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RESEARCH ARTICLE

Habitual foot strike pattern does not affect simulated triceps surae muscle metabolic energy consumption during running

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ABSTRACT

Foot strike pattern affects ankle joint work and triceps surae muscle–tendon dynamics during running. Whether these changes in muscle–tendon dynamics also affect triceps surae muscle energy consumption is still unknown. In addition, as the triceps surae muscle accounts for a substantial amount of the whole-body metabolic energy consumption, changes in triceps surae energy consumption may affect whole-body metabolic energy consumption. However, direct measurements of muscle metabolic energy consumption during dynamic movements is difficult. Model-based approaches can be used to estimate individual muscle and whole-body metabolic energy consumption based on Hill type muscle models. In this study, we use an integrated experimental and dynamic optimization approach to compute muscle states (muscle forces, lengths, velocities, excitations and activations) of 10 habitual midfoot/forefoot striking and nine habitual rearfoot striking runners while running at 10 and 14 km h^{-1}. The Achilles tendon stiffness of the musculoskeletal model was adapted to fit experimental ultrasound data of the gastrocnemius medialis muscle during ground contact. Next, we calculated triceps surae muscle and whole-body metabolic energy consumption using four different metabolic energy models provided in the literature. Neither triceps surae metabolic energy consumption ($P>0.35$) nor whole-body metabolic energy consumption ($P>0.14$) was different between foot strike patterns, regardless of the energy model used or running speed tested. Our results provide new evidence that midfoot/forefoot and rearfoot strike patterns are metabolically equivalent.

KEY WORDS: Dynamic optimization, Forefoot strike, Gastrocnemius medialis, Rearfoot strike, Soleus, Ultrasound

INTRODUCTION

The metabolic energy consumed during submaximal running, often referred to as running economy, is an important factor determining endurance running performance (Jones and Carter, 2000). Reduced energy consumption corresponds to improved running economy and hence superior endurance performance (Hoogkamer et al., 2016; Kipp et al., 2019). As such, researchers try to identify running patterns with minimal metabolic energy consumption (Moore, 2016). One aspect of people's running pattern is foot strike pattern. Although foot strike pattern is a continuum, generally three different foot strike patterns are considered: forefoot strike, midfoot strike and rearfoot strike (Cavanagh and Lafortune, 1980).

Although rearfoot striking is the most common running pattern during shod running (Hasegawa et al., 2007; Kasmer et al., 2013; Larson et al., 2011), there seems to be a widespread belief that forefoot striking is more economical than rearfoot striking. This belief is based upon evidence that a greater percentage of midfoot/forefoot strikers appear among the first finishers in long-distance races (de Almeida et al., 2015; Hasegawa et al., 2007), suggesting forefoot striking to be more economical. However, studies comparing metabolic energy consumption between habitual forefoot and habitual rearfoot strikers found no difference in whole-body metabolic energy consumption (Gruber et al., 2013) or even lower energy consumption in rearfoot strikers compared with their forefoot striking colleagues at 11 and 13 km h^{-1} but not at 15 km h^{-1} (Ogueta-Alday et al., 2014).

Available analyses of the kinetic and kinematic differences between foot strike patterns do not clearly provide evidence for either differences in or unchanged energy consumption with foot strike patterns. Differences in foot strike patterns induce changes in negative ankle work, with forefoot striking demonstrating greater negative ankle work (Stearne et al., 2014). This ankle work is predominantly absorbed by the muscle–tendon unit (MTU) spanning the ankle joint, i.e. triceps surae muscle and the in-series connected tendinous tissue (series elastic element). Hence, differences in ankle work may affect the MTU and subsequently the energy consumption of this triceps surae muscle. We recently demonstrated that during early stance, one of the triceps surae muscles, the gastrocnemius medialis (GM), produces greater muscle force at lower contraction velocity in midfoot/forefoot strikers compared with rearfoot strikers. Higher muscle force production suggests more muscle activation and thus higher metabolic energy consumption, whereas lower contraction velocities appear to be more force efficient and would therefore reduce muscle activation and thus metabolic energy consumption (Hill, 1922; van der Zee et al., 2019). Hence, we hypothesized that the differences in metabolic energy consumption would counteract each other and no difference in GM metabolic energy consumption would exist (Swinnen et al., 2019). Although it is still unknown whether foot strike pattern induces differences in gastrocnemius lateralis (GL) and soleus (SOL), the other two triceps surae muscles, previous research estimated that the triceps surae accounts for 25 to 40% of the whole-body metabolic energy consumption (Fletcher and MacIntosh, 2017). Consequently, if triceps surae muscle metabolic energy consumption is similar between foot strike patterns, we would expect no differences in whole-body metabolic energy consumption between foot strike patterns either.

Model-based approaches have been used to estimate individual muscle and whole-body metabolic energy consumption based on Hill type muscle models (Bhargava et al., 2004; Miller, 2014; Uchida et al., 2016; Umberger, 2010; Umberger et al., 2003).

