Inter-individual variability in muscle fiber type distribution affects running economy but not running gait at submaximal running speeds

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Abstract

Running economy is an important determinant of endurance running performance, yet insights into characteristics contributing to its inter-individual variability remain limited. Although slow-twitch muscle fibers are more energy-efficient than fast-twitch fibers during the (near-)isometric contractions common during submaximal running, current literature lacks a consensus on whether a relationship between muscle fiber type distribution and running economy exists. This study aims to resolve the ongoing debate by addressing potential confounding factors often overlooked in prior research, such as the effect of different running speeds, the homogeneity of investigated groups, and the potential impact of the adopted running gait. We selected two groups with predetermined distinct muscle fiber type distribution in their triceps surae muscle by measurement of carnosine via ^{1}H-MRS, one predominantly slow (ST; n = 11; carnosine z-score = -1.31) and the other predominantly fast (FT; n = 10; z-score = 0.83). Across a range of running speeds (2 – 4 m/s), we measured running economy (W/kg) through indirect calorimetry, along with running kinematics, kinetics and muscle activity of the lower limb. The ST-group exhibited, on average, 7.8% better running economy than the FT-group (p = 0.01) and this difference was consistent across speeds. Both groups demonstrated almost identical kinematics, kinetics and muscle activity patterns across submaximal running speeds. Overall, our findings indicate that distinct muscle fiber type distribution explains some of the observed variability in running economy, for which a predominance of energy-efficient slow-twitch fibers appear beneficial. In contrast, muscle fiber type distribution does not affect running gait substantially.

Introduction

Maximal oxygen uptake ($\dot{\mathrm{V}}\mathrm{O}_2\mathrm{max}$), percentage of $\dot{\mathrm{V}}\mathrm{O}_2\mathrm{max}$ at lactate threshold, and running economy are key physiological determinants of endurance running performance[1]. A lower metabolic rate at the same speed indicates a better running economy and translates to improved endurance performance[2]. Although, it has been recognized that inter-individual variations in running economy result from a complex interplay between training, metabolic, cardiorespiratory, biomechanical, and neuromuscular factors[3], a deeper understanding of how these specific factors impact running economy can facilitate the development of personalized training programs to enhance performance.

Skeletal muscles are the major energy consumers while running and, importantly, the energy consumed by these muscles is highly determined by the fiber type of the activated muscle fibers. It is well established that slow-twitch (type I) fibers are substantially more economical during isometric or low velocity contractions compared to fast-twitch (type II) muscle fibers[4–6]. While the distribution of these muscle fiber types appears highly variable among individuals[7,8], some of the most energy demanding muscles during running operate close to isometric contraction velocities[9–12]. Therefore, the prevailing theoretical consensus is that a greater proportion of slow-twitch muscle fibers is associated with more efficient ATP hydrolysis, especially during isometric contractions. Consequently, it is often suggested that individuals with greater proportions of slow-twitch muscle fibers would have a better running economy. However, a consensus on the association between muscle fiber typology and running economy is lacking. Some studies have indeed observed that a greater distribution of slow-twitch muscle fibers was correlated with better running economy[13–15]. In contrast, other studies did not find any correlation between muscle fiber type distribution and running economy[15–20], or even observed opposite correlations suggesting that larger distributions of fast muscle fibers are beneficial for running economy at some speeds[17,19,20].

