

RESEARCH ARTICLE

Shorter muscle fascicle operating lengths increase the metabolic cost of cyclic force production

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Abstract

During locomotion, force-producing limb muscles are predominantly responsible for an animal's whole body metabolic energy expenditure. Animals can change the length of their force-producing muscle fascicles by altering body posture (e.g., joint angles), the structural properties of their biological tissues over time (e.g., tendon stiffness), or the body's kinetics (e.g., body weight). Currently, it is uncertain whether relative muscle fascicle operating lengths have a measurable effect on the metabolic energy expended during cyclic locomotion-like contractions. To address this uncertainty, we quantified the metabolic energy expenditure of human participants, as they cyclically produced two distinct ankle moments at three ankle angles (90°, 105°, and 120°) on a fixed-position dynamometer using their soleus. Overall, increasing participant ankle angle from 90° to 120° (more plantar flexion) reduced minimum soleus fascicle length by 17% (both moment levels, $P < 0.001$) and increased metabolic energy expenditure by an average of 208% across both moment levels (both $P < 0.001$). For both moment levels, the increased metabolic energy expenditure was not related to greater fascicle positive mechanical work (higher moment level, $P = 0.591$), fascicle force rate (both $P \geq 0.235$), or model-estimated active muscle volume (both $P \geq 0.122$). Alternatively, metabolic energy expenditure correlated with average relative soleus fascicle length ($r = -0.72$, $P = 0.002$) and activation ($r = 0.51$, $P < 0.001$). Therefore, increasing active muscle fascicle operating lengths may reduce metabolic energy expended during locomotion.

NEW & NOTEWORTHY During locomotion, active muscles undergo cyclic length-changing contractions. In this study, we isolated confounding variables and revealed that cyclically producing force at relatively shorter fascicle lengths increases metabolic energy expenditure. Therefore, muscle fascicle operating lengths likely have a measurable effect on the metabolic energy expenditure during locomotion.

dynamometer; economy; efficiency; energetic; length

INTRODUCTION

During locomotion, many limb extensor muscles operate at shorter lengths than optimal for active force production (1–6). For instance, during the stance phase of human walking and running, soleus fascicles operate between ~0.65 and 1.01 of their optimal length (1, 2). A shorter than optimal fascicle operating range is functionally relevant because muscles produce less force per unit activation (7–9) and per adenosine triphosphate (ATP) utilization (10–13) further down the ascending limb of their force-length relationship (Fig. 1). That is because at shorter than optimal lengths, sarcomere geometry yields fewer overlapping actin-myosin filaments (7), less force per cross-bridge cycle (17), and greater passive force that places tension along the muscle fascicle (10, 18). Thus, to produce the requisite force and sustain locomotion with shorter muscle operating lengths (19, 20), animals must activate additional ATP-consuming cross bridges and ion pumps than they otherwise would at optimal lengths (21–23).

Despite the aforementioned rationale, muscle operating lengths are not often considered to have a notable effect on whole body metabolic energy expenditure during locomotion (2, 20, 24–27). This omission may be because the metabolic influence of producing force at different muscle lengths is conventionally studied during isolated isometric contractions at a given activation (10, 11, 13). This is different than integrated cyclic length changing contractions at a given average force, which emulates important aspects of locomotion mechanics. It is also difficult to separate the metabolic effect of muscle operating length per se from other biomechanical parameters during locomotor-like contractions (9). For example, during concentric contractions, force-producing muscles expend more metabolic energy the further that they shorten (28). As such, scientists commonly attribute increased metabolic energy expenditure to greater muscle shortening (28) and/or mechanical work production (27–30). However, in some cases, the measured metabolic increase may be attributed to muscles producing force at



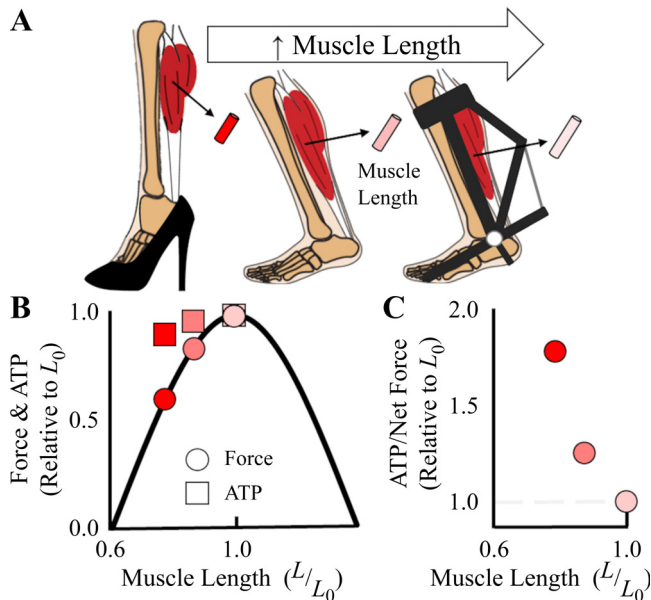


Figure 1. Representation of soleus fascicle length during midstance of walking in high-heeled shoes (14, 15), barefoot, and with an ankle exoskeleton (16; A). B: conceptual graph showing isometric muscle fascicle force production and adenosine triphosphate (ATP) utilization relative to muscle length (10). C: actin-myosin ATP utilization per net isometric muscle fascicle force production at a given activation vs. muscle fascicle operating length (10). L and L_0 indicate actual and optimal muscle fascicle length, respectively.

less economical lengths. Experimentally disentangling the metabolic effect of muscle operating lengths from other metabolically relevant biomechanical parameters during locomotion (e.g., force, work, and velocity) is challenging, particularly during walking and running. Fortunately, a well-controlled experiment using isolated contractions to emulate aspects of locomotion may be revealing.

Thus, to help reveal the link between locomotion mechanics and metabolic energy expenditure, our goal was to determine the metabolic influence of cyclically producing a fixed submaximal force at different muscle fascicle lengths. To accomplish this goal, we quantified the mechanics and metabolic energy expenditure of human soleus muscles, as they cyclically produced force and changed length within different regions of the force-length relationship. We hypothesized that cyclically producing the same submaximal force with relatively shorter muscle fascicles would increase metabolic energy expenditure.