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> **List of symbols and abbreviations**
> $\dot{E}$ metabolic energy consumption rate
> EMG   electromyography
> FF   midfoot/forefoot strike
> GL   gastrocnemius lateralis
> GM   gastrocnemius medialis
> $\dot{H}_{A}$ activation heat rate
> $\dot{H}_{M}$ maintenance heat rate
> $\dot{H}_{SL}$ shortening/lengthening heat rate
> MTU   muscle–tendon unit
> RF   rearfoot strike
> SOL   soleus
> $\dot{W}$ mechanical work rate

However, to obtain reliable simulation results, a close match between simulated and experimental data is essential. Here, we used experimental dynamics ultrasound data from the GM to improve our dynamic optimization and, as such, ensure more reliable estimations of muscle metabolic energy consumption. We used four different metabolic energy models (Bhargava et al., 2004; Uchida et al., 2016; Umberger, 2010; Umberger et al., 2003) to calculate triceps surae muscle and whole-body metabolic energy consumption of habitual midfoot/forefoot and rearfoot strikers running at 10 and 14 km h^{-1}. We hypothesized that neither triceps surae nor whole-body metabolic energy consumption would be different between foot strike patterns. A secondary aim was to assess whether these findings are robust to the metabolic energy models used.

MATERIALS AND METHODS
Participants
Ten habitual midfoot/forefoot strikers (6 males, 4 females) and nine habitual rearfoot strikers (6 males, 3 females) participated in this study (Table 1). All participants were regular runners with at least 2 years running experience, running 30 km week^{-1} or more and were able to run 10 km within 45 min. They did not have any Achilles tendon or calf injuries in the last 6 months and had no prior Achilles tendon surgery. Written informed consent, approved by the local ethical committee (Medical Ethical Committee of UZ Leuven), was obtained at the start of the experiment.

Experimental procedure
The experimental procedures have been described in detail in our earlier publication on gastrocnemius medialis muscle–tendon interaction and muscle force production in this group of runners (Swinnen et al., 2019). Briefly, after a 10 min warm-up, participants ran 5 min on a force measuring treadmill (Motekforce Link, Amsterdam, The Netherlands): 2.5 min at 10 and 14 km h^{-1}, in randomized order. We collected kinetic, kinematic, muscle activation and ultrasound data of at least four strides during the last minute of each running speed. All measurements were synchronized through a trigger pulse signal sent from the ultrasound device.

Table 1. Participant demographics

	Forefoot strikers	Rearfoot strikers
Body mass (kg)	65.2±7.7	72.7±12.5
Body height (m)	1.78±0.07	1.81±0.08
Training volume (km week^{-1})	53±23	49±15

All data are expressed as means±s.d. There were no significant differences between groups.

Kinetics, kinematic and foot strike angle
Thirteen infrared cameras (Vicon, Oxford Metrics, UK) captured the motion of an extended plug-in-gait marker set (47 reflective markers; Fig. S1) at a sampling frequency of 150 Hz. We used OpenSim 3.3 (OpenSim, Stanford, CA, USA) to first scale the Hamner musculoskeletal model based on the subject's dimensions (Hamner et al., 2010) and to subsequently compute joint kinematics using a Kalman smoothing algorithm (De Groote et al., 2008). MTU lengths were calculated using OpenSim's Muscle Analysis Tool.

Ground reaction force data, sampled at 900 Hz, were first low-pass filtered with a cut-off frequency of 20 Hz and used to determine ground contact phase adopting a 30 N threshold. We determined foot strike angle using a marker-based method (Altman and Davis, 2012). At initial ground contact, we drew a line through the first metatarsal–phalangeal joint marker and heel marker of the left foot. The angle between this line and the ground was calculated and considered as the foot strike angle. Following Altman and Davis (2012), runners with a foot strike angle greater than 8 deg were considered rearfoot strikers, while runners with a foot strike angle under 8 deg were considered midfoot/forefoot strikers. Foot strike angle was averaged over the strides used for ultrasound analysis. Foot strike type (rearfoot or midfoot/forefoot) was consistent within subjects across running speeds.

We calculated joint torques using OpenSim's Inverse Dynamics Tool based on joint kinematics and ground reaction forces. Joint torques were low-pass filtered using a recursive fourth-order Butterworth filter with a cut-off frequency of 20 Hz.

Dynamic ultrasound imaging
We collected dynamic ultrasound images of the GM muscle fascicles of the left leg with a B-mode ultrasound system (Telemed Echoblaster 128 CEXT system) sampling at 86 Hz. The linear transducer (UAB Telemed, Vilnius, Lithuania, LV 7.5/60/128Z-2) was placed on the mid-belly of the muscle, aligned with the muscle fascicles and attached to the calf with tape and bandages. To analyze the GM muscle fascicle lengths and pennation angles, we used a semi-automatic tracking algorithm (Farris and Lichtwark, 2016). We analyzed at least four strides and calculated fascicle length changes relative to fascicle length at toe-off. All data were splined to 100 data points per ground contact, starting at initial contact.

Muscle activity
We used surface electromyography (EMG) to determine GM and SOL muscle activity of the right leg through a wireless EMG acquisition system (ZeroWire EMG Aurion, Milano, Italy) measuring at 900 Hz. EMG signals were first band-pass filtered (20-400 Hz), rectified and low-pass filtered (20 Hz). For each subject and muscle, EMG waveforms were normalized to maximal activation, determined as the maximal activation of each muscle using a moving average over 10 data points. Owing to technical issues, the EMG data of the GM of one participant (midfoot/forefoot striker) and the SOL of three participants (two midfoot/forefoot strikers and one rearfoot striker) could not be used.