This lack of consensus in literature may stem from the relative homogeneity of the populations tested and/or the speed at which running economy was assessed. Most previous studies examining the effect of muscle fiber typology on running economy were performed with endurance trained runners. A good running economy is particularly important for them and they tend to have a predominance of slow-twitch muscle fibers[7,8]. This homogeneity in muscle fiber typology, combined with the multifaceted determinants affecting running economy may have contributed to the lack of clear conclusions across studies. Additionally, running speed could potentially confound the effect of muscle fiber type distribution on running economy. Studies reporting a significant correlation between muscle fiber type distribution and running economy often assessed slower running speeds than the studies lacking such a correlation, suggesting that running speed may present a confounding effect. Moreover, Kyrölainen and colleagues (2003)[17] even reported better running economy when more fast muscle fibers were present at their fastest running speed tested (7 m/s), whereas at slower speeds no correlation was found. Similarly, Pellegrino et al. (2016)[20] found significantly better running economy with greater proportions of fast muscle fibers at their fastest speed (4.56 m/s and 1% grade) but not at slower speeds. Franch et al. (1998)[15] observed a positive correlation between the percentage of fast muscle fibers and running $\dot{V}O_2$ at their slowest speed (3.42 m/s), indicating worse running economy with greater proportion of fast fibers, but not at their faster speeds (3.72 and 4 m/s). Contrary to these findings, Hunter and colleagues (2015)[19] found a significant correlation between the proportion of fast muscle fibers and running economy at their slowest speed (2.68 m/s). Despite the broad range of running speeds previously tested, it has not been directly investigated whether an interaction effect between muscle fiber type distribution and running speed on running economy exists.

Additionally, the preferred running gait of individuals with different muscle fiber type distributions may be different, potentially offsetting differences in running economy. The faster cross-bridge cycling rate of fast fibers, primarily responsible for the higher energy rate during isometric contractions, enables higher maximal contraction velocities[4,21]. Moreover, fast fibers' maximal mechanical efficiencies are reached at higher contraction velocities[22]. As humans are remarkably good in self-optimizing their locomotion pattern[23], i.e. they adopt a gait pattern which appears close to their metabolic optimum, distinct muscle fiber type distributions may induce different running gaits between individuals. Such differences could result in altered muscle activation patterns, different spatiotemporal variables and even different joint power distributions among the lower limb joints. Despite the importance of preferred locomotion patterns for injury prevention and performance enhancement, there is no data on whether muscle fiber type distribution affects one's habitual running gait.

In this study, we aimed to assess how distinct muscle fiber type distributions, assessed by non-invasive MR spectroscopy of the gastrocnemius medialis and soleus muscle, impact running economy and running gait across a range of running speeds. We hypothesized that individuals with predominantly slow muscle fibers would demonstrate superior running economy at slower running speeds, and that this metabolic advantage would reduce at faster speeds. Additionally, we explored whether muscle fiber type distribution affects their running gait, by assessing spatiotemporal variables, joint powers and muscle activities of the lower limb.

Materials and methods

Participants. 31 physically active males were invited for a proton magnetic resonance spectroscopy scan (^{1}H-MRS) using a 3T whole-body MRI scanner (Siemens, Healthineers AG, Germany). All subjects participated voluntarily and gave written informed consent, approved by KU Leuven social and societal ethics committee (approval number: G-2021-4008). To ensure a large range in muscle fiber type distributions, running was not a prerequisite to participate in the study. While some participants ran regularly, for many, running was not their primary sport (e.g., soccer, basketball, squash, track & field sprints) with the weekly training volume for all participants ranging from 5 to 25 hours, with no significant differences between groups (Table 1). We computed each participant's muscle carnosine content of the right soleus and gastrocnemius medialis muscle using ^{1}H-MRS[24]. To estimate each participant's muscle fiber type distribution, these carnosine concentrations were converted into z-scores, based on the normal distribution of a previously collected reference dataset[25]. Participants were divided into three groups based on their z-scores, and the middle (e.g. intermediate; n = 10) group was excluded for subsequent experimental testing. Consequently, we had two groups, i.e. participants with either a low z-score (n = 11; ST-group) or a high z-score (n = 10; FT-group) with distinct muscle fiber type distributions (Table 1).

