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RESEARCH ARTICLE

Faster triceps surae muscle cyclic contractions alter muscle activity and whole body metabolic rate

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Abstract

Hundred years ago, Fenn demonstrated that when a muscle shortens faster, its energy liberation increases. Fenn's results were the first of many that led to the general understanding that isometric muscle contractions are energetically cheaper than concentric contractions. However, this evidence is still primarily based on single fiber or isolated (ex vivo) muscle studies and it remains unknown whether this translates to whole body metabolic rate. In this study, we specifically changed the contraction velocity of the ankle plantar flexors and quantified the effects on triceps surae muscle activity and whole body metabolic rate during cyclic plantar flexion (PF) contractions. Fifteen participants performed submaximal ankle plantar flexions (~1/3 s activation and ~2/3 s relaxation) on a dynamometer at three different ankle angular velocities: isometric (10° PF), isokinetic at 30°/s (5–15° PF), and isokinetic at 60°/s (0–20° PF) while target torque (25% MVC) and cycle frequency were kept constant. In addition, to directly determine the effect of ankle angular velocity on muscle kinematics we collected gastrocnemius medialis muscle fascicle ultrasound data. As expected, increasing ankle angular velocity increased gastrocnemius medialis muscle fascicle contraction velocity and positive mechanical work ($P < 0.01$), increased mean and peak triceps surae muscle activity ($P < 0.01$), and considerably increased net whole body metabolic rate ($P < 0.01$). Interestingly, the increase in triceps surae muscle activity with fast ankle angular velocities was most pronounced in the gastrocnemius lateralis ($P < 0.05$). Overall, our results support the original findings from Fenn in 1923 and we demonstrated that greater triceps surae muscle contraction velocities translate to increased whole body metabolic rate.

NEW & NOTEWORTHY Single muscle fiber studies or research on isolated (ex vivo) muscles demonstrated that faster concentric muscle contractions yield increased energy consumption. Here we translated this knowledge to muscle activation and whole body metabolic rate. Increasing ankle angular velocity increased triceps surae contraction velocity and mechanical work, increasing triceps surae muscle activity and substantially elevating whole body metabolic rate. Additionally, we demonstrated that triceps surae muscle activation strategy depends on the mechanical demands of the task.

energetics; gastrocnemius medialis; locomotion; muscle mechanical work

INTRODUCTION

Human skeletal muscles are the driving tissues for any kind of functional movement from quiet standing, accurate object manipulation to sprinting or jumping. During locomotion, the leg muscles produce force to support the body and accelerate it forward. Therefore, skeletal muscles are the major energy-consuming tissues during locomotion and as such determine the whole body metabolic rate (1). Reducing someone's metabolic rate during locomotion has been demonstrated to enhance endurance running performance (2) and suggested to increase preferred walking speed and decrease fatigue in older adults (3). Hence, enabling muscles to operate at more metabolically favorable conditions will reduce a muscle's energy consumption rate and improve the locomotor ability.

One-hundred years ago, Fenn (4) demonstrated that the energy liberation of the frog sartorius muscle was elevated during shortening contractions as compared with an isometric contraction. Moreover, he stated that "the excess energy due to shortening of the muscle is nearly identical to the work done," a theory which is still known as the "Fenn-effect." Although the Fenn effect may not be generally valid (5), Hill (6) generalized the velocity dependence of a muscle force into the well-established force-velocity relationship of a muscle. The force potential of a muscle decreases with increasing shortening velocity. Since then, the increased energy liberation with increasing contraction velocity was extensively described in amphibian muscle fibers (6, 7), mammalian muscle fibers (8), and even in human muscle fibers (9, 10). In 1982, Stainsby (11) demonstrated the relationship between a muscle's oxygen consumption rate and increased work or shortening in situ in the dog gastrocnemius plantaris muscle and more recently, Ortega et al. (12) demonstrated the "Fenn-effect" in the human first dorsal

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interosseous muscle. Using magnetic resonance spectroscopy, these latter researchers showed a nearly 50% increase in muscle ATP consumption during shortening contractions compared with isometric or lengthening contractions. These studies have led to our general understanding that slower or isometric muscle contractions are more economical than fast concentric contractions.

Although researchers often attribute differences in whole body metabolic rate during full-body exercises to altered muscle contraction velocities, the evidence is still primarily based on single fibers or isolated (ex vivo) muscles and no study has translated the velocity effect from the single fiber level to the whole body level. Especially the muscle contraction velocity of the triceps surae muscle, an important muscle during locomotion and a muscle that is relatively easy to assess in vivo using ultrasound imaging has often been related to the metabolic cost of locomotion (13–17). Moreover, the triceps surae in series connected tendinous tissue, muscle synergies, and neural motor control make the whole body a lot more complex than a single muscle fiber and may question whether single muscle fiber studies or studies on isolated ex vivo muscle do translate to the whole body. Still, given the substantial increase in energy liberation with higher contraction velocities observed in single fibers, we expect that an increase in muscle contraction velocity while keeping muscle force production and duration constant would increase muscle activation, muscle metabolic rate, and therefore whole body metabolic rate.