Comparison between experimental EMG and simulated activation of the GM and SOL demonstrated similar trends, yet owing to our optimization criteria (minimization of muscle activation squared), pre-activation is not predicted (Fig. S2).

Estimating muscle and whole-body metabolic energy consumption
Several models for estimating muscle metabolic energy rate have been proposed, and it is still unclear which model yields the most

valid results. Therefore, we used multiple models primarily to assure that our results are independent from the metabolic energy model used. Our goal was not to compare the different energy models as we do not have experimental data of whole-body metabolic energy consumption for comparison (for comparison between metabolic energy models, see Miller, 2014 and Koelewijn et al., 2019). All models required the muscle states (i.e. muscle activations, excitations, lengths, velocities and forces) as inputs. To obtain these muscle states, we solved the muscle redundancy problem using a dynamic optimization algorithm that takes into account muscle–tendon dynamics (i.e. muscle activation and contraction dynamics) of the 43 lower limb muscles of the left leg in our model (De Groote et al., 2009, 2016). Individual muscle moment arms, MTU lengths and muscle properties were extracted from the scaled OpenSim model and were input to the muscle redundancy solver. We scaled maximal isometric muscle force based on the subject's body mass and height (Handsfield et al., 2014). To avoid maximal muscle activations and unrealistically high reserve actuator forces, muscle forces were multiplied by 3 for all participants. The triceps surae muscles, containing the GM, GL and SOL, were modeled as three separate MTUs, with the tendon representing the Achilles tendon. To ensure a close match between experimental GM muscle fascicle length changes and simulated GM muscle fascicle lengths, we adjusted the normalized tendon stiffness, a scaling factor to calculate GM, GL and SOL tendon stiffness based on the ratio between maximal isometric force and tendon slack length, to a value of 5 for all participants. As such,

neither average contraction velocity ($P>0.24$) nor contraction range during ground contact ($P>0.19$) of our simulated GM muscle fascicle length changes were different from our experimental muscle fascicle length changes (Fig. 1). Gerus et al. (2015) previously stated that the Achilles tendon is more compliant than the generic tendon stiffness as described by Zajac (1989). We tested multiple other values (ranging from 4 to 35), where 5 gave the best match. The normalized stiffness for all other muscles was kept to the default value of 35. Joint torques served as inputs to solve the muscle redundancy problem by minimizing the squared muscle activation. We solved the dynamic optimization problem through direct collocation using GPOP-II software (Patterson and Rao, 2014). Subsequently, the resulting nonlinear equations were solved using ipopt (Wächter and Biegler, 2006). In nine out of the 154 ground contacts analysed, the optimization algorithm failed to find an optimal solution; these strides were excluded.

Next, the simulated muscle states were used as input in four models to estimate muscle metabolic energy rate $\dot{E}$ that are consistent with Hill-based muscle dynamics: Umberger et al. (2003), Bhargava et al. (2004), Umberger (2010) and Uchida et al. (2016). All of these models had the same general form to calculate energy expenditure:

$$\dot{E} = \dot{H}_A + \dot{H}_M + \dot{H}_{SL} + c\dot{W}, \qquad (1)$$

where $\dot{H}_A$, $\dot{H}_M$ and $\dot{H}_{SL}$ are the heat production rates of the muscles for activation, maintenance and shortening/lengthening,
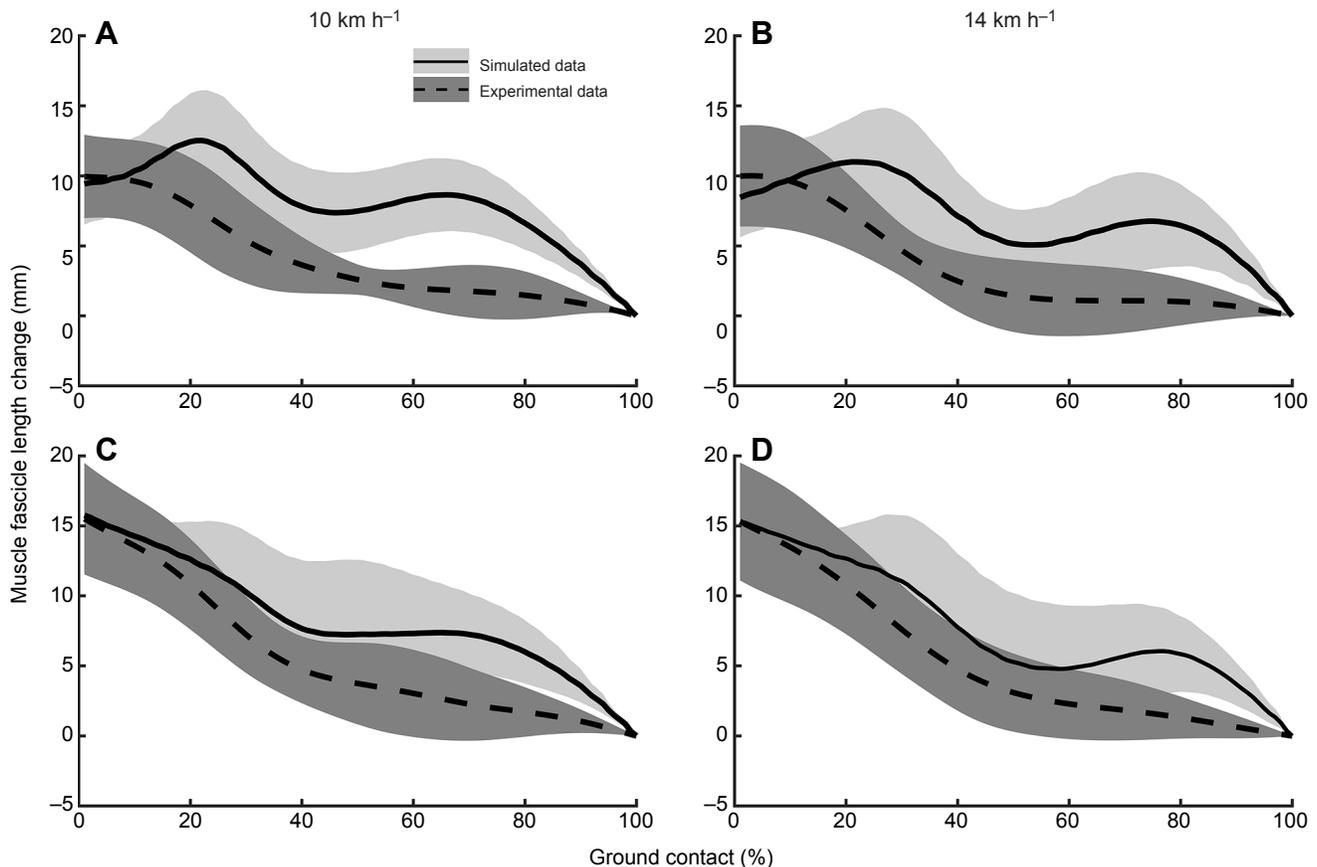