Table 1. Muscle fiber typology group characteristics

	ST-group	**FT-group**

Z-score*	-1.31 ± 0.61	+0.83 ± 0.38
Age (y)	24 ± 5	23 ± 2
Body mass (kg)	75.2 ± 7.4	74.7 ± 6.1
Body height (m)	1.82 ± 0.08	1.82 ± 0.06
Hours/week sport	12.0 ± 5.0	10.5 ± 2.9
km/week running	29 ± 23	20 ± 7
$\mathbf{\dot{V}O_2peak}\ (\boldsymbol{mL \cdot min^{-1} \cdot kg^{-1}})$	66.3 ± 7.3	62.7 ± 7.9
Speed at $\mathbf{\dot{V}O_2peak}$ (km/h)*	19.9 ± 1.2	18.5 ± 1.4
Speed at 2nd ventilatory threshold (km/h)*	16.5 ± 1.1	15.2 ± 1.2

*Indicates significant difference between muscle fiber typology groups ($p < 0.05$).

Experimental sessions. The experimental testing consisted of two sessions: a biomechanics and a metabolic session, in random order. For both sessions, participants performed running trials at five different running speeds: 2 m/s (7.2 km/h), 2.5 m/s (9.0 km/h), 3 m/s (10.8 km/h), 3.5 m/s (12.6 km/h), and 4 m/s (14.4 km/h) while running in standardized running shoes (Li Ning Marathon; heel-to-toe drop: 4 mm; mass: 200 – 265 grams depending on shoe size). During the biomechanical session we collected spatiotemporal variables, joint kinematics and kinetics, and muscle activation of the tibialis anterior, soleus, gastrocnemius medialis, gastrocnemius lateralis, vastus lateralis and vastus medialis of the right leg using surface electromyography (1000 Hz, Cometa, Italy) while running on a force measuring treadmill (1000 Hz, M-gait Motekforce Link, the Netherlands). This study was part of a larger project which also involved data collection while walking at 2 m/s[5]. After arrival in the lab the participants were prepared for the measurement session by shaving and cleaning the skin before we applied bipolar EMG electrodes onto the respective muscle bellies, and placed 28 retroreflective markers on anatomical landmarks and 12 technical cluster markers (4 on the torso, 4 on the pelvis, 5 on each thigh, 5 on each shank and 6 on each foot; 1 marker on each thigh and shank were only used for scaling purposes). After a 10-minute warm-up at self-selected speed, participants performed five 3-minute running trials with *ad libitum* rest between trials (ranging from no rest to 5 minutes rest between trials). Data was collected during the last minute of the trial for at least fifteen strides. We ordered the running trials from slow to fast to minimize the effect of fatigue (potentially elicited at the faster speeds).

In the metabolic session we determined the participant's running economy and $\dot{\mathrm{V}}\mathrm{O}_2\mathrm{peak}$. After a 10-minute warm-up, participants ran for 6-minutes at five different speeds, interspersed by 5 minutes of rest, while we collected oxygen uptake and carbon dioxide production rates (K5, Cosmed, Italy). After determining each participant's running economy, participants were allowed *ad libitum* rest (ranging from 5 to 13 minutes) before starting the $\dot{\mathrm{V}}\mathrm{O}_2\mathrm{peak}$ protocol. Here, the treadmill was set to 2.5 m/s (9 km/h) at the start and speed was increased every 1 minute with 1 km/h until exhaustion (treadmill inclination kept to zero degrees). In order to be able to reliably calculate whole-body metabolic rate from oxygen uptake rates and carbon dioxide production rates we asked our participants to refrain from caffeine (for at least 12 hours) and any caloric intake (for at least 2 hours) prior to the start of the experiment.

Running kinematics, kinetics & spatiotemporal variables. Thirteen infrared cameras (200 Hz, Vicon Oxford Metrics, UK) captured the trajectories of the 40 retroreflective markers while participants ran on the force instrumented treadmill. To compute stride frequency, ground contact time and duty factor, ground reaction forces were first low pass filtered using a fourth order Butterworth filter with a cut-off frequency of 20 Hz before applying a 50 N threshold to determine foot-ground contact.