One potential reason why the increased metabolic rate with increasing contraction velocity has not been demonstrated on the whole body level may be the difficulty of isolating muscle contraction velocity from other factors affecting a muscle's metabolic rate. The energy consumption rate of a muscle is not only defined by its contraction velocity but also highly depends on the duration of activation, the force magnitude, and the length of the muscle (18). Moreover, other factors such as the frequency of muscle activation (19) and duty factor (20) have been associated with changes in muscle metabolic rates. During almost any human movement, multiple factors change. However, on a dynamometer, we can specifically target one joint and control for joint angular velocities during cyclic torque production. Imposing a change in muscle contraction velocity while keeping muscle force constant will inherently alter a muscle's mechanical power (force $\times$ velocity) and work (the integral of power). Hence, using the dynamometer we can (indirectly) control muscle fascicle contraction velocities and mechanical work of the muscles crossing the joint while keeping most of the other factors affecting a muscle's metabolic rate constant.

Human muscles contain numerous muscle fibers, of different muscle fiber types, with distinct mechanical and metabolic properties. Traditionally, human muscle fiber types are divided into three categories: slow (type I), intermediate (type IIa), and fast (type IIx) muscle fibers. Studies on single muscle fibers have demonstrated that the force-velocity relationship highly depends on the muscle fiber type. Fast-twitch muscle fibers demonstrate double to triple the maximal contraction velocity of slow-twitch fibers and the force-velocity relationship appears less curved (8, 21). As a result, fast-twitch fibers can generate more power, especially at high concentric contraction velocities (22). Therefore, it has been suggested that the recruitment of muscle fibers with different typologies enables muscles to optimize power production at a wide range of movements with different velocities (21). Furthermore, the distribution of muscle fiber types within one person is different across muscles and even synergistic muscles demonstrate substantial differences (23). For example, the human soleus (SOL) muscle contains ~85% slow-twitch fibers, making it the "slowest" human muscle, whereas the gastrocnemius medialis (GM) and gastrocnemius lateralis (GL)—synergistic plantar flexor muscles—contain only ~50% and ~45% slow-twitch fibers in the same "average" person, respectively (23). Hence, changing the mechanical demands of a muscle by inducing different contraction velocities may also induce a change in the coordination strategy of these synergistic muscles. Such changes in recruitment in which muscles with larger proportions of fast-twitch fibers (i.e., the gastrocnemii muscles) are preferably activated during faster muscle movements (e.g., movement with the highest joint angular velocity) have been observed in animals (24–26) and humans (27, 28).

Here, we set out to advance our insights into the effect of increased muscle contraction velocity on whole body metabolic rate and muscle activation patterns during cyclic contractions. To do so, we used a protocol in which participants had to cyclically produce locomotion-like ankle torques (i.e., similar durations of force production and relaxation as during walking and running) at different ankle angular velocities. In line with the original research by Fenn (1923), we hypothesize that with increasing ankle angular velocities the muscle force potential reduces, leading to increased triceps surae muscle activation and elevated whole body metabolic rate. In addition, we predict that with increasing ankle angular velocity the increase in muscle activation will be more pronounced in the relatively fast gastrocnemii muscles compared with the slower soleus muscle.

METHODS

Participants

Fifteen male volunteers completed the experimental protocol (body mass = 74.6 ± 6.2 kg; resting metabolic rate = 134 ± 18 W; Achilles tendon moment arm = 5.7 ± 0.4 cm). Prior to the experimental data collection, the experimental protocol was explained to the participants and they gave written informed consent approved by the local ethical committee (Social and societal ethics committee of the KU Leuven). All participants were free from any musculoskeletal injury.

Experimental Protocol

Upon arrival in the laboratory, each participant was positioned in a prone position on the dynamometer with the right foot securely strapped to the footplate and the ankle axis of rotation aligned with the dynamometer's axis of rotation (Biodex System 3, Biodex Medical Systems, Inc., NY). In this position and once the participants were already lying down for at least 6 min, we collected the participant's resting metabolic rate through indirect calorimetry (Cosmed K5, COSMED Srl, Rome, Italy). Next, participants performed a warm-up in which they executed five isometric plantar

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flexion contractions with increasing intensity. Following the warm-up, participants performed three maximal voluntary contractions (MVCs) of the right ankle plantar flexors while laying prone (extended knee) with the ankle angle fixed at 10° plantar flexion (PF). In addition, in the same position, three MVCs of the ankle dorsiflexors were obtained. Between each MVC participants were allowed 1 min of rest to avoid fatigue (29). Passive resting torques were used to adjust the produced torques during MVC.

Subsequently, participants performed six, 6 min trials interspersed by 5 min of rest. During these trials, participants were asked to cyclically perform plantar flexion contractions for ~1/3 s to reach a target torque (25% of MVC), followed by a 2/3 s period of rest. To guide the participants during torque production, we used both an audible metronome and a monitor displaying visual feedback with the target torque and the produced torque. Participants performed the trials at three different ankle angular velocities: *1*) isometric (ISO), i.e., no angular rotation, with the ankle angle fixed at 10° PF, *2*) isokinetic at a relatively slow angular velocity (30°/s) during which the ankle rotated from 5° PF to 15° PF, and *3*) isokinetic at a relatively fast angular velocity (60°/s) during which the ankle rotated from 0° PF tot 20° PF. The protocol was designed to have most of the active force produced during ankle plantar flexion (i.e., concentric contraction of the plantar flexors) while during the relaxation period, the foot and foot plate rotated toward their initial position under the influence of gravity. The order of the conditions was randomized and duplicated in a mirrored design making six trials in total. During each trial, we collected ankle torque, angle and angular velocity from the dynamometer, whole body metabolic rate (Cosmed K5, COSMED Srl, Rome, Italy), and muscle activation data of the triceps surae and tibialis anterior muscle using surface electromyography (1,000 Hz) (Zerowire, CA). After the six trials, we collected another two plantar flexion MVCs to quantify any potential fatigue.

