0.980	0.033*
Hallux	0.038	0.138	0.487	0.005	-0.059	0.798	0.048	-0.367	0.432
Heel _{Average}	<0.001	-0.027	0.939	0.063	-0.355	0.368	0.073	-0.785	0.330
Mid-foot	0.173	0.182	0.123	0.292	0.273	0.037*	0.240	0.507	0.064

*. Correlation is significant at the 0.05 level (2-tailed).

E Ground reaction moment arm at peak/maximum ankle plantar flexion (cm)

Speed	1.25 ms ⁻¹			1.75 ms ⁻¹			2.00 ms ⁻¹		
	R ²	Slope	P-value	R ²	Slope	P-value	R ²	Slope	P-value
Heel	0.117	-0.010	0.212	0.113	-0.010	0.220	0.198	-0.012	0.096
Hallux	0.093	-0.009	0.269	0.096	-0.009	0.261	0.193	-0.012	0.102
Heel _{Average}	0.025	-0.008	0.575	0.033	-0.009	0.515	0.117	-0.016	0.212
Mid-foot	0.475	0.012	0.005*	0.510	0.013	0.003*	0.510	0.012	0.003*

*. Correlation is significant at the 0.05 level (2-tailed).

Table S3. Regressions between unnormalized foot anthropometric measurements (cm) and dependent variables (N=15).

Definitions:

- **Heel:** The horizontal distance between the lateral malleolus and the most posterior point of the Achilles tendon.
- **Hallux:** The horizontal distance from the first metatarsal head to the most anterior aspect of the toe.
- **Heel_{Average}:** The average of 1) horizontal distance between the lateral malleolus and posterior point of the Achilles tendon and 2) horizontal distance between the medial malleolus and the most posterior point of the Achilles tendon.
- **Mid-foot:** The horizontal distance between the medial malleolus and the first metatarsal head.
- **Hallux/Heel:** Ratio of hallux length over lateral heel length.
- **Mid-foot/Heel:** Ratio of mid-foot length over lateral heel length.

A Soleus average shortening velocity (mms⁻¹)

Speed	1.25 ms ⁻¹			1.75 ms ⁻¹			2.00 ms ⁻¹		
	R ²	Slope	P-value	R ²	Slope	P-value	R ²	Slope	P-value
Heel	0.003	0.212	0.844	0.011	-0.336	0.713	<0.001	-0.056	0.962
Hallux	<0.001	-0.010	0.992	0.049	-0.678	0.430 [†]	<0.001	-0.077	0.944
Heel _{Average}	0.018	0.811	0.633	0.010	0.519	0.719	0.002	-0.309	0.867
Mid-foot	<0.001	-0.010	0.991	0.166	-1.131	0.131	0.049	-0.781	0.427
Hallux/Heel	0.003	-0.652	0.836	0.006	-0.729	0.786	0.001	-0.428	0.900
Mid-foot/Heel	0.002	-0.216	0.879	0.013	-0.481	0.689	0.020	-0.770	0.613

*. Correlation is significant at the 0.05 level (2-tailed).

†. Cook's distance values indicated a possible significant outlier. We removed the outlier, and we reran the analysis (N=14). The output was: R² = 0.305, Slope = -1.967 and P-value = 0.041.

B Soleus shortening velocity at peak/maximum ankle plantar flexion moment (mms⁻¹)

Speed	1.25 ms ⁻¹			1.75 ms ⁻¹			2.00 ms ⁻¹		
	R ²	Slope	P-value	R ²	Slope	P-value	R ²	Slope	P-value
Heel	0.127	7.331	0.193	0.240	9.306	0.064 [†]	<0.001	0.238	0.946
Hallux	0.039	-3.862	0.481	0.013	2.079	0.683	0.100	-3.737	0.250
Heel _{Average}	0.081	9.262	0.305	0.160	12.037	0.139	0.003	-1.127	0.839
Mid-foot	0.027	-2.880	0.561	0.127	-5.808	0.192	0.246	-5.273	0.060
Hallux/ Heel	0.388	-37.657	0.013*	0.287	-29.864	0.040*	0.101	-11.562	0.249
Mid-foot/ Heel	0.220	-12.729	0.078	0.494	-17.594	0.003*	0.094	-5.023	0.266

*. Correlation is significant at the 0.05 level (2-tailed).