Next, we scaled a musculoskeletal model in OpenSim[26] according to each participant's anthropometry based on their body mass and marker positions measured during a standing static trial. Raw marker data was filtered with a Woltring filter with cut-off frequency of 20 Hz before computing the joint angles and joint torques using an inverse kinematics and inverse dynamics approach, respectively. Next, we calculated joint powers in the sagittal plane by multiplying each joint torque by the joint angular velocity, determined as the time derivative of the respective joint angles. We calculated net average joint power by time-integrating joint power and dividing the computed joint work by stride time. Positive average joint power was calculated by time-integrating only the positive joint power. Lastly, relative contributions of each joint to the total positive joint power were determined by dividing joint positive power by the total positive lower limb joint power during the stride. For one participant technical issues with the motion capture cameras caused very poor marker quality and this individual (FT-group) was excluded from the kinematic/kinetics analysis. Joint powers were normalized to body mass and to visually present joint powers we resampled them to 101 datapoints per stride.

Muscle activation. Raw EMG signals were band pass filtered (20-400 Hz), full-wave rectified and low pass filtered (20 Hz). These filtered signals were subsequently normalized by the peak muscle activation obtained while running at the range of speeds (2 – 4 m/s) or when walking at 2 m/s. Mean muscle activity was computed as the area under the normalized EMG curve divided by the stride time. Due to technical issues some of the EMG data was excluded (Figure 3, Supplementary Table 1). To visually present muscle activation, data was resampled to 101 datapoints per stride.

Running energetics and $\dot{\mathrm{V}}\mathrm{O}_2\mathrm{peak}$. The oxygen uptake and carbon dioxide production rates of the last two minutes of each running trial were averaged and used as inputs into the Péronnet-Massicotte equation[27] ($whole - body\ metabolic\ rate = 16.89 * \dot{V}O_2 + 4.84 * \dot{V}CO_2$) to calculate running economy, expressed in Watts. To determine each participant's $\dot{\mathrm{V}}\mathrm{O}_2\mathrm{peak}$, we computed the maximal $\dot{\mathrm{V}}\mathrm{O}_2$ over a 30-seconds time window. Both $\dot{\mathrm{V}}\mathrm{O}_2\mathrm{peak}$ and running economy were normalized to body mass. To reliably calculate whole-body metabolic rate using indirect calorimetry, participants have to run at submaximal intensity which we verified using respiratory exchange ratio (RER). At 3.5 m/s one participant's (FT-group) and at 4 m/s seven participants' (4 FT, 3 ST) RER exceeded 1.0. These individuals' data for those speeds were excluded from the analysis. For one participant (ST-group) technical issues halfway through the measurement forced us to discard the running economy data while running at 3.5 and 4 m/s, as well as $\dot{\mathrm{V}}\mathrm{O}_2\mathrm{peak}$.

Statistics. To assess differences between groups and running speeds and to determine muscle typology group × speed interaction effects, we used linear mixed-effect models (fixed effects: muscle typology group and running speeds; random effect: participant). When we observed an interaction effect, we calculated the model-predicted estimated marginal means to detect significant differences between groups at each condition separately. If there was no interaction effect, we removed the interaction term from our linear mixed-effect model to only test for significant main effects. Additionally, we evaluated differences in $\dot{\mathrm{V}}\mathrm{O}_2\mathrm{peak}$, 2nd ventilatory threshold, and running volume between muscle typology groups using an unpaired t-test; and differences in maximal speed reached during the $\dot{\mathrm{V}}\mathrm{O}_2\mathrm{peak}$ test through a Mann-Whitney U test (data not normally distributed). R statistical software and specific packages (lmer and emmeans) were used for all analyses, and the significance level was set at 0.05. Individual data is available as supplementary material.