Finally, the aforementioned cyclic contraction conditions (isometric, 30°/s, 60°/s) were repeated for 1 min to collect in vivo GM muscle fascicle data. By changing the ankle angular velocity, we can indirectly change the triceps surae muscle fascicle velocity. To quantify the effect of ankle angular velocity on triceps surae muscle fascicle velocity, we used dynamic ultrasound images of the GM muscle. We placed an ultrasound transducer on the GM muscle belly to collect in vivo muscle fascicle behavior. To allow for good quality surface electromyography data as well as GM muscle fascicle ultrasound images, electromyographic (EMG) and ultrasound data collections were separated as both devices are placed in a similar position on the calf muscle.

Dynamometer Data

Ankle torque, angle, and angular velocity data were measured at 1,000 Hz (Biodex System 3, Biodex Medical Systems, Inc., NY) and raw data was low-pass filtered with a 4th order Butterworth filter at 6 Hz (20). We used the plantar flexion torque data to detect and define the different cycles adopting a torque threshold of 2.5% of the participant's MVC. For every cycle, we calculated the mean torque, as the area under the torque-time curve divided by the cycle time, peak torque, and ankle angle at the instant of peak torque. In addition, we calculated duty factor (active torque production time/total cycle time). Torque data were normalized to MVC torques to obtain a percentage of MVC and all time series data were splined into 101 data points per cycle (0 to 100%). Cycles that were shorter than 0.8 or longer than 1.2 s were discarded from the analysis primarily to avoid that artificial cycles (e.g., either multiple cycles identified as one cycle or when the ankle torque during rest exceeded the torque threshold very briefly) were included in the analysis.

Whole Body Metabolic Rate

To determine whole body metabolic rate during rest and during the cyclic plantar flexion contractions, we used the oxygen consumption and carbon dioxide production rates of the last 2 min as inputs into the equation proposed by Péronnet and Masicotte (30) to calculate whole body metabolic rate. We duplicated each condition to increase reliability and we used the mean of both trials as the metabolic rate at the respective condition. Only incorporating either the 1st or 2nd trial did not affect any of the conclusions based on whole body metabolic rate. Since we were primarily interested in the metabolic rate associated with the exercise, we subtracted the resting metabolic rate —measured in the same position on the dynamometer and before the start of any exercise—from the metabolic rates during exercise to obtain net metabolic rate and as such omit the metabolic rate associated with the basal metabolism. We excluded a total of 5 (out of 105) trials as respiratory exchange ratio did not reflect a ratio indicative of fat and/or carbohydrate oxidation.

Electromyography

Muscle activation data of all three triceps surae muscles (GM, GL, and SOL) and tibialis anterior muscle of the right leg were collected. Before placing the bipolar electrodes (Ag/AgCl electrodes, 10 mm recording diameter, Ambu), the skin was shaved and cleaned with an alcohol solution. Next, we placed the electrodes on the muscle belly of each muscle with an interelectrode distance of 2 cm. EMG signals were band-pass filtered (20–400 Hz), rectified, and low-pass filtered (20 Hz). Muscle activity data were normalized to peak activation of each respective muscle during MVC (i.e., plantar flexion MVCs for triceps surae and dorsiflexion MVCs for tibialis anterior). We calculated the mean muscle activity for each cycle by integrating the muscle activation over time and subsequently dividing the integrated activation by cycle time. In addition, we determined the peak activation and interpolated all muscle activity time series data into 101 data points. Two trials were discarded due to clearly visible tibialis anterior coactivation during the exercise, quantified as the mean tibialis anterior (TA) activity in the discarded trial being more than threefold the TA activation of the (duplicated) nondiscarded trial.

To assess differences in coordination strategy within the triceps surae with changing ankle angular velocity, we calculated the relative increase in muscle activity with increasing ankle angular velocity by normalizing the cycle mean muscle activity to the mean activity during the isometric condition.

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Dynamic Ultrasound Imaging

We used B-mode ultrasound (Telemed ArtUs, Vilnius, Lithuania) to determine GM muscle fascicle kinematics during at least seven consecutive cycles in each condition. The linear transducer, operating at 8 MHz and sampling at 78 Hz, was placed on the GM muscle belly and securely wrapped around the calf. A semiautomatic tracking algorithm (31) was used to process the muscle fascicle lengths and pennation angles. We visually checked every frame and manually adjusted the position of the fascicle and/or aponeurosis if necessary. GM muscle fascicle lengths and pennation angles were low-pass filtered at 6 Hz and we took the time derivative of the fascicle lengths to determine fascicle velocities. We calculated the mean GM muscle velocity as the mean contraction velocity of the fascicles from the start of the cycle to peak torque production.

Next, we calculated the triceps surae muscle-tendon force by dividing the ankle joint torque by the subject-specific Achilles tendon moment arm, measured with a tape measure at neutral position and averaged over the medial and lateral side (32) and taking into account the effect of the ankle joint angle on the muscle-tendon moment arm (33, 34). We multiplied the triceps surae muscle-tendon force by the relative physiological cross-sectional area of the GM muscle to the entire triceps surae (35) to obtain GM muscle-tendon force and divided this muscle-tendon force by the cosine of the pennation angle to eventually obtain GM muscle force. In addition, we calculated GM muscle instantaneous mechanical power as GM muscle force multiplied by the GM muscle fascicle velocity (13). Finally, we calculated the net and positive muscle mechanical work per cycle by integrating the respective net and positive mechanical power over time. All time series data (muscle fascicle length and velocity) were splined into 101 data points to allow for comparison.