Fig. 1. Simulated (solid) and experimental (dashed) gastrocnemius medialis muscle fascicle length changes during ground contact. Data are for midfoot/forefoot strikers (A,B; n=10) and rearfoot strikers (C,D; n=9) at 10 km h^{-1} (A,C) and 14 km h^{-1} (B,D). Muscle fascicle length changes are normalized to muscle fascicle length at toe-off. Shaded area represents standard deviation.

respectively, $\dot{W}$ is the muscle mechanical work rate where concentric work is defined positively, and c is a weighting factor depending on the type of work (concentric or eccentric). The major differences between the models are how they treat eccentric muscle work and how they weigh muscle lengthening heat rate. In Umberger et al. (2003) and Uchida et al. (2016), negative mechanical work (i.e. metabolic energy generation) is incorporated, whereas Bhargava et al. (2004) and Umberger (2010) are restricted to positive mechanical work only, negative mechanical work is excluded and the lengthening heat rate coefficient is adapted. Apart from these differences, the heat rate calculations have similar terms between the models, though the scaling factors used are different. Activation and maintenance heat rates are generally defined by muscle mass/force, length and fiber type composition whereas shortening/lengthening heat rate depends on muscle contraction velocity. Umberger et al. (2003), Umberger (2010) and Uchida et al. (2016) scale these heat rates by muscle activation, whereas Bhargava et al. (2004) does not. We refer to the specific papers for more detailed information on the models.

Muscle metabolic energy rate was integrated over time to obtain metabolic energy consumption during one stance phase, which was then multiplied by 2 to account for both legs, and multiplied by the stride frequency to obtain metabolic energy rate in Watts. The metabolic energy consumed by the triceps surae muscles was normalized to their respective muscle mass. We computed whole-body metabolic energy expenditure as the sum of metabolic energy consumed by all 43 muscles included in the model and added a basal rate of 1.2 W kg^{-1} (Waters and Mulroy, 1999). Whole-body metabolic energy consumption was normalized to body mass.

Statistics
All data are presented as means±s.d. We categorized our data into four groups: midfoot/forefoot strike at 10 km h^{-1} (FF10), midfoot/forefoot strike at 14 km h^{-1} (FF14), rearfoot strike at 10 km h^{-1} (RF10) and rearfoot strike at 14 km h^{-1} (RF14). First, normality was checked with the Shapiro–Wilk test. If data from all groups followed a normal distribution, a mixed ANOVA was used to determine interaction and main effects (foot strike pattern and running speed) using SPSS v.24 (IBM SPSS, Armonk, New York, NY, USA). Yet, if not all the data in the groups followed a normal distribution, the non-parametric Mann–Whitney U-test was performed to compare foot strike pattern differences at 10 and 14 km h^{-1} separately. To determine the effect of running speed for these datasets, the data were first grouped according to running speed and again checked upon normality. If both datasets were then normally distributed, a paired t-test was performed; if not, we performed a Wilcoxon signed-rank test. Statistical significance was considered when $P<0.05$.