METHODS

Participants

Nine volunteers completed the protocol [average \pm SD; 8 male and 1 female; age: 26.3 ± 2.6 yr; standing height: 1.77 ± 0.07 m; mass: 74.9 ± 11.4 kg; resting metabolic power 87 ± 12 W; optimal soleus fascicle length: 41 ± 6 mm; maximum soleus fascicle shortening velocity: 182 ± 25 mm/s (2)]. We estimated maximum soleus fascicle shortening velocity to equal 4.4 resting lengths per second (2) based on the assumption that only slow oxidative soleus fibers are active during sustained submaximal metabolic trials (31). Before

the study, each participant gave informed written consent. The study protocol was approved by the Georgia Institute of Technology Central Institutional Review Board.

Protocol

Participants arrived at the laboratory in the morning following an overnight fast. Upon arrival, participants laid supine on a dynamometer with custom attachments that supported their legs in the testing position: right knee and ankle were supported at 50° and 90° , respectively (Fig. 2). Ninety degree indicates perpendicular segments and more acute angles indicate joint (dorsi)flexion. In this position, participants rested for 10 min while breathing into a mouthpiece that channeled expired air to a metabolic cart (TrueOne 2400, ParvoMedic, Sandy, UT). Next, we shaved participant's leg hair and used electrode preparation gel to lightly abrade the skin superficial to their right soleus, lateral gastrocnemius, and tibialis anterior (NuPrep, Weaver and Co., Aurora, CO). We placed bipolar surface electrodes over the skin superficial to each respective muscle belly and in approximately the same orientation as the muscle fascicles (Delsys Inc., Natick, MA). We secured a linear-array B-mode ultrasound probe to the skin superficial of each participant's right medial soleus (Telemed, Vilnius, Lithuania). We placed reflective markers on the dynamometer at its axis of rotation, 10 cm above the axis of rotation, as well as on the participant's skin/clothes superficial to their right leg's medial knee-joint center, medial malleolus, and first metatarsal head (Fig. 2). We measured each participant's Achilles tendon moment arm during barefoot standing (ankle angle: 90°). Then, we estimated each participant's triceps surae muscle-tendon unit length as well as the Achilles tendon moment arms at 105° and 120° using Eq. 13 from Bobbert et al. (32). Average \pm SD participant Achilles tendon moment arm distance at 90° , 105° , and 120° equaled 49 ± 4 mm, 54 ± 4 mm, and 59 ± 5 mm, respectively.

In a random order, participants performed four maximum voluntary contractions (MVCs) with their ankle joint at 90° in-line with the dynamometer's axis of rotation (Biodex Medical Systems Inc., NY) and their knee at 70° , 60° , and 50° : three plantar flexion MVCs and one dorsiflexion MVC. At least 2 min of rest preceded each MVC to mitigate fatigue (33). Because MVC ankle moment did not increase with more extended knee angles, we deemed the contribution of the biarticular gastrocnemius on ankle moment to be negligible (1). In addition, soleus' force-producing capacity is $\sim 2\times$ that of all uniaxial plantar flexor muscles combined (34), thus we simply attributed ankle moment generation to soleus force production.

Subsequently, participants performed six, 5-min trials with their knee at 50° separated by at least 5 min of rest. Participants performed trials at each of the two dynamometer torque levels (10 N·m and 15 N·m) at the following ankle angles: 90° , 105° , and 120° . These trials consisted of each participant repeatedly producing plantar flexor moments on a fixed-position dynamometer foot-pedal following the sound of an audible metronome (metronome frequency 0.75 Hz and duty cycle 0.5; Fig. 2). To guide ankle plantar flexor moments throughout each trial, participants watched a computer screen that displayed the

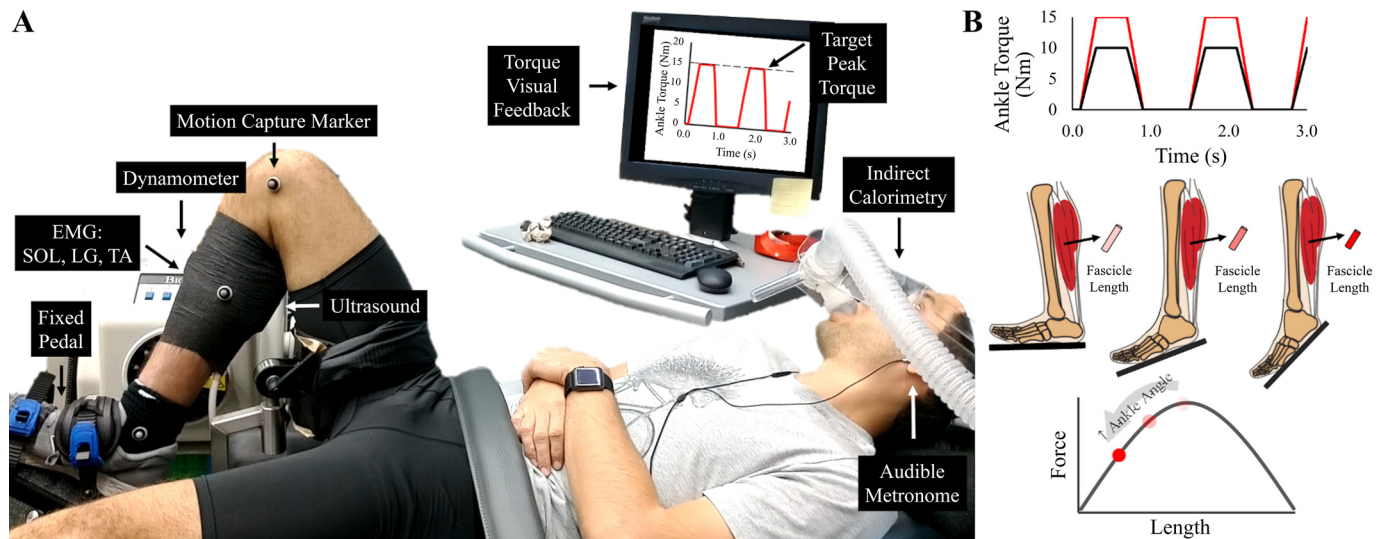


Figure 2. A: experimental setup of a participant cyclically generating soleus muscle force to produce a plantar flexor moment that exerts an external torque on a fixed dynamometer pedal following the cues of an audible metronome and visual feedback. B: illustrations of the two target torque levels (peak torque: 10 N·m and 15 N·m), three ankle angles (90°, 105°, and 120°) with the corresponding hypothetical minimum soleus fascicle operating lengths and their respective location on a muscle force-length relationship. EMG, electromyography; LG, lateral gastrocnemius; SOL, soleus; TA, tibialis anterior.