Statistics

To assess statistical differences between ankle angular velocity conditions, we performed repeated-measure ANOVAs or, if the data did not follow a normal distribution, the nonparametric Friedman test. To check whether our data followed a normal distribution, we used the Shapiro–Wilk test and our sphericity criterion was tested using Mauchly's test. If the data followed a normal distribution but the assumption of sphericity was violated we performed a repeated-measure ANOVA with a Greenhouse–Geisser correction. We used a Kruskal–Wallis test (data not normally distributed) to statistically test for differences in relative increase in mean muscle activity between triceps surae muscles. If we found a statistically significant main effect, a Bonferroni-adjusted pairwise comparison between conditions was used to test for significant differences between each condition.

RESULTS

Ankle Torque, Spatiotemporal, and Kinematic Data

Mean (P = 0.247) and peak (P = 0.344) ankle plantar flexion torque were not different across ankle angular velocity conditions (Fig. 1A; Table 1). In addition, also cycle time (P = 0.057) and duty factor (P = 0.247) were not different across conditions. Furthermore, although the different ankle angular velocity conditions inherently implied differences in joint angles, the joint angle at the instance of peak torque was not different across conditions (P = 0.127).

Gastrocnemius Medialis Muscle Kinematics and Work

At the start of force production, GM muscle fascicle length was larger due to differences in ankle joint position (i.e., less

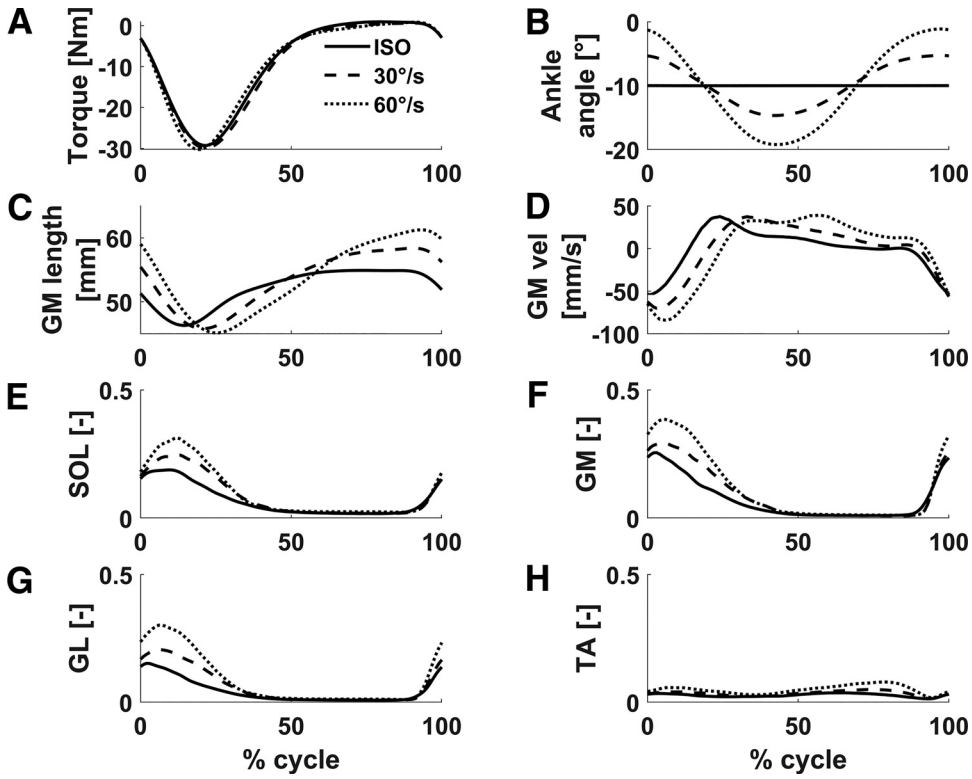


Figure 1. Mean ankle torque (*A*), angle (*B*), gastrocnemius medialis (GM) muscle kinematics (*C* and *D*), and muscle activations (*E*–*H*) throughout the cycle at three different ankle angular velocities (n = 15 subjects). For clarity, standard deviations were omitted. GL, gastrocnemius lateralis; SOL, soleus; TA, tibialis anterior.

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Table 1. *Dynamometer data, mean gastrocnemius medialis muscle fascicle length, velocity, and length at peak torque*

	ISO	30°/s	60°/s
Mean torque, % MVC	8.0 ± 1.7	8.4 ± 1.9	8.0 ± 1.2
Peak torque, % MVC	27.2 ± 2.7	27.6 ± 2.8	27.2 ± 2.3
Cycle time, s	1.00 ± 0.01	1.00 ± 0.01	0.99 ± 0.01
Duty factor	0.49 ± 0.07	0.52 ± 0.10	0.52 ± 0.10
Ankle angle at peak torque, °	−10.0 ± 0.6	−11.1 ± 1.2	−10.8 ± 2.1
GM length at peak torque, mm	45.9 ± 7.9	45.3 ± 8.0	45.3 ± 8.3
Mean GM length during active torque production, mm	48.5 ± 8.3	48.4 ± 8.3	48.7 ± 8.7
Mean GM velocity start to peak torque, mm/s*	27.1 ± 13.1‡§	52.3 ± 15.4†§	72.5 ± 22.0†‡