RESULTS
Although mean foot strike angle was more than 15 deg different between both foot strike groups ($P<0.01$; Table 2), triceps surae metabolic energy consumption was not different between foot strike patterns, regardless of speed or metabolic energy model ($P>0.35$; Fig. 2). Moreover, metabolic energy consumed by the individual triceps surae muscles, i.e. GM, GL and SOL, was not different between foot strike patterns ($P>0.10$) regardless of the model used or running speed. Furthermore, estimated whole-body metabolic energy consumption was not different between foot strike patterns regardless of the model or running speed tested ($P>0.14$; Fig. 3). As one would expect, running faster resulted in greater metabolic energy consumption in the triceps surae muscle group ($P<0.01$) as

Table 2. Comparison between midfoot/forefoot and rearfoot strikers and between 10 and 14 km h^{-1}

	Model	Speed (km h^{-1})	Forefoot strikers	Rearfoot strikers
Foot strike angle (deg)[a]	–	10	−0.4±4.4	14.8±3.7
		14	0.3±5.3	17.2±5.4
Ratio (%) ($\dot{E}_{TS}/\dot{E}_{WB}$)	Umberger et al. (2003)[c]	10	26±4	22±8
		14	25±3	25±8
	Bhargava et al. (2004)[b]	10	26±3	27±6
		14	23±4	26±6
	Umberger (2010)[b]	10	27±4	28±9
		14	28±5	32±10
	Uchida et al. (2016)[c]	10	27±4	23±8
		14	26±3	26±9

All data are expressed as means±s.d. $\dot{E}_{TS}$, triceps surae energy expenditure; $\dot{E}_{WB}$, whole-body energy expenditure.
[a]Significant main foot strike effect.
[b]Significant running speed effect.
[c]Significant interaction effect.

well as in all three triceps surae muscles individually ($P<0.02$). Also, whole-body metabolic energy consumption was greater when running at 14 km h^{-1} compared with 10 km h^{-1} ($P<0.01$).

The ratio of metabolic energy consumed by the triceps surae relative to whole-body metabolic energy consumption ranged between 22 and 32% across foot strike patterns and running speeds but was not different between foot strike patterns ($P>0.19$). In contrast, the different models revealed inconsistent results when the effect of speed on this ratio was considered. While Umberger et al. (2003) and Uchida et al. (2016) did not show significant differences in this ratio between running speeds ($P>0.07$), Umberger (2010) showed a significant greater ratio at 14 km h^{-1} compared with 10 km h^{-1} ($P=0.01$), whereas Bhargava et al. (2004) showed a significant smaller ratio at 14 km h^{-1} than at 10 km h^{-1} ($P=0.02$).

DISCUSSION
This study investigated the effect of habitual foot strike pattern on simulated triceps surae muscle and whole-body metabolic energy consumption. We used a dynamic optimization approach in which the Achilles tendon stiffness of the musculoskeletal model was adapted to better match experimental GM ultrasound data (Fig. 1). Four different metabolic energy models were incorporated to ensure model independency. In line with our hypothesis, none of the individual triceps surae muscles, nor whole-body metabolic energy consumption, demonstrated significant differences between midfoot/forefoot strikers and rearfoot strikers (Figs 2 and 3). Faster running increased both simulated triceps surae muscle and whole-body metabolic energy consumption. These findings were independent of the metabolic energy model used.