trial's target peak dynamometer torque and the recorded dynamometer torque profile over the previous 5–10 s. We randomized the trial order and collected metabolic data, dynamometer torque data (100 Hz), motion capture data (200 Hz; Vicon Motion Systems, UK), soleus fascicle length and orientation data (100 Hz), as well as the surface electromyography signals from the soleus, tibialis anterior, and lateral gastrocnemius (1,000 Hz; Fig. 2).

Soleus Fascicle Mechanics

To determine soleus fascicle kinematics, we recorded B-mode ultrasound images containing the posterior-medial soleus compartment. We recorded soleus fascicle images during 20 s in the last 2 min of the metabolic trials. Within these 20 s, we postprocessed soleus fascicle lengths and pennation angles throughout six consecutive moment generation cycles using a semiautomated tracking software (35). We filtered soleus fascicle pennation angle and length using a fourth-order low-pass Butterworth filter (6 Hz) and took the derivative of fascicle length with respect to time to determine fascicle velocity.

To quantify soleus kinetics, we used a custom MATLAB script (Mathworks Inc., Natick, MA) that filtered motion capture data using a fourth-order low-pass Butterworth filter (6 Hz) and subtracted the gravitational dynamometer torque from the corresponding trial. We computed net dynamometer torque from 12 consecutive moment generation cycles that encompassed the analyzed fascicle kinematic data. Due to small fluctuations in dynamometer torque, we implemented a 1 N·m dynamometer torque threshold to determine the duration of active force production. Using filtered data, we calculated net ankle moment using dynamometer torque and the position of the ankle's axis of rotation relative to the dynamometer's axis of rotation. Using the estimated change in soleus muscle-tendon moment arm distance at each ankle angle (32), we divided net ankle

moment (m_{ank}) by the respective Achilles tendon moment arm distance (r_{AT}) to calculate muscle-tendon force. In turn, we divided muscle-tendon force by the cosine of fascicle pennation angle (θ_p) to calculate active soleus fascicle force (F_{sol}).

$$F_{\text{sol}} = \frac{m_{\text{ank}}}{r_{\text{AT}} \cos(\theta_p)}. \quad (1)$$

We assumed passive muscle fascicle forces are negligible. We also omitted data from one 5-min metabolic trial because the participant achieved an average maximum ankle moment that was >5 N·m more than targeted. Further, we assumed that optimal soleus fascicle length was consistent across muscle activation magnitudes (36) and that it was the value that we measured during resting at a 90° ankle angle (31, 37).

Relating Biomechanics to Metabolism

Recently, two studies performed similar experimental protocols and linked the mechanics of muscle fascicles cyclically producing force to metabolic energy expenditure. One study (27) indicated that the overall rate of metabolic energy expenditure (\dot{E}_{met}) scaled with metabolic rate associated with the rate of peak force production and force production cycle frequency ($\dot{E}_{\text{FR}} \propto \dot{F}_{\text{peak}} \cdot f$), the rate of mechanical work ($\dot{E}_W \propto \dot{W}$), and the force-time integral ($\dot{E}_{\text{FT}} \propto \int F dt$) (Eq. 2). The other study (31) suggested that metabolic energy expenditure (\dot{E}_{met}) is well-explained by active muscle volume, which was calculated using active muscle fascicle force production (F_{act}), optimal fascicle length (l_0), stress (σ), and the fascicle's force-length and force-velocity force potential as per a Hill-type muscle model (FL and FV , respectively; Eq. 3; 38). Due to the similarities between these previous studies (27, 31) and the current study, our secondary objective was to test whether these published biomechanical equations could explain the present study's metabolic data (Eqs. 2 and 3).

$$\dot{E}_{met} = \dot{E}_{FR} + \dot{E}_W + \dot{E}_{FT}. \quad (2)$$

$$\dot{E}_{met} \propto V_{act} = \frac{F_{act} \cdot l_0}{\sigma \cdot FL \cdot FV}. \quad (3)$$

Muscle Activation

We band-pass filtered raw soleus, lateral gastrocnemius, and tibialis anterior, electromyography signals between 20 and 450 Hz from the same 12 consecutive torque generation cycles that we used to assess net ankle moment. We full wave rectified the filtered electromyography signals and calculated the mean of the rectified signals using a 40 ms moving window. Due to technical issues, we were unable to collect one participant's tibialis anterior activation during the metabolic trials.

Metabolic Energy Expenditure

During the resting trial and each cyclic force-production trial, we used open-circuit expired gas analysis to record the participant's rates of oxygen uptake ($\dot{V}O_2$) and carbon dioxide production ($\dot{V}CO_2$). We averaged $\dot{V}O_2$ and $\dot{V}CO_2$ over the last minute of each trial and used a standard equation to calculate metabolic power (Watts; 39). Next, we subtracted each participant's resting metabolic power from their experimental values to yield net metabolic power. We removed three metabolic values (of 54) from our analyses because the corresponding respiratory exchange ratio did not reflect a respiratory quotient value that was indicative of fat and/or carbohydrate oxidation (39).

Statistical Analyses

Unless otherwise specified, we performed all statistical tests within the targeted lower and higher ankle moment trials independently. We performed a *t* test to determine whether the targeted lower and higher cycle-average torque trials elicited different average ankle moments. We performed linear mixed models to determine the influence of ankle angle on kinetics, kinematics, muscle activity, and net metabolic power. We also performed linear mixed models with two independent variables (average muscle fascicle length and positive mechanical work) and one dependent variable (net metabolic power). Across both moment levels, we performed independent linear regressions to determine the correlation between average relative muscle fascicle length, positive muscle fascicle mechanical work, and average soleus muscle activation on net metabolic power. We set the significance level ($\alpha = 0.05$) and performed statistical analyses using RSTUDIO software (RSTUDIO, Inc., Boston, MA).