Results

While whole-body metabolic rate increased with increasing running speed ($p < 0.001$; Figure 1), we did not observe a muscle typology group × speed interaction effect ($p = 0.53$). However, across all speeds the ST-group was on average 7.8 % more economical than the FT-group ($p = 0.01$). The greater whole-body metabolic rate was associated with higher oxygen consumption rates ($p = 0.01$; Table 1) in the FT-group compared to the ST-group, whereas RER-values were similar ($p = 0.93$). Additionally, while $\dot{\mathrm{V}}\mathrm{O}_2\mathrm{peak}$ was not different between muscle typology groups ($p = 0.30$), the running speed reached at $\dot{\mathrm{V}}\mathrm{O}_2\mathrm{peak}$ was higher in the ST- compared to FT-group ($p = 0.03$; Table 1).

When considering the spatiotemporal variables while running, regardless of muscle fiber type distribution, step frequency increased whereas ground contact time and duty factor decreased when running faster ($p < 0.001$; Table 2). We found a significant muscle typology group × speed interaction effect ($p = 0.04$) for step frequency, but not for ground contact time ($p = 0.43$) nor duty factor ($p = 0.07$). This interaction effect demonstrates that stride frequency increased more in the FT-group compared to ST-group when running speed increased. Post hoc pairwise comparison demonstrated no significant difference in step frequency at any of the running speeds between muscle fiber type groups

($p > 0.21$). Furthermore, duty factor ($p = 0.06$) nor ground contact time were different between muscle fiber type groups ($p = 0.23$).

In general, running kinematics, lower limb joint torques and powers were remarkably similar between muscle fiber type groups (Supplementary Figures 1 and 2; Figure 2). Net average ankle and knee joint power decreased when running faster while net average hip joint power increased ($p < 0.001$; Figure 2). Average positive joint power increased for all three lower limb joints when speed was increased ($p < 0.001$; Figure 2). For average net ankle ($p < 0.001$; Figure 2B) and average positive knee joint power ($p < 0.001$; Figure 2F), we found significant muscle typology group × speed interaction effects indicating that average net ankle power decreased less and average positive knee joint power increased more in the ST- compared to the FT-group when running faster. Yet, post hoc pairwise comparison revealed no significant group difference at any of the speeds ($p > 0.14$). Also, for all other net or positive average joint powers there was no group effect ($p > 0.34$). The relative contribution of the ankle and knee to total lower limb positive power production decreased when running faster, whereas the relative contribution of the hip increased ($p < 0.001$; Figure 3). The contributions of the ankle and hip to the total positive power was similar between muscle fiber type groups ($p > 0.46$). For the contribution of the knee joint, we observed a muscle typology group × speed interaction effect ($p = 0.007$), indicating that the reduction in contribution of positive knee joint power when running faster was smaller in the ST-group. Yet, pairwise comparisons revealed no significant difference at any of the running speeds ($p > 0.29$).

Mean activation of all measured lower limb muscles increased when running faster ($p < 0.01$; Figure 4). However, only for gastrocnemius medialis mean muscle activation we observed a significant muscle typology group x speed effect with a greater increase in mean activation in the ST- compared to the FT-group with speed ($p < 0.01$; Figure 4D), but no significant difference between muscle fiber type groups at any speed ($p > 0.22$). Similarly, there was no muscle fiber type group effect for any of the other muscles ($p > 0.17$).