Our results provide additional scientific evidence that midfoot/forefoot and rearfoot strike patterns are energetically equivalent. We recently showed that GM muscle force production is greater while muscle contraction velocity is smaller in midfoot/forefoot strikers compared with rearfoot strikers, especially during early ground contact (Swinnen et al., 2019). Here, we provide further evidence that the greater muscle forces in midfoot/forefoot strikers are more economically produced owing to the lower muscle contraction velocities, and hence no difference in GM, GL or SOL metabolic energy consumption between foot strike patterns exist. Moreover, previous experimental research already demonstrated that differences in whole-body metabolic energy consumption between foot strike patterns are small (Ogueta-Alday et al., 2014)
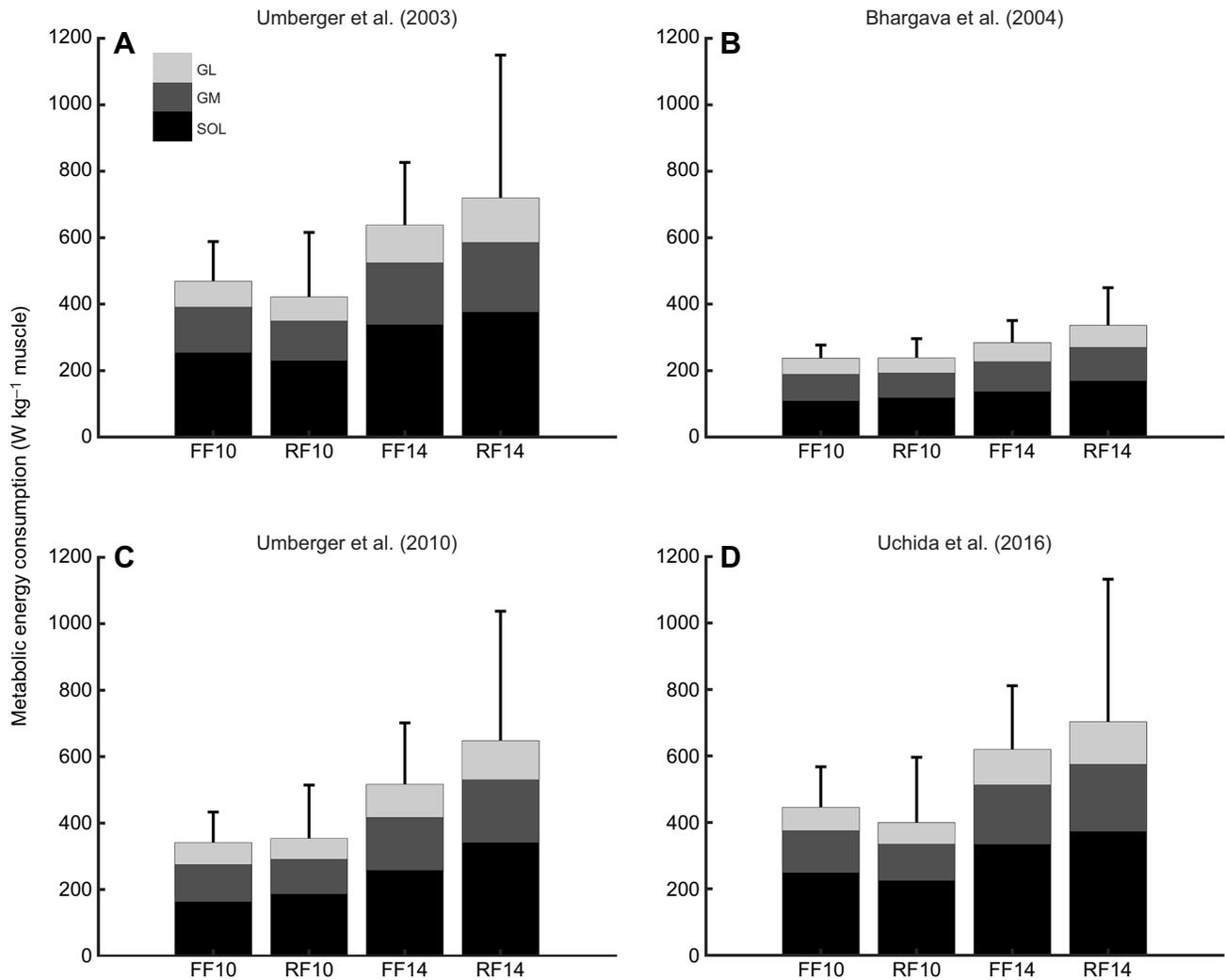
Fig. 2. Triceps surae metabolic energy consumption including individual muscles: soleus (SOL; black), gastrocnemius medialis (GM; dark grey) and gastrocnemius lateralis (GL; light grey) in midfoot/forefoot strikers (FF, $n=10$) and rearfoot strikers (RF, $n=9$) at 10 and 14 km h^{-1}. The following models were used: (A) Umberger et al. (2003), (B) Bhargava et al. (2004), (C) Umberger (2010) and (D) Uchida et al. (2016). Mixed ANOVA or Mann–Whitney U-test demonstrated no significant difference in metabolic energy consumed between foot strike patterns, individual triceps surae muscles ($P>0.10$) or all three muscles together ($P>0.35$). Mixed ANOVA, paired t-test or Wilcoxon signed-rank test demonstrated significant greater energy consumption at 14 km h^{-1} compared with 10 km h^{-1} ($P<0.01$).

or even non-existent (Cunningham et al., 2010; Gruber et al., 2013; Lussiana et al., 2017; Perl et al., 2012). Studies investigating the effect of gait retraining from rearfoot to forefoot strike running did not find an effect on the metabolic energy consumption during running when enough training sessions (eight or more) were offered (Ekizos et al., 2018; Roper et al., 2017). However, when only two training sessions were provided, an initial increase in metabolic cost was reported (Ekizos et al., 2018), indicating the need for habituation. Although it remains possible that more training sessions may further reduce metabolic cost once switched, in general, switching foot strike pattern seems to be ineffective from a performance point of view.

The contribution of the triceps surae to the whole-body metabolic energy rate (i.e. ratio) was also not different between foot strike patterns. However, the effect of running speed was less clear. Two models [Umberger et al. (2003) and Uchida et al. (2016)] did not find a speed effect, whereas Umberger (2010) and Bhargava et al. (2004) did find a speed effect, but in opposing directions. With faster running, the relative contribution of joint power/work during

ground contact seems to gradually shift more towards proximal joints (i.e. hip), especially at running speeds closer to sprinting (Schache et al., 2015). Hence, if a shift in muscle metabolic energy consumption had occurred, a shift in the same direction as joint power would have been expected, implying a decreased relative contribution of the triceps surae with increasing running speed. However, the difference in running speeds tested in this study was small and our fastest speed did not approach sprinting. Therefore, to better understand the effect of running speed on the distribution of muscle metabolic energy consumption across lower extremity muscles, a wider range of running speeds should be investigated. Moreover, by testing a wider range of running speeds, one could also examine whether triceps surae metabolic energy consumption between foot strike patterns remains similar outside our tested range of running speeds. Faster running speeds would be an especially interesting future direction, as with faster running, more people tend to midfoot/forefoot strike (Breine et al., 2014).