RESULTS

Biomechanics

Consistent with the study design, participants produced two distinct cycle average \pm SD ankle moment levels: 4.85 ± 0.72 N·m and 6.58 ± 0.94 N·m ($P < 0.001$; Fig. 3). Within each moment level, the duration of active force production (both $P \geq 0.158$), force production cycle frequency (both $P \geq 0.375$), and cycle average ankle moment (both $P \geq 0.678$) remained constant across ankle angles. However, not

all metrics remained constant across ankle angles. Plantar flexing the ankle angle 30° increased the distance of participant Achilles tendon moment arms by ~ 0.9 cm (32), thereby decreasing average soleus muscle-tendon force (both $P \leq 0.002$; Fig. 3). Greater ankle angles also increased average and maximum soleus fascicle pennation angles (both $P \leq 0.001$; Fig. 3), which yielded statistically similar cycle average soleus fascicle force production across ankle angles for the low moment level ($P = 0.063$) but not the higher moment level ($P = 0.003$; Fig. 3). Similarly, at the lower moment level, soleus fascicle force-time integral was independent of ankle angle ($P = 0.070$), but it decreased by 19% due to increasing ankle angle from 90° to 120° within the higher moment level ($P = 0.003$; Fig. 4).

Increasing ankle angle systematically shortened soleus fascicle lengths, but it did not alter many biomechanical parameters that previous dynamometer studies linked to net metabolic power. Regarding Eq. 2 (27), as aforementioned, soleus fascicle force-time integral remained constant or slightly decreased at greater ankle angles (Fig. 4). Soleus fascicle force-rate was independent of ankle angle (both $P \geq 0.235$; Fig. 4), whereas positive soleus fascicle work increased across ankle angles within the lower ankle moment level ($P < 0.001$), but not within the higher ankle moment level ($P = 0.591$; Fig. 4). Regarding Eq. 3 (38), both average and minimum soleus fascicle operating lengths decreased with increasing ankle angle (both $P < 0.001$). These shorter fascicle operating lengths reduced the average soleus fascicle force-length potential by 7%–8% across ankle moment levels ($P < 0.001$; Fig. 5). Greater ankle angles yielded faster maximum soleus fascicle shortening velocities within the lower ankle moment level ($P < 0.001$), but not statistically in the higher ankle moment level ($P = 0.099$). Combining cycle average fascicle force production and force-length-velocity potential (38), ankle angle did not affect the model-estimated cycle average soleus active muscle volume (both $P \geq 0.122$; Fig. 5). Therefore, neither of the published equations (Eqs. 2 and 3) would predict an increased metabolic energy expenditure at more plantar-flexed ankle angles due to constant and decreasing mechanical variables.

Metabolic Power

Ankle angle dramatically affected the metabolic power of cyclic force production. Changing ankle angle from 90° to 120° increased net metabolic power by 189% and 228% within the lower and higher ankle moment levels, respectively (both $P < 0.001$; Fig. 6). Unlike previous dynamometer studies (27, 31), neither the combined cost of muscle force-time integral, positive mechanical work, and force rate (Eq. 2); nor modeled active muscle volume (Eq. 3) could explain the metabolic data. This is especially evident within the higher moment level where net metabolic power increased by 228% across ankle angles, but all of the biomechanical variables were either unchanged or decreased with increasing ankle angle: force-time integral (Fig. 4), force rate (Fig. 4), positive mechanical work (Fig. 4), and active muscle volume (Fig. 5). Within each moment level, positive mechanical work did not relate to net metabolic power while controlling for average fascicle length ($P \geq 0.405$). On the contrary, while controlling for positive mechanical work, decreasing average fascicle