[†]. Cook's distance values indicated a possible significant outlier. We removed the outlier, and we reran the analysis (N=14). The output: R² = 0.088, Slope = 3.842 and P-value = 0.302.

C Peak/maximum ankle plantar flexion (Nmkg⁻¹)

Speed	1.25 ms ⁻¹			1.75 ms ⁻¹			2.00 ms ⁻¹		
	R ²	Slope	P-value	R ²	Slope	P-value	R ²	Slope	P-value
Heel	0.220	0.102	0.078	0.124	0.094	0.198	0.135	0.112	0.178
Hallux	0.346	0.121	0.021*	0.249	0.126	0.058	0.287	0.156	0.039*
Heel _{Average}	0.113	0.116	0.220	0.035	0.079	0.503	0.062	0.120	0.372
Mid-foot	0.439	0.123	0.007*	0.517	0.164	0.003*	0.569	0.198	0.001*
Hallux/ Heel	0.013	-0.074	0.682	0.001	-0.024	0.913	<0.001	-0.001	0.996
Mid-foot/ Heel	0.068	-0.075	0.347	0.007	-0.030	0.759	0.003	-0.023	0.839

*. Correlation is significant at the 0.05 level (2-tailed).

D Cost of transport ($\text{Jkg}^{-1}\text{m}^{-1}$)

Speed	1.25 ms^{-1}			1.75 ms^{-1}			2.00 ms^{-1}		
	R ²	Slope	P-value	R ²	Slope	P-value	R ²	Slope	P-value
Heel	0.020	-0.056	0.615	0.251	-0.227	0.057	0.440	-0.616	0.007*
Hallux	0.012	0.040	0.702	0.064	-0.109	0.361	0.191	-0.386	0.103
Heel _{Average}	0.010	-0.062	0.722	0.206	-0.326	0.089	0.285	-0.786	0.040*
Mid-foot	0.072	-0.091	0.333	0.184	-0.167	0.110	0.359	-0.478	0.018*
Hallux/ Heel	0.027	0.190	0.558	0.131	0.481	0.186	0.160	1.091	0.140
Mid-foot/ Heel	<0.001	-0.011	0.940	0.155	0.235	0.146	0.229	0.587	0.071

*. Correlation is significant at the 0.05 level (2-tailed).

E Ground reaction moment arm at peak/maximum ankle plantar flexion (cm)

Speed	1.25 ms^{-1}			1.75 ms^{-1}			2.00 ms^{-1}		
	R ²	Slope	P-value	R ²	Slope	P-value	R ²	Slope	P-value
Heel	0.243	-0.008	0.062	0.234	-0.008	0.068	0.342	-0.009	0.022*
Hallux	0.303	-0.008	0.033*	0.300	-0.008	0.035*	0.448	-0.009	0.006*
Heel _{Average}	0.224	-0.012	0.075	0.237	-0.012	0.066	0.400	-0.015	0.011*
Mid-foot	0.506	-0.009	0.003*	0.519	-0.010	0.002*	0.525	-0.009	0.002*

*. Correlation is significant at the 0.05 level (2-tailed).

Table S4. Regressions between normalized foot anthropometric measurements (%height) and normalized stance-integrated electromyography (EMG) data (N=14). The integrated EMG data for the 1.25 ms⁻¹ was used as the reference value, and thus no statistical analysis was applied (i.e., NaN).

A Lateral Gastrocnemius

Speed	1.25 ms ⁻¹			1.75 ms ⁻¹			2.00 ms ⁻¹		
	R ²	Slope	P-value	R ²	Slope	P-value	R ²	Slope	P-value
Heel	NaN	NaN	NaN	0.187	-0.299	0.122	0.205	-0.434	0.104
Hallux	NaN	NaN	NaN	0.014	-0.079	0.684	0.035	-0.171	0.523

*. Correlation is significant at the 0.05 level (2-tailed).