Dynamic optimization allowed us to account for muscle–tendon interactions when estimating muscle states. A good match between
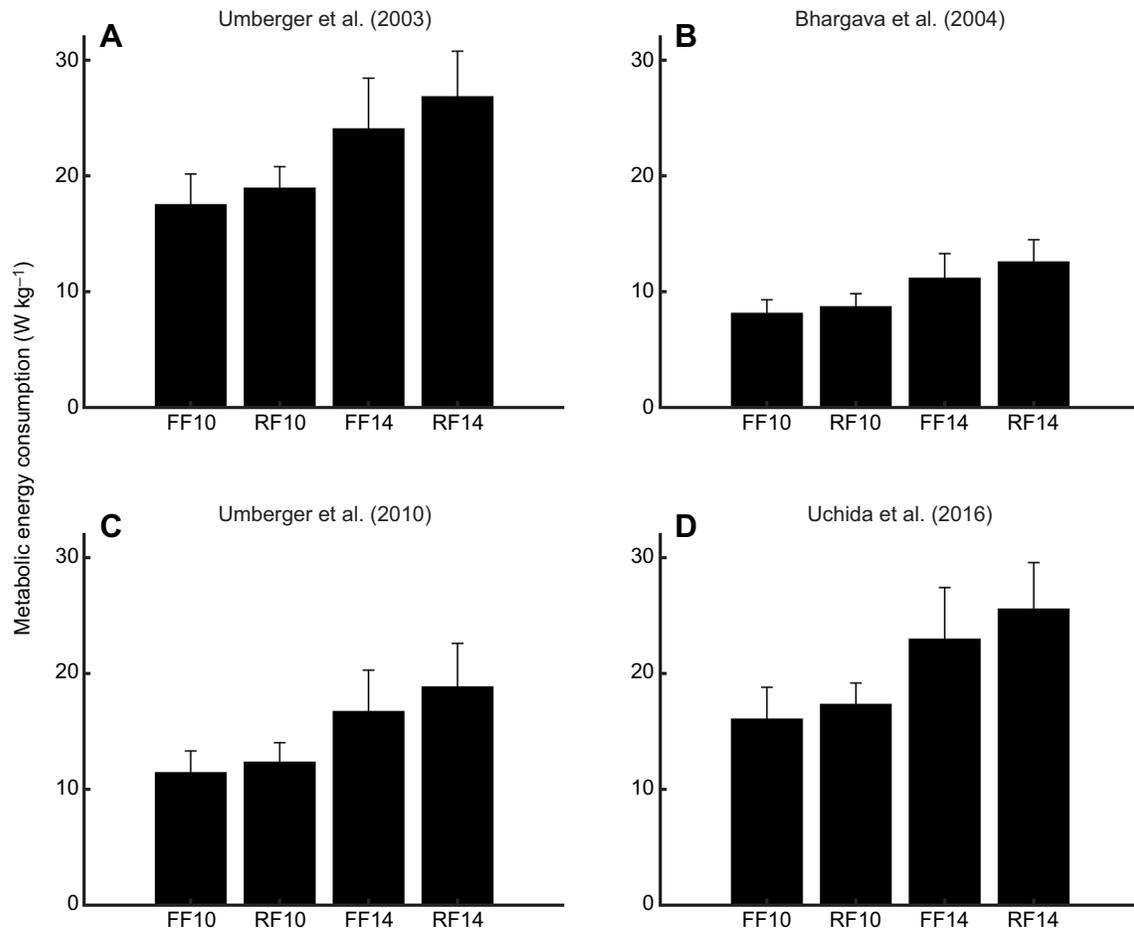
Fig. 3. Estimated whole-body metabolic energy consumption for all four metabolic energy models used for midfoot/forefoot strikers at 10 km h^{-1} (FF10) and 14 km h^{-1} (FF14) and rearfoot strikers at 10 km h^{-1} (RF10) and 14 km h^{-1} (RF14). The following models were used: (A) Umberger et al. (2003), (B) Bhargava et al. (2004), (C) Umberger (2010) and (D) Uchida et al. (2016). Mixed ANOVA or Mann–Whitney U-test demonstrated no significant difference between foot strike patterns (P>0.14). Mixed ANOVA, paired t-test or Wilcoxon signed-rank test demonstrated a significant increase in energy consumption when running at 14 km h^{-1} compared with 10 km h^{-1}.

experimental and predicted muscle states is crucial for good estimations of muscle metabolic energy. We found that it was important to adapt Achilles tendon stiffness to obtain a close match between simulated and measured GM fiber lengths. Using a generic normalized tendon stiffness value of 35 resulted in negligible length changes of the tendinous tissues and, as a consequence, muscle fascicle length changes were no longer uncoupled from length changes of the entire MTU (Fig. S3). Nevertheless, there is ample experimental evidence that the tendinous tissue interacts with the triceps surae muscles, uncoupling the muscle fascicle length changes from the length changes of the entire MTU (Fukunaga et al., 2002; Lai et al., 2015; Lichtwark and Wilson, 2008), allowing the muscle fascicles to contract at much slower – more force-efficient – velocities, implying lower metabolic energy consumption (Hill, 1922; van der Zee et al., 2019). As a result, predicted triceps surae muscle metabolic energy consumption with the generic stiff tendon was on average 80% higher compared with the adapted Achilles tendon stiffness (Fig. S4). Also, estimated whole-body metabolic energy consumption was on average 23% higher compared with the adapted Achilles tendon stiffness (Fig. S5). The discrepancy between the results based on the generic and adapted tendon stiffness values illustrates the importance of a good match between computed and experimental muscle states to obtain reliable results of muscle metabolic energy consumption. Moreover, the

increased metabolic energy consumption associated with the stiff tendon emphasizes the importance of the MTU interaction on the metabolic energy consumption during running.