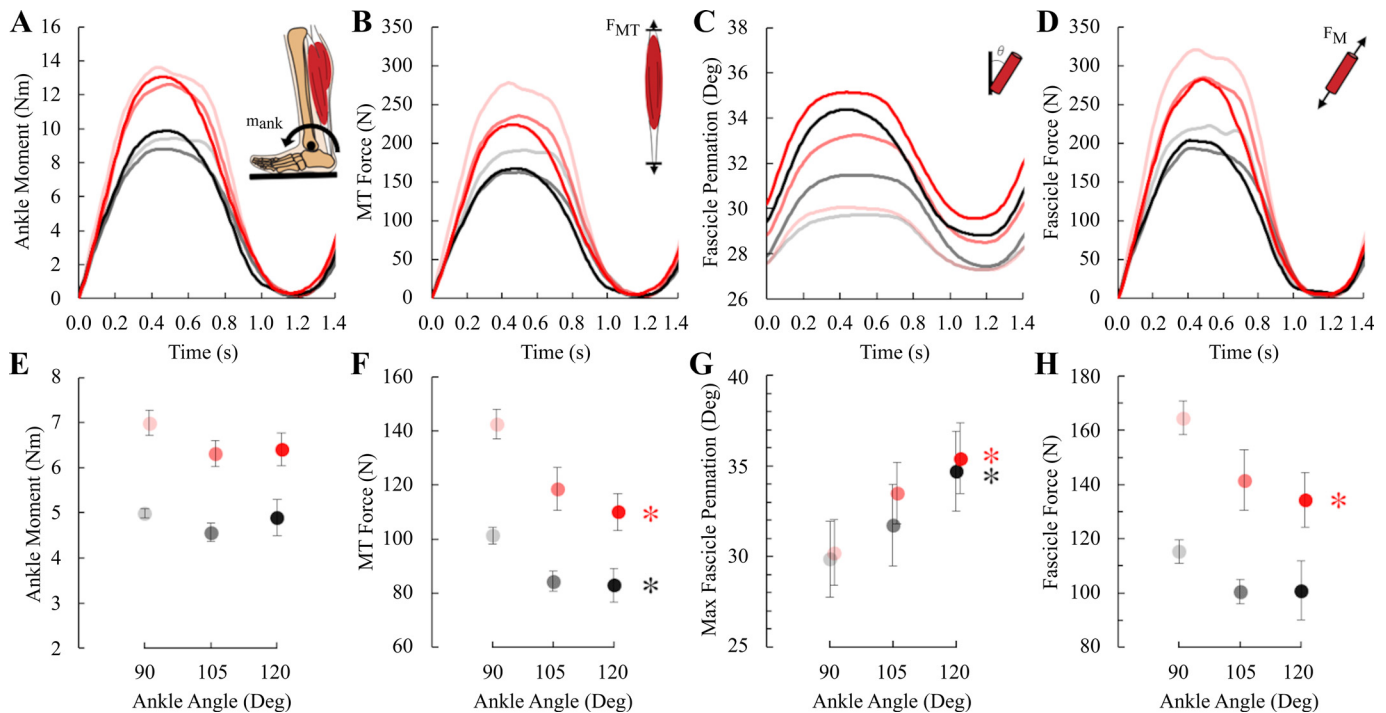


Figure 3. Top row: time-series plots of average ankle moment (m_{ank} ; A), muscle-tendon force (F_{MT} ; B), soleus fascicle pennation angle (C), and active soleus fascicle force (F_{M} ; D). Bottom row: average \pm SE average ankle moment (E), average MT force (F), maximum fascicle pennation angle (G), and average soleus fascicle force vs. ankle angle (H). Black and red symbols are offset for clarity and indicate the lower and higher ankle moment levels, respectively. Lighter to darker colors indicate more dorsiflexed to plantar-flexed ankle angles per moment level. Figure details: sample size: 9; sex: 8 male/1 female; statistical tests: linear mixed model. Black and red asterisks (*) indicate that there is an effect of ankle angle on the indicated moment level's dependent variable ($P < 0.05$). MT, muscle-tendon.

length was associated with an increased net metabolic power (both $\beta = -1.4$ to -3.1 ; $P \leq 0.047$). Pooled across ankle moment levels and participants, without controlling for other mechanical parameters, average relative muscle fascicle operating length inversely correlated with net metabolic power ($r = -0.72$, $P = 0.002$), whereas positive muscle fascicle mechanical work was not correlated to net metabolic power ($P = 0.125$). In addition, average soleus activation positively correlated with net metabolic power across ankle moment levels and participants ($r = 0.51$, $P < 0.001$; Fig. 6). Therefore, cyclically producing force with 16%–17% shorter muscle fascicles yielded $\sim 200\%$ more metabolic energy expenditure.

Muscle Activation

Cyclically producing force at different ankle angles altered plantar flexor muscle activation. Both soleus and lateral gastrocnemius muscle activation increased by 146%–196% with increasing ankle angle within each moment level (all $P < 0.001$; Fig. 7). Even though tibialis anterior activation statistically increased at greater ankle angles (both $P \leq 0.027$), we considered its influence on net metabolic power to be trivial because its cycle average activation was merely 0.02–0.05 of its MVC value across conditions.

DISCUSSION

During locomotion, muscle fascicle operating lengths depend on body segment geometry, the structural properties of biological tissues, and the body's kinetics. In the present study, we controlled for participant structural properties

(within participant design), limb-joint kinetics (constant ankle moment cycle), and independently altered muscle fascicle operating lengths via geometric changes (changing ankle angle). Using this protocol, we revealed that shorter muscle fascicle operating lengths increased metabolic energy expenditure during cyclic force production—supporting our hypothesis.

Producing a constant force with shorter muscle fascicles than optimal likely elicits multiple neuromechanical changes that increase metabolic energy expenditure. Consistent with the sliding filament (40, 41) and cross-bridge (42, 43) theories, at relatively short muscle lengths there is less overlap between actin and myosin filaments (7), reducing the number of force-producing cross bridges per active sarcomere. At shorter lengths, sarcomere force production decreases faster than the corresponding ATP utilization within a given muscle fiber, eliciting less economical force production. For example, Hilber et al. (10) demonstrated that rabbit psoas muscles produced force $\sim 27\%$ and 88% less economically at 0.8 and 0.6 of the muscle's optimal length versus at the optimal length, respectively. In addition, to keep producing the same force, the body needs to activate more force-producing sarcomeres, which further increases metabolic energy expenditure due to additional ATP use for ion pumping (calcium and sodium-potassium pumping; 22, 44). Second, the distance between actin and myosin filaments increases at shorter muscle lengths than optimal (increased lattice spacing; 17). This increased lattice spacing changes cross-bridge geometry and kinetics such that there is less force produced per cross-bridge cycle, and therefore less force per ATP utilization (17). Thus, to produce