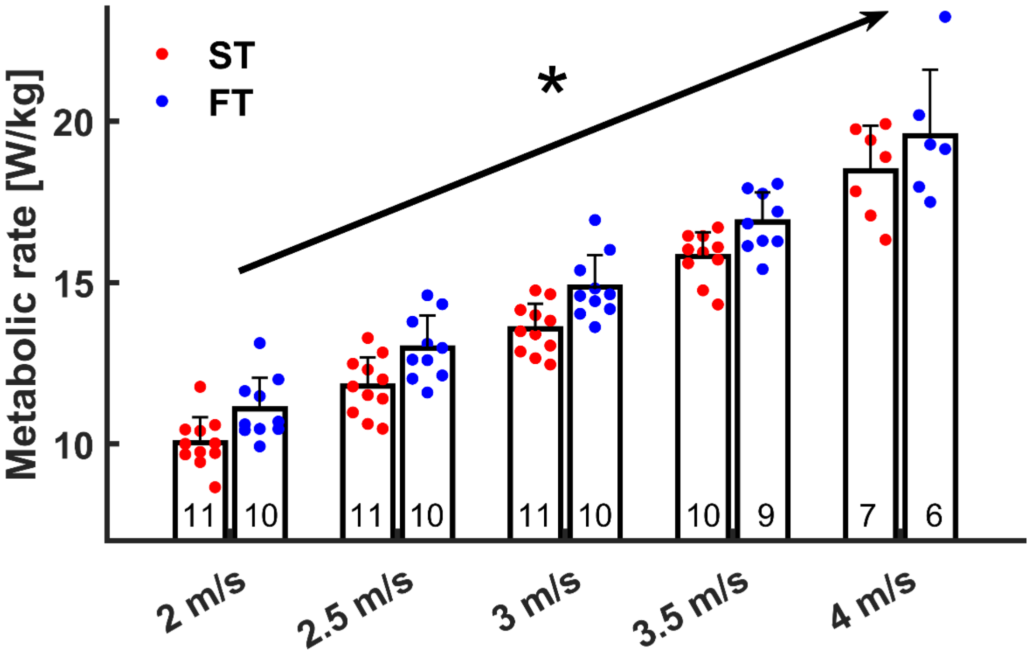

*Figure 1. Running economy, expressed as whole-body metabolic rate in Watts/kg, across a range of speeds in two groups with either a slow (Red, ST-group) or fast (Blue, FT-group) muscle fiber type distribution. Dots present the individual data with mean and standard deviation represented by the bar graphs. *indicates a significant group effect and the arrow represents a significant speed effect ($p < 0.05$). The number in the bar graphs indicate the number of participants included in the analysis.*

Table 2. Spatiotemporal variables in two groups with either a slow (ST-group) or fast (FT-group) muscle fiber type distribution across a range of speeds.

		2 m/s	**2.5 m/s**	**3 m/s**	**3.5 m/s**	**4 m/s**
Step frequency (steps/min)^{a,b}	ST	158 ± 9	159 ± 11	162 ± 11	165 ± 11	169 ± 11
	FT	153 ± 5	154 ± 6	158 ± 6	162 ± 7	168 ± 7
Ground contact time (ms)^{a}	ST	307 ± 36	274 ± 27	253 ± 22	234 ± 19	219 ± 17
	FT	291 ± 21	267 ± 19	241 ± 16	225 ± 13	210 ± 14
Duty factor (-)^{a}	ST	0.40 ± 0.04	0.36 ± 0.03	0.34 ± 0.03	0.32 ± 0.03	0.31 ± 0.03
	FT	0.37 ± 0.02	0.34 ± 0.02	0.32 ± 0.02	0.30 ± 0.02	0.29 ± 0.02

$\dot{V}O_2$ $(mL * min^{-1} * kg^{-1})$[a,c]	ST	28.4 ± 2.2	33.3 ± 2.6	38.3 ± 2.2	44.4 ± 2.4	51.6 ± 4.2
	FT	31.5 ± 2.9	36.7 ± 2.9	42.1 ± 2.9	47.3 ± 3.0	54.6 ± 5.9
RER (-)[a]	ST	0.89 ± 0.05	0.90 ± 0.05	0.90 ± 0.05	0.92 ± 0.06	0.95 ± 0.05
	FT	0.87 ± 0.07	0.90 ± 0.07	0.89 ± 0.06	0.94 ± 0.05	0.95 ± 0.04

[a] *significant speed effect ($p < 0.05$);* [b] *significant muscle typology × speed interaction effect ($p < 0.05$);* [c] *Significant group effect ($p < 0.05$).*

Discussion

We demonstrated that individuals possessing predominantly slow muscle fibers were more economical runners than individuals with predominantly fast muscle fibers at speeds ranging from 2 – 4 m/s. Contrary to our hypothesis, we did not observe an interaction effect between running speed and muscle typology group, indicating that the metabolic benefit of having a large proportion of slow-twitch fibers is independent of speed within the speed range we evaluated. Despite some interaction effects in spatiotemporal (e.g. stride frequency) and average joint powers (e.g. net ankle and positive knee) between muscle typology group and running speed, at submaximal running speeds, the running gaits adopted by both groups appear very similar.