Although our conclusions are independent of the metabolic energy model used, the wide variability in absolute energy rates between the metabolic energy models is remarkable. Whereas Bhargava et al. (2004) and Umberger (2010) predict whole-body metabolic energy consumption rather close to that from experimental data, whole-body metabolic energy consumption predicted by Umberger et al. (2003) and Uchida et al. (2016) is almost twice as high as that experimentally observed (Batliner et al., 2018; Kipp et al., 2018). The major difference is that the Umberger et al. (2003) and Uchida et al. (2016) models neglect eccentric work whereas the Bhargava et al. (2004) and Umberger (2010) models account for eccentric work. Instead of accounting for negative work, Umberger et al. (2003) and Uchida et al. (2016) reduce the lengthening heat rate coefficient. Our results [lower energy rates with the Umberger et al. (2003) and Uchida et al. (2016) models] illustrate that the reduction of the lengthening heat rate more than offsets the exclusion of eccentric muscle work. Although we seem to have a good understanding of the energy cost of isometric and concentric muscle contractions, the energy cost during eccentric or stretch–shortening muscle contraction is more debatable. It is clear that eccentric muscle work is more efficiently produced compared

with concentric muscle work (Hill, 1960), and therefore it appears reasonable to allow eccentric muscle work and muscle lengthening to reduce the metabolic energy consumption rate of a muscle; however, a clear consensus on how to treat eccentric work is still lacking. Also, the energy cost associated with the stretch–shortening of a muscle is still controversial (Holt et al., 2014; van der Zee et al., 2019). Nevertheless, in contrast to the absolute differences, the relative increase in metabolic energy consumption based on all muscle metabolic models when running faster corresponds quite well with the experimental data. Experimental data indicate that increasing the running speed from 10 to 14 km h^{-1} would correspond with an increase in whole-body metabolic energy consumption of approximately 40 to 45% (Batliner et al., 2018; Kipp et al., 2018). The energy models predict similar increases of 40% (Umberger et al., 2003), 41% (Bhargava et al., 2004), 49% (Umberger, 2010) and 45% (Uchida et al., 2016). In summary, although metabolic energy models do a good job of predicting relative changes, absolute values are not in accordance with experimental data. Therefore, experimental muscle research on how to account for the energy cost of eccentric and stretch–shortening muscle contractions is necessary before recommendations on how to implement these contractions in metabolic energy models can be made.

Our study has some limitations. First, we did not measure Achilles tendon stiffness from our participants and assumed equal normalized Achilles tendon stiffness for all subjects. Kubo et al. (2015) found no difference in Achilles tendon stiffness between foot strike patterns and thus, on average, we can assume equal normalized Achilles tendon stiffness. Midfoot/forefoot strikers are reported to activate their gastrocnemii muscles earlier (Ahn et al., 2014; Swinnen et al., 2019); however, owing to our optimization criteria (i.e. minimization of muscle activation squared), pre-activation of the triceps surae muscles is not predicted. Still, our simulations demonstrate a slightly earlier triceps surae muscle activation in midfoot/forefoot strikers than rearfoot strikers (Fig. S2). Furthermore, musculoskeletal modelling simplifies human anatomy and functionality. For example, our musculoskeletal model lacks a midfoot arch, which has been shown to store and release energy and subsequently reduce the metabolic rate during running (Ker et al., 1987; Stearne et al., 2016). Model parameters describing muscle properties are often derived from cadaver studies and as such may not represent actual muscle properties in healthy men or women. We model the Achilles tendon moment arm as a function of the ankle angle; however, Rasske et al. (2017) demonstrated that Achilles tendon moment arm is also load dependent. Moreover, we only took metabolic energy expenditure during ground contact into account; according to Arellano and Kram (2014), only considering ground contact would lead to an underestimation of 7% of the net metabolic energy expenditure. We used ultrasound data to validate our simulations, and a well-known limitation of ultrasound data is that these 2D images represents a 3D muscle structure, possibly resulting in underestimation of muscle fascicle length changes when there is out of plane muscle movement. Although we seem to have equally trained runners in both groups (Table 1), we did not collect running performance metrics or whole-body metabolic energy consumption and therefore it remains possible that whole-body energy consumption or running performance was still different between our groups.

In conclusion, we demonstrated that – in contrast with the widespread belief in the running community – none of the foot strike patterns induce a reduction in metabolic energy consumption of the triceps surae muscle while running. In agreement with previous experimental research, simulated whole-body metabolic energy consumption was also similar between foot strike patterns. Hence, we conclude that none of the foot strike patterns can be associated with a superior running energetics. However, we looked into differences in metabolic rate during sub-maximal running, an important performance parameter in distance running. It should be noted that for sprinting, energy rate is not as important owing to the short distance/time.

Supplementary information
Supplementary information available online at
http://jeb.biologists.org/lookup/doi/10.1242/jeb.212449.supplemental

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