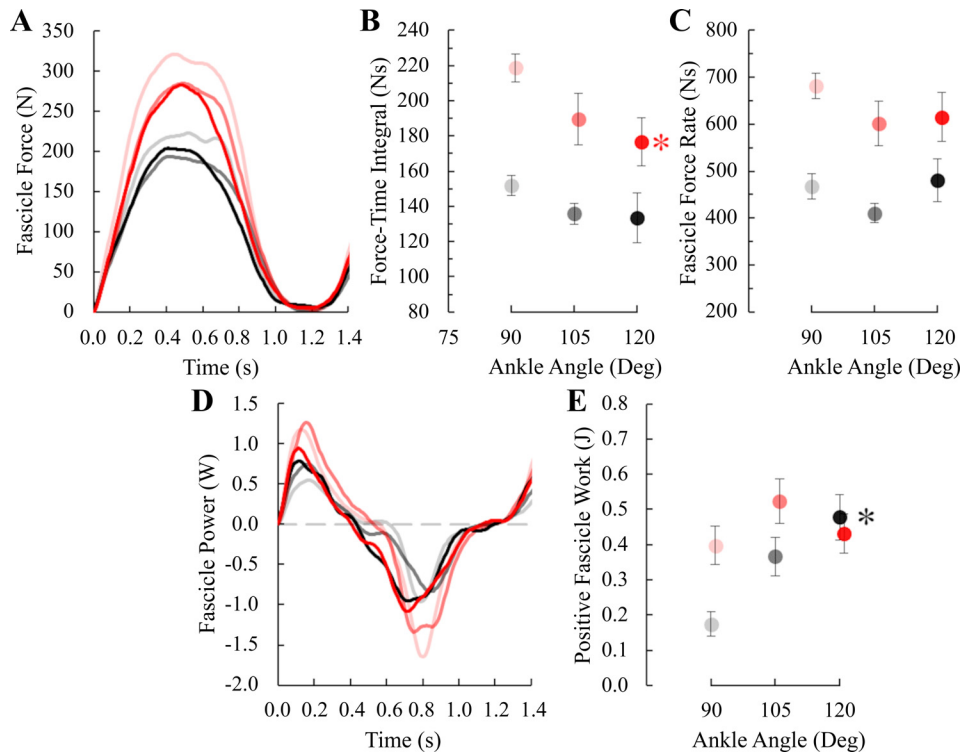


Figure 4. Time-series plots of average soleus fascicle force (A) and power (D), as well as average \pm SE soleus fascicle total force-time integral (B), force rate (C), and positive mechanical work (E). Black and red symbols are offset for clarity and indicate the lower and higher ankle moment levels, respectively. Lighter to darker colors indicate more dorsiflexed to plantar-flexed ankle angles per moment level. Figure details: sample size: 9; sex: 8 male/1 female; statistical tests: linear mixed model. Black and red asterisks (*) indicate that there is an effect of ankle angle on the indicated moment level's dependent variable ($P < 0.05$).

the same force at shorter lengths than optimal requires the body to activate more force-producing cross bridges, increasing metabolic energy expenditure due to additional cross-bridge cycling and ion pumping. Finally, as muscles shorten, filaments compress, various intra- and extracellular components deform (e.g., extracellular matrix and blood), and subtle volumetric changes provide force that attempts to lengthen the muscle (10, 18). To counteract these lengthening forces and produce the same net fascicle

force, the body likely activates additional motor units; again, increasing metabolic energy expenditure due to both greater cross-bridge cycling and ion pumping. Altogether, producing the same net force with shorter fascicles than optimal has multiple effects: reduced actin-myosin overlap, increased lattice spacing, and increased lengthening forces that collectively increase the metabolic energy expended due to the greater cost of cross-bridge cycling and ion pumping.

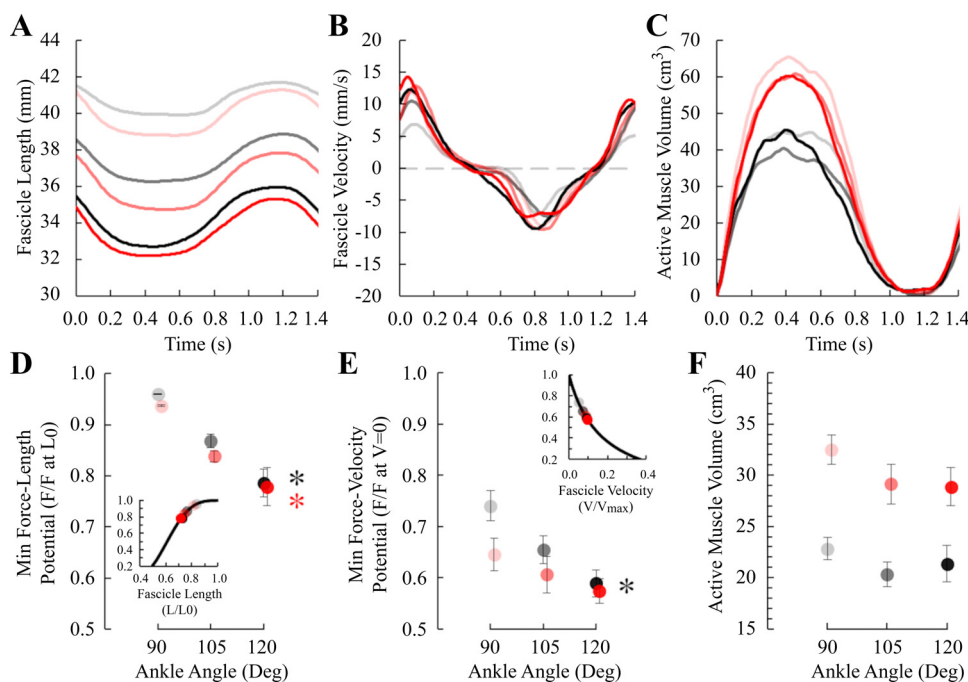
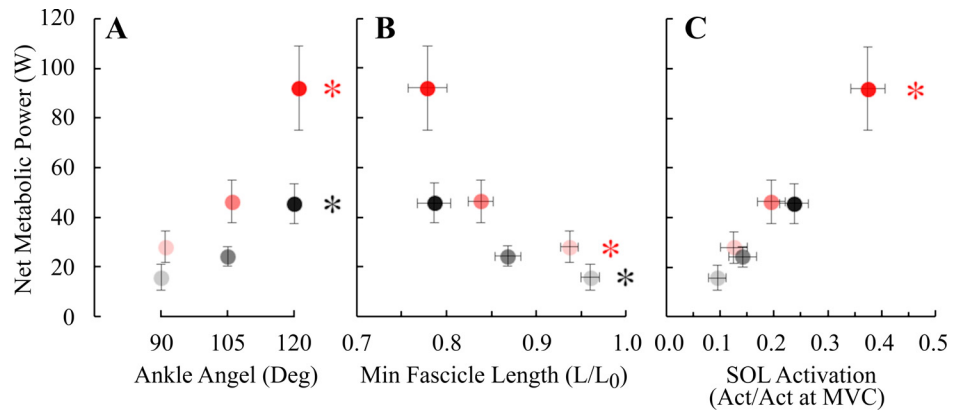


Figure 5. Top row: time-series plots of average soleus fascicle length (A), fascicle velocity (B), and active muscle volume (C). Bottom row: average \pm SE minimum Hill-type force-length potential (D), minimum Hill-type force-velocity potential (E), and average active muscle volume vs. ankle angle (F). Within D and E are the respective force-potentials plotted on the force-length and force-velocity curves, respectively. Regarding fascicle velocity, shortening and lengthening equals positive and negative velocity, respectively. Black and red symbols are offset for clarity and indicate the lower and higher ankle moment levels, respectively. Lighter to darker colors indicate more dorsiflexed to plantar-flexed ankle angles per moment level. Figure details: sample size: 9; sex: 8 male/1 female; statistical tests: linear mixed model. Black and red asterisks (*) indicate that there is an effect of ankle angle on the indicated moment level's dependent variable ($P < 0.05$).