Data are presented as means ± SD. n = 15 subjects (Mean and peak torque, cycle time, duty factor, angle at peak torque: Friedman; GM length and velocity: repeated-measures ANOVA). *Significant effect of ankle angular velocity with $P < 0.001$; †significantly different from isometric condition ($P < 0.05$); ‡significantly different from 30°/s condition ($P < 0.05$); §significantly different from 60°/s condition ($P < 0.05$). GM, gastrocnemius medialis; MVC, maximal voluntary contraction.

plantar flexed with increasing angular velocity; Fig. 1, *B* and *C*). Yet, neither mean GM muscle fascicle length during torque production (P = 0.856) nor fascicle length at peak torque (P = 0.592) was different across conditions. Increasing ankle angular velocity increased GM muscle fascicle contraction velocity (Fig. 1*B*), with mean muscle fascicle contraction velocity significantly different between conditions ($P < 0.001$; Table 1). Similarly, GM positive and net muscle mechanical work per cycle increased with increasing ankle angular velocity ($P < 0.001$; Fig. 2).

Muscle Activity

Both cycle mean and peak muscle activity of all three triceps surae muscles increased with increasing ankle angular velocity ($P < 0.001$; Fig. 3 and Supplemental Fig. S1; see https://doi.org/10.6084/m9.figshare.21222236). Post hoc analysis revealed that mean and peak muscle activity of all three triceps surae muscles were significantly different between all three conditions ($P < 0.031$). Mean and peak activation of the tibialis anterior muscle was significantly higher during the fastest (60°/s) isokinetic condition compared with the slow (30°/s) and isometric conditions ($P < 0.01$) but was not different between the slow and isometric conditions (P = 0.61).

The relative increase in mean GL muscle activity at 60°/s was greater than the relative increase in mean SOL (P = 0.013) and GM (P = 0.016) muscle activation (Fig. 4). The relative increase in mean muscle activity at 30°/s was not different between any of the triceps surae muscles (P = 0.08).

Whole Body Metabolic Rate

Increasing ankle angular velocity also increased net whole body metabolic rate (ISO = 49.9 ± 30.3 W; 30°/s = 71.2 ± 31.4 W; 60°/s = 100.4 ± 27.1 W; $P < 0.001$; Fig. 5). Post hoc analysis revealed significant differences between all angular velocity conditions ($P < 0.001$).

Pre- versus Postexercise MVC

Maximally produced ankle torque was 5.5% lower after the cyclic contraction exercises than before the exercises (P = 0.027; Supplemental Fig. S2; see https://doi.org/10.6084/m9.figshare.21222242).

DISCUSSION

In this study, we changed the ankle angular velocity during locomotion-like cyclic ankle plantar flexor contractions (i.e., similar durations of force production and relaxation as during walking and running) while keeping other factors associated with a muscle's metabolic rate as constant as possible. In line with our first hypothesis, increasing ankle angular velocity resulted in increased triceps surae muscle activations. An increase in muscle activity is a clear, but not conclusive, indicator for increased muscle metabolic rate, which is likely to be reflected in increased whole body metabolic rate. Indeed, we found considerably higher net whole body metabolic rates when ankle angular velocity was increased. In addition, we found that with increasing ankle

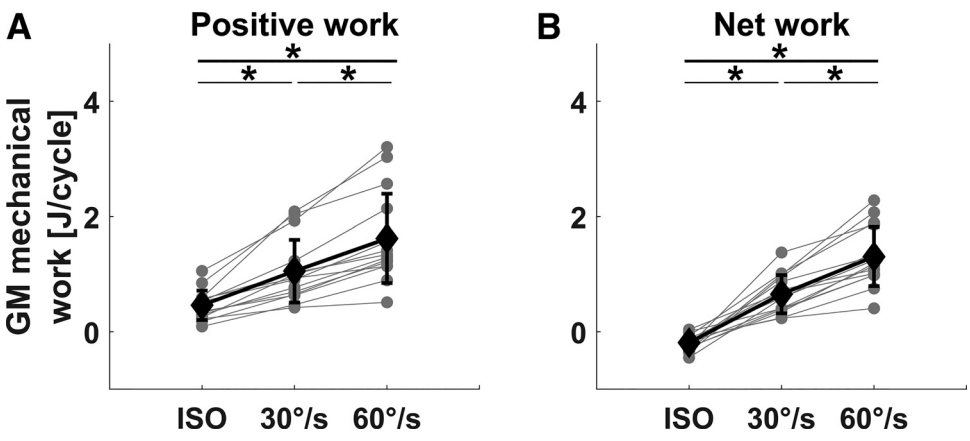


Figure 2. Gastrocnemius medialis (GM) positive (*A*) and net (*B*) mechanical work per cycle compared between three different ankle angular velocities. Black diamonds represent group mean data with the corresponding standard deviation, gray lines and dots represent individual data. *Significant difference between conditions (n = 15 subjects, positive work: Friedman test; net work: repeated-measure ANOVA).