B Medial Gastrocnemius

Speed	1.25 ms ⁻¹			1.75 ms ⁻¹			2.00 ms ⁻¹		
	R ²	Slope	P-value	R ²	Slope	P-value	R ²	Slope	P-value
Heel	NaN	NaN	NaN	0.676	-0.270	<0.001*	0.376	-0.331	0.020*
Hallux	NaN	NaN	NaN	0.144	-0.119	0.181	0.065	-0.132	0.378

*. Correlation is significant at the 0.05 level (2-tailed).

C Soleus

Speed	1.25 ms ⁻¹			1.75 ms ⁻¹			2.00 ms ⁻¹		
	R ²	Slope	P-value	R ²	Slope	P-value	R ²	Slope	P-value
Heel	NaN	NaN	NaN	0.306	-0.203	0.040*	0.263	-0.249	0.061
Hallux	NaN	NaN	NaN	0.005	0.024	0.819	0.074	0.126	0.345

*. Correlation is significant at the 0.05 level (2-tailed).

D Tibialis Anterior

Speed	1.25 ms ⁻¹			1.75 ms ⁻¹			2.00 ms ⁻¹		
	R ²	Slope	P-value	R ²	Slope	P-value	R ²	Slope	P-value
Heel	NaN	NaN	NaN	0.039	0.110	0.498	0.038	0.117	0.503
Hallux	NaN	NaN	NaN	0.010	-0.052	0.740	<0.001	-0.004	0.983

*. Correlation is significant at the 0.05 level (2-tailed).

Table S5. Regressions between unnormalized foot anthropometric measurements (cm) and normalized stance-integrated electromyography (EMG) data (N=14). The integrated EMG data for the 1.25 ms⁻¹ was used as the reference value, and thus no statistical analysis was applied (i.e., NaN).

A Lateral Gastrocnemius

Speed	1.25 ms ⁻¹			1.75 ms ⁻¹			2.00 ms ⁻¹		
	R ²	Slope	P-value	R ²	Slope	P-value	R ²	Slope	P-value
Heel	NaN	NaN	NaN	0.153	-0.140	0.167	0.176	-0.208	0.135
Hallux	NaN	NaN	NaN	0.008	-0.031	0.757	0.028	-0.078	0.570

*. Correlation is significant at the 0.05 level (2-tailed).

B Medial Gastrocnemius

Speed	1.25 ms ⁻¹			1.75 ms ⁻¹			2.00 ms ⁻¹		
	R ²	Slope	P-value	R ²	Slope	P-value	R ²	Slope	P-value
Heel	NaN	NaN	NaN	0.710	-0.143	<0.001*	0.422	-0.182	0.012*
Hallux	NaN	NaN	NaN	0.232	-0.078	0.081	0.134	-0.097	0.198

*. Correlation is significant at the 0.05 level (2-tailed).

C Soleus

Speed	1.25 ms ⁻¹			1.75 ms ⁻¹			2.00 ms ⁻¹		
	R ²	Slope	P-value	R ²	Slope	P-value	R ²	Slope	P-value
Heel	NaN	NaN	NaN	0.323	-0.108	0.034*	0.298	-0.138	0.043*
Hallux	NaN	NaN	NaN	0.001	-0.006	0.911	0.017	0.031	0.655

*. Correlation is significant at the 0.05 level (2-tailed).

D Tibialis Anterior

Speed	1.25 ms ⁻¹			1.75 ms ⁻¹			2.00 ms ⁻¹		
	R ²	Slope	P-value	R ²	Slope	P-value	R ²	Slope	P-value
Heel	NaN	NaN	NaN	0.010	0.028	0.738	0.025	0.050	0.587
Hallux	NaN	NaN	NaN	0.047	-0.059	0.459	0.001	-0.010	0.912

*. Correlation is significant at the 0.05 level (2-tailed).