Figure 6. Average \pm SE net metabolic power (A), minimum fascicle length (B), and average soleus activation (C) vs. ankle angle. Black and red symbols are offset for clarity and indicate the lower and higher ankle moment levels, respectively. Lighter to darker colors indicate more dorsiflexed to plantar-flexed ankle angles per moment level. Figure details: sample size: 9; sex: 8 male/1 female; statistical tests: linear mixed model. Black and red asterisks (*) indicate that there is an effect of ankle angle on the indicated moment level's dependent variable ($P < 0.05$). MVC, maximum voluntary contraction.



In addition to testing our hypothesis, we also revealed that two published equations were unable to relate our participants' soleus fascicles mechanics to the corresponding metabolic energy expenditure (Eqs. 2 and 3; 27, 31). One such equation (Eq. 2; 27) did not include muscle operating length in the estimate of metabolic energy expenditure. Interestingly, the other equation (Eq. 3; 38) did include an idealized Hill-type muscle force-length potential and still failed to predict our measured metabolic data. The inability of this second equation (Eq. 3) to predict our participant's metabolic energy expenditure (or muscle activity) suggests that Hill-type muscle models under-predict physiological changes that occur when

intact leg muscles cyclically produce force at different operating lengths. Although we were unable to completely rule out the potential effects of other mechanical parameters (e.g., differences in muscle shortening velocities), our results suggest that muscle operating lengths affect metabolic energy expenditure more than conventionally thought. Therefore, future attempts to link biomechanics to metabolic energy expenditure during cyclic muscle contractions may benefit from directly considering the influence of muscle operating lengths.

As like studies are added to the literature, we encourage researchers to compare data sets and form testable hypotheses

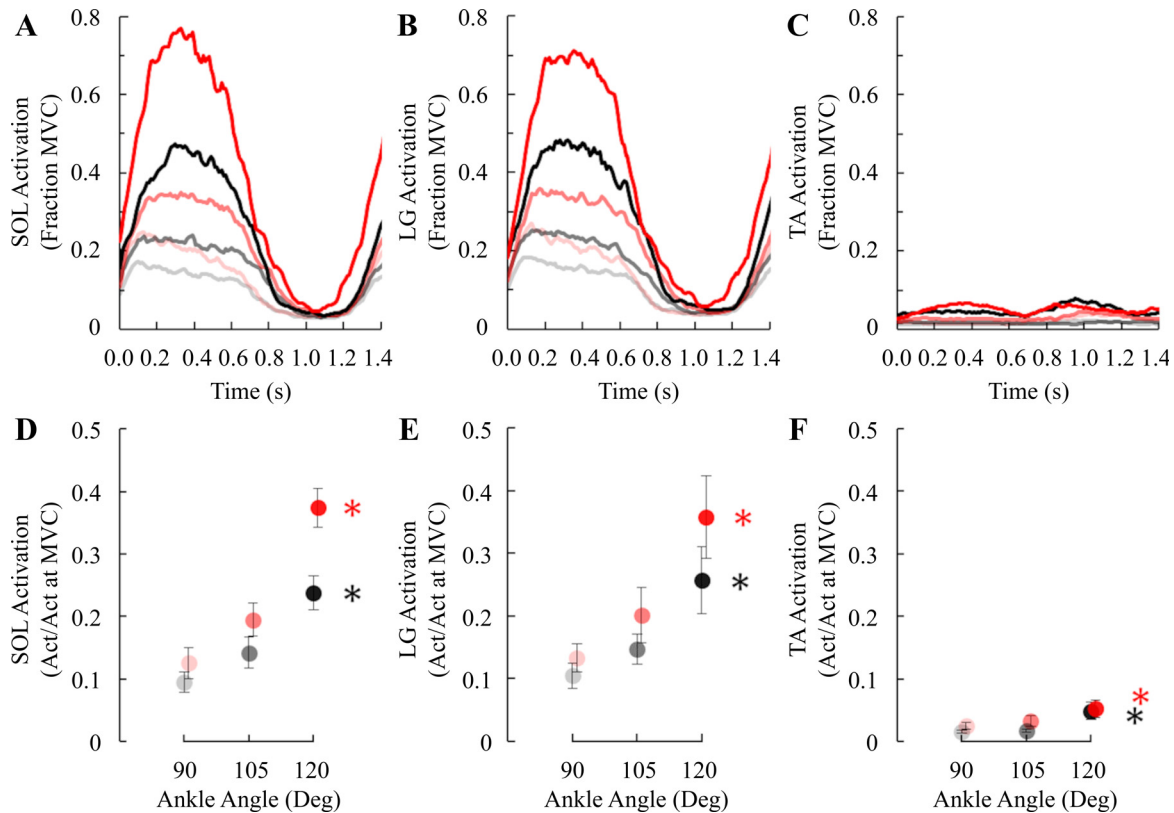


Figure 7. Top row: time-series plots of average soleus (SOL) activation (Act; A), lateral gastrocnemius (LG) activation (B), and tibialis anterior (TA) activation (C). Bottom row: average \pm SE SOL activation (D), LG activation (E), and TA activation (F) vs. ankle angle. MVC is maximum voluntary contraction. Black and red symbols are offset for clarity and indicate the lower and higher ankle moment levels, respectively. Lighter to darker colors indicate more dorsiflexed to plantar flexed ankle angles per moment level. Figure details: sample size: 9; sex: 8 male/1 female; statistical tests: linear mixed model. Black and red asterisks (*) indicate that there is an effect of ankle angle on the indicated moment level's dependent variable ($P < 0.05$).