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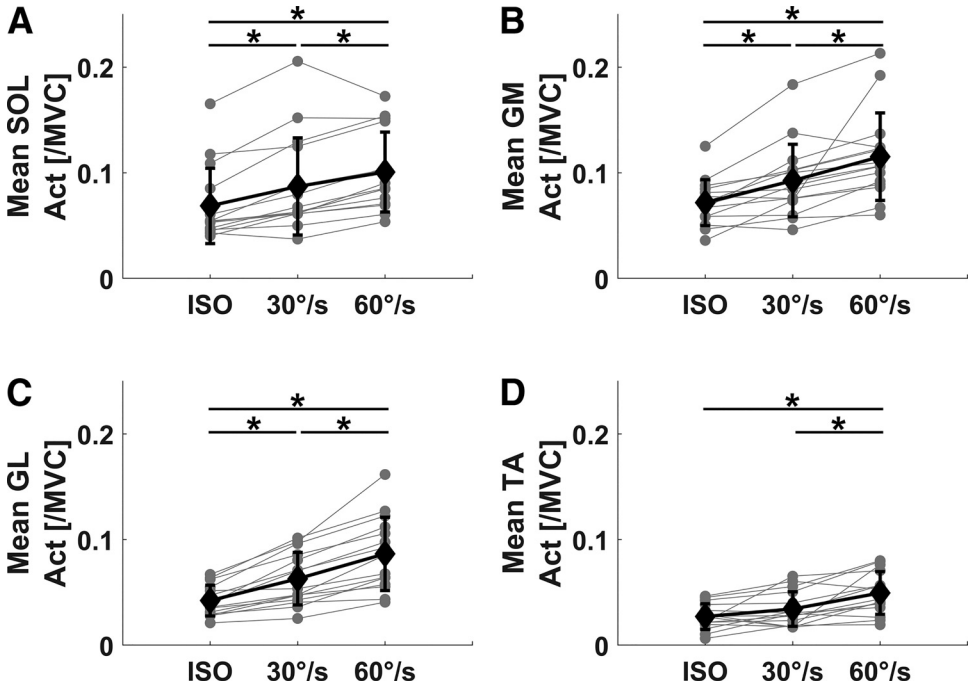


Figure 3. Cycle mean muscle activation of the soleus (SOL, *A*), gastrocnemius medialis (GM, *B*), gastrocnemius lateralis (GL, *C*), and tibialis anterior (TA, *D*) during three different ankle angular velocities. Activation data is normalized to the respective activations during MVC. Black diamonds represent group mean data with the corresponding standard deviation, gray lines and dots represent individual data. *Significant difference between conditions (n = 15 subjects, SOL and TA: Friedman test; GM and GL: repeated-measure ANOVA). MVC, maximal voluntary contraction.

angular velocity, the GL muscle, containing a larger relative distribution of fast-twitch fibers, but not the GM, increased its activation more compared with the SOL which only partially supports our second hypothesis.

Increasing ankle angular velocity resulted in increased GM muscle fascicle velocity and mechanical work, requiring higher triceps surae muscle activations to produce the same torque and increasing net whole body metabolic rate. Although mean and peak ankle plantar flexion torques were not different across ankle angular velocity conditions, net whole body metabolic rate clearly increased with increasing ankle angular velocity. Compared with the isometric condition, net whole body metabolic rate increased by 43% and 101% at the intermediate (30°/s) and fastest (60°/s) ankle angular velocities, respectively. Other factors known to affect muscle metabolic rates such as mean muscle fascicle length (36), cycle frequency (19, 37), and duty factor (20) were not significantly different across conditions (Table 1). In contrast, in vivo GM ultrasound data demonstrated that higher ankle angular velocities resulted in faster GM contraction velocities (Fig. 1*D*) and substantially increased positive and net GM muscle mechanical work per cycle (Fig. 2). Notably, even in the "isometric" condition, the GM muscle did produce some work even though the muscle-tendon unit did not (no change in ankle or knee joint angle). The discrepancy between the triceps surae muscle and muscle-tendon unit work highlights the effect of the in series connected tendinous tissue of the triceps surae muscle-tendon unit, i.e., the muscle shortens, producing mechanical work, by lengthening the tendinous tissue. Nevertheless, the net mechanical work performed by the GM muscle per cycle in the isometric condition was nearly zero.

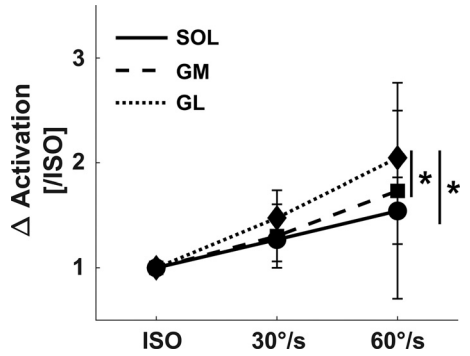


Figure 4. Relative increase in mean soleus (SOL, solid), gastrocnemius medialis (GM, dashed), and gastrocnemius lateralis (GL, dotted) muscle activation with increasing ankle angular velocity. Activation is expressed relative to the isometric ankle angular velocity condition. *Significant difference between muscles (n = 15 subjects, Kruskal–Wallis test).