regarding how locomotor-like mechanics affect metabolic energy expenditure. However, numerous methodological discrepancies limit the utility of interstudy comparisons. For example, the present study's net metabolic power values are 2–6× greater than those reported from a study that involved cyclic bilateral knee moments at roughly similar torque magnitudes and cycle frequencies (27). Although this comparison is thought provoking, there is not enough information to deduce the factor(s) responsible for the metabolic differences. Simply using different protocols and testing different participants introduces discrepancies that affect interstudy comparisons. Further, compared with the knee extensors, soleus muscles are typically more pennate and have shorter moment arms (45), thereby eliciting greater muscle force production per unit joint moment. Moreover, the soleus' relatively greater force production, more compliant tendon (46, 47), and optimally shorter muscle fascicles (48) likely yielded greater relative muscle fascicle shortening compared with that of the knee extensors—contributing to the metabolic differences between the studies (27–30). Even when muscle mechanics are identical, metabolic power can vary due to dissimilar rates of enzymatic activity (e.g., ATPase activity; 21). Hence, due to a myriad of potential factors affecting interstudy comparisons, we encourage researchers to independently test their hypotheses and thoroughly detail their experimental methods and results.

It is unlikely that the neuromechanics of nonsoleus plantar flexors affect our conclusion that soleus metabolic power increased ~200% across ankle angles and muscle lengths. In our study, for simplicity, we assumed that gastrocnemius metabolic power remained constant across ankle angles because, due to the prescribed knee joint angle, it was severely limited in its force and mechanical work capacity (see METHODS). We recognize that lateral gastrocnemius activation increased like that of the soleus at more plantar-flexed ankle angles (Fig. 7), and thus it may have also increased its metabolic power like that of the soleus. If we update our assumption to state that the gastrocnemius muscles increased their metabolic power proportional to their activation, our conclusions regarding soleus metabolism would remain unchanged. That is because lateral gastrocnemius and soleus activation both increased by roughly the same percentage across ankle angles (~200%; Fig. 7). Simply stated, if the gastrocnemius (and other synergistic plantar flexors) increased their metabolic energy expenditure ~200% across ankle angles, the absolute magnitude of soleus metabolic energy expenditure would change, but its relative increase across ankle angles would remain the same. An unlikely scenario where the soleus would not increase its metabolic power ~200% across ankle angles would only occur if synergistic muscles collectively increased their metabolic power much more than that of the soleus across ankle angle conditions. We are dubious of this scenario because the soleus is ~130% more massive than the combination of all synergistic muscles that could produce plantar flexor moment in our study (45). Therefore, even if the synergistic muscles increased their metabolic power across ankle angles, it remains likely that the soleus increased its metabolic power by ~200% across ankle angles.

We acknowledge that there are multiple assumptions that may limit the findings of this study. First, we assumed that

the soleus had uniform fascicle mechanics throughout the entire muscle, which oversimplifies the muscle's complex architecture (49). Although passively changing muscle-tendon length alters soleus fascicle lengths and pennation angles in the same direction across muscle compartments (49), perhaps our ultrasound imaged compartment had less fascicle shortening across ankle angles compared with other compartments. If so, the greater fascicle shortening throughout the other compartments would yield a lower overall muscle force potential and a greater increase in activation and metabolic energy expenditure across ankle angles. Second, we assumed that the soleus is primarily comprised of homogeneous muscle fibers (50) and that these fibers are exclusively recruited during the present study's submaximal metabolic trials (51). Hence, we deemed that all active soleus muscle fascicles have the same maximum shortening velocity across experimental activation levels (2). Third, we assumed that soleus' optimal fascicle length equaled the resting fascicle length at a 90° ankle angle (37). This assumption straddles the conflicting reports that optimal soleus sarcomere length occurs at more dorsiflexed (52) and plantar flexed (53) ankle angles. If the optimal soleus sarcomere length occurred at an ankle angle <90°, we may have underestimated the decrease in force potential across ankle angles due to operating along steeper regions of the force-length relationship. Fourth, we assumed that each participant's optimal soleus fascicle length remained the same value across the experimental conditions. This assumption does not correspond with the notion that optimal muscle length decreases with greater activation (54, 55). An activation-dependent decrease in optimal muscle length may have reduced the difference in the soleus' force-length operating region between the 120° versus 90° ankle angle conditions. Alternatively, decreasing optimal fascicle length would also elicit a narrower force-length relationship (in millimeters), such that an absolute decrease in fascicle length would travel further down the ascending limb of the force-length relationship. Thus, it is difficult to predict how an activation-dependent shift in optimal fascicle length affects soleus force potential across ankle angles. Fifth, our surface electromyography measurements were likely influenced by changing muscle geometry across ankle angles (56, 57). Sixth, we also assumed that the participants used ideal force-length and force-velocity profiles (7, 8, 58). Regardless of these assumptions, our conclusion that cyclically producing force with relatively shorter muscle fascicles increases metabolic energy expenditure remains sound. We also find assurance when comparing our results to the most analogous locomotion experiment—walking and running in footwear with different heel heights. Similar to our study, increasing footwear heel height elicits postural changes that decrease relative muscle fascicle operating lengths (14, 15) and increase metabolic energy expenditure during walking and running compared with baseline conditions (i.e., barefoot or in flats; 59, 60).

Conclusions

In conclusion, increasing the operating length of muscle fascicles that produce force on the ascending limb of their force-length relationship may measurably decrease metabolic energy expenditure during locomotion. This finding

may help resolve why the locomotion economy differs within and across animal species, in addition to informing biomechanical interventions that reduce user metabolic energy expenditure.

DATA AVAILABILITY

The data that support this study are available at: <https://doi.org/10.6084/m9.figshare.20060891.v1>.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

O.N.B., J.R.F., and G.S.S. conceived and designed research; O.N.B., L.H.T., and J.N.S. performed experiments; O.N.B. analyzed data; O.N.B., J.R.F., and G.S.S. interpreted results of experiments; O.N.B. prepared figures; O.N.B. drafted manuscript; O.N.B., L.H.T., J.N.S., J.R.F., and G.S.S. edited and revised manuscript; O.N.B., L.H.T., J.N.S., J.R.F., and G.S.S. approved final version of manuscript.

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