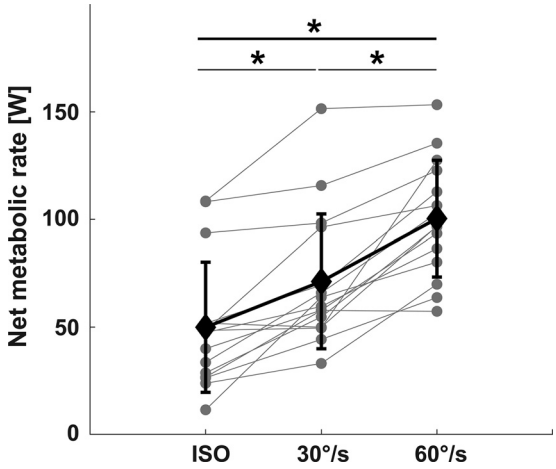


Figure 5. Net whole body metabolic rate while performing cyclic ankle plantar flexor contractions at three different ankle angular velocities. Black diamonds represent group mean data with the corresponding standard deviation, gray lines and dots represent individual data. *Significant difference between conditions (n = 15 subjects, Friedman test).

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Similar to the present study, Fletcher et al. (38) used a dynamometer to investigate whether muscle shortening alone was able to explain differences in the energy cost of the GM muscle during contraction. Remarkably, they found that the condition in which the smallest amount of muscular work was performed (isokinetic condition) was associated with the highest estimated energy cost, which clearly contradicts the results found in this study and the original findings from Fenn (4). In contrast to our study, many factors affecting a muscle's energy cost were not controlled limiting the comparability with this study. First, ankle plantar flexor torque was different between conditions, explaining why muscular work was higher in the isometric compared with the isokinetic condition. Also, fascicle length at peak torque and contraction duration was significantly longer in the isometric condition compared with the isokinetic condition, differences which may have contributed to the reduced energy consumption during the "isometric" (but associated with greatest muscular work) condition (19, 36, 39). In addition, in line with our results, van der Zee et al. (40) demonstrated that greater knee joint power increased whole body metabolic rate.

Higher concentric contraction velocities reduce the muscle's force potential (41, 42). If a muscle has to produce the same force but with a reduced force potential its neural drive should be increased, likely associated with increased muscle activation (43). Gabaldón et al. (43) demonstrated that when the relative contraction velocity of the ankle extensor muscles of wild turkeys increased but force demand remained similar, the integrated muscle activity of these muscles increased. Similarly, we found that all three triceps surae muscles increased their mean and peak activation with increasing ankle angular velocity indicating that the triceps surae muscles' metabolic rate is increased (Fig. 3 and Supplemental Fig. S1). This increase in muscle activation likely reflects an increase in active muscle volume, postulated to closely relate to whole body metabolic rate when running at different speeds (44). Interestingly, the increase in mean muscle activity when ankle angular velocity increased from isometric to 60°/s may not fully explain the increase in net whole body metabolic rate. The underlying assumption when relating active muscle volume with whole body metabolic rate is that muscles contract isometrically, or at least at the same contraction velocity across conditions, implying that the energy consumption per unit of active muscle volume remains constant. Clearly, in our study contraction velocity is not constant. Greater contraction velocities relate to faster cross-bridge attachment/detachment (45) and, as cross-bridge detachment is an energy-consuming process, a muscle's metabolic rate per unit of active muscle volume will also increase. As such, when a muscle is required to produce the same force but with a faster contraction velocity, its energy consumption rate increases due to a greater number of fibers recruited as well as a faster rate of energy consumption per activated fiber due to faster cross-bridge attachment/detachment. Furthermore, coactivation of the tibialis anterior muscle increased with angular velocity, especially at the highest angular velocity (Fig. 3*D* and Supplemental Fig. S1*D*). Since this increased coactivation primarily occurred during the relaxing phase of the cycle (Fig. 1*H*), when triceps surae muscles were not or only marginally active, we do not expect this coactivation to affect triceps surae muscle activation or metabolic rate. Still, greater tibialis anterior activation will probably have led to greater tibialis anterior muscle metabolic rate, which may have contributed to the increased whole body metabolic rate at the fastest ankle angular velocity. However, as this absolute increase in activation is relatively small compared with the absolute increase in activation of the triceps surae muscles, we argue that increased tibialis anterior muscle metabolic energy will only account for a small portion of the increased whole body metabolic rate. Overall, our results provide relatively strong evidence that increasing the ankle angular velocity while producing a similar torque profile increases triceps surae muscle contraction velocity and positive mechanical work produced per cycle, leading to increased triceps surae muscle activity, which eventually also increases whole body metabolic rate.

Remarkably, the relative increase in triceps surae muscle activation with faster ankle angular velocities was not consistent within the individual triceps surae muscles, suggesting that the coordination strategy adopted between synergistic muscles likely depends on the mechanical demand of the exercise. At the fastest ankle angular velocity condition, mean GL muscle activity was increased by 104% compared with the isometric condition, which was significantly more than the relative increase in SOL and GM cycle mean muscle activation of 47% and 61%, respectively (Fig. 4). The percentage of slow-twitch fibers in the SOL muscle (~85%) is considerably larger than the percentage of slow-twitch fibers in the GM (~50%) and GL (~45%) muscle (23) and has been proposed to explain a shift in coordination strategy (27, 28, 46). Moreover, Lai et al. (47) demonstrated that adjusting the motor unit recruitment strategy based on the mechanical demand of the task is metabolically beneficial. Although the difference in muscle fiber type composition can potentially explain increased relative activation of the GL compared with SOL, it is unlikely to explain the differences between both gastrocnemii muscles. An alternative explanation is a difference in relative contraction velocity of the triceps surae muscle due to distinct muscle fascicle resting lengths. Previous studies demonstrated that the GL muscle contains substantially longer muscle fascicles compared with the GM (15%–20% longer) and SOL muscle (60%–70% longer) (35, 48). When assuming that the absolute shortening velocity within the triceps surae muscles is similar, the in-series coupled sarcomeres will have to shorten more (and thus faster) in the shorter GM muscle compared with the GL. As such, the reduction in force potential of the GL is potentially less compared with the GM. Higher reliance on the muscles with better-preserved force potential (e.g., GL) is likely beneficial from a whole body metabolic perspective. More specifically the sum of muscle activations squared—a commonly used neuromuscular strategy underlying force sharing (49)—is smaller when GL would be activated relatively more compared with GM and SOL. Yet, as we did not measure contraction velocity of the GL or SOL nor the muscle fiber type distributions within our subjects, these explanations remain theoretical. Future research measuring optimal fascicle lengths and muscle fascicle contraction velocities of all individual triceps surae muscle and/or collecting data on the inter- and intrasubject variability in triceps surae muscle fiber type distribution can further elaborate on why coordination patterns within this synergistic muscle may be altered.

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In this study, we aimed to only change the contraction velocity of the triceps surae muscles while keeping other factors associated with muscle metabolic rate, such as muscle fascicle length (36), constant. However, altering a muscle's contraction velocity is inherently linked to changes in muscle fascicle lengths and, although we designed our experiment to minimize differences in muscle fascicle lengths across conditions, differences in fascicle lengths at the start and end of active torque production may have influenced our results. Furthermore, to determine GM muscle fascicle work, we assumed that the force contribution of each muscle is linearly related to its physiological cross-sectional area. As the GL was preferentially recruited during fast trials, this might not be true. It is hard to determine whether a change in relative muscle activity also translates to a change in relative muscle force as muscle force is also determined by operating length, velocity, and pennation angle. If the relative contribution of the GM decreased at higher ankle angular velocities, in line with the decreased relative activation, this would imply that we slightly overestimated the increase in GM muscle mechanical work with increasing ankle angular velocity. However, with increasing ankle angular velocity from zero (isometric condition) to 60°/s, we observed a ~3.5-fold increase in positive GM fascicle work that greatly exceeds the potential change in GM force due to a shift in force distribution. Therefore, we believe that conclusions regarding fascicle work were not sensitive to the underlying assumptions about force sharing. In addition, we found a reduction in postexercise MVC compared with pre-exercise MVC, which suggests that there may be some fatigue (Supplemental Fig. S2). However, given the relatively small reduction (−5.5% on average) and the randomized counterbalanced order of trials, we believe that fatigue did not influence our conclusions. Finally, we report ankle plantar flexor torque as a proxy for triceps surae muscle forces. Obviously, when considering the metabolic rate of a muscle, muscle force rather than ankle torque is of interest. The main reason why we only report ankle torques and not (GM) muscle fascicle forces is due to the limited number of cycles for which we collected GM muscle fascicle kinematics (7–10 cycles compared with ~300 for ankle torque production), necessary to obtain pennation angles, and the fact that we did not collect whole body metabolic rate during these contractions. Yet, when using the GM muscle fascicle kinematic data, it was clear that muscle fascicle force closely followed ankle torque production. Moreover, we estimated mean and peak Achilles tendon force and—just like ankle torque—forces were similar across ankle angular velocity conditions.

Translating our results to locomotion (e.g., walking and running), we suggest that fine-tuned triceps surae muscle-tendon interaction is important to aid with minimizing whole body metabolic rate. During the stance phase of locomotion, several muscle-tendon units undergo stretch-shortening cycles. However, dynamic ultrasound studies have clearly demonstrated that the triceps surae muscles shorten (i.e., contract concentrically) throughout the stance of locomotion, especially during running, and the length changes are primarily covered by the in-series connected elastic tissue (14, 50–53). Although peak ankle angular velocity in walking [130°/s–330°/s (54)] and running [320 –800°/s (55, 56)] are substantially greater than the ankle angular velocity conditions in this study, mean GM muscle fascicle contraction velocities during stance appear comparable [−25 to −35 mm/s in walking (57) and −40 to −72 mm/s in running (14, 53)]. Theoretically, an optimal muscle-tendon interaction, including adequate stiffness of the in-series connected tissue, could facilitate little to no triceps surae muscle mechanical work. Increasing triceps surae in series connected elastic tissue stiffness through strength training for example, is reported to reduce whole body metabolic rate during running (58, 59) and recently Bohm et al. (59) have related the reduced whole body metabolic rate to reduced SOL shortening velocity during the propulsion phase. In general, our results provide evidence that triceps surae muscle contraction velocity can affect whole body metabolic rate and therefore highlight the importance of a fine-tuned muscle-tendon interaction, allowing for slow concentric contractions, or—ideally—isometric contractions, for energy-efficient locomotion.

DATA AVAILABILITY

The data that support this study are available at https://doi.org/10.6084/m9.figshare.21221912.

SUPPLEMENTAL DATA

Supplemental Fig. S1: https://doi.org/10.6084/m9.figshare.21222236.

Supplemental Fig. S2: https://doi.org/10.6084/m9.figshare.21222242.

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DISCLOSURES

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

AUTHOR CONTRIBUTIONS

W.S., W.H., F.D.G., and B.V. conceived and designed research; W.S. performed experiments; W.S. analyzed data; W.S. and B.V. interpreted results of experiments; W.S. prepared figures; W.S. drafted manuscript; W.S., W.H., F.D.G., and B.V. edited and revised manuscript; W.S., W.H., F.D.G., and B.V. approved final version of manuscript.

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