Our findings support the notion that variations in the distribution of muscle fiber types of the soleus and gastrocnemius medialis muscles across individuals contribute to differences in running economy. Moreover, the similar running gaits and muscle activations between muscle fiber type groups suggest that the superior running economy of the ST-group is directly related to the different metabolic rates of the activated muscle fibers. The faster cross-bridge cycling rate of fast muscle fibers is fundamental to the larger maximal contraction velocity achievable by these fibers[4]. However, as every cross-bridge cycle has an energetic cost of 1 ATP, these fast fibers consume three to five times more energy during isometric contractions[4]. Importantly, dynamic ultrasound studies revealed that muscles crucial for running, i.e. triceps surae and vastus lateralis muscle, operate at relatively slow, close to isometric, contraction velocities[9–12]. Recently, we demonstrated that the net whole-body metabolic energy expenditure of performing isolated triceps surae muscle contractions at low contraction speeds was twice as high in individuals with predominantly fast compared to individuals with predominantly slow muscle fibers[5]. Based on these combined observations, we contend that the energy-efficient force production of slow fibers, operating at relatively slow speeds in these major energy-consuming muscles while running, explains the superior running economy observed in the group with a high proportion of slow muscle fibers.

We tested whether the disparity observed in previous studies could be attributed to the different running speeds tested. Our data did not reveal a significant interaction effect between running speed and muscle fiber type group for speeds between 2 and 4 m/s. This suggests that the superior running economy in the ST-group is independent of running speed. The underlying assumption for the hypothesized reduced difference in running economy at faster speeds was that increased running speed leads to faster muscle contraction velocities, thereby diminishing the metabolic advantage of slow muscle fibers. Remarkably, faster running has only a small and inconsistent effect on muscle contraction velocity. While there is some increase in triceps surae muscle contraction velocity when running faster[11,12], the vastus lateralis muscle contraction velocity seems to actually decrease[9], this therefore might explain why slow-twitch fibers remain more efficient with slight increases in speed. Consistent with our results, Bellinger and colleagues[14], using a similar non-invasive methodology to assess muscle fiber type distribution, observed that a slow muscle fiber typology was beneficial for running economy at six different speeds (85 – 110% of gas exchange threshold; 3.57 – 4.60 m/s) in well trained middle distance runners possessing a slow or intermediate (but not fast) muscle fiber typology. In contrast to our findings, Kyrölainen and colleagues[17] and Pellegrino and colleagues (2016)[20] reported positive correlations between the distribution of fast muscle fibers and running economy at their fastest speed (7 m/s and 4.56 m/s and 1% grade respectively). It is worth noting that at this speed the subjects, although well-trained runners, exhibited substantial lactate production, compromising the validity of running economy values. Additionally, the brief duration ran at the highest speed in

Kyrölainen et al.[17] (1 minute, with data collected during the last 20 seconds) further reduces the validity of these results. Nevertheless, we acknowledge that the fastest speed tested in our study was only moderately fast (4 m/s) and one should be cautious when extrapolating our results to even faster speeds. Most participants were not highly trained runners and could not sustain faster aerobic running speeds (note that 7 out of 21 subjects were already excluded from our fastest speed as their RER exceeded 1.0).

Additionally, the lack of consensus in previous studies may stem from the limited variation in muscle fiber type distributions within each study, particularly in those that found no correlation. Remarkably, in studies showing no association between muscle fiber type distribution and running economy, the average percentage of slow-twitch fibers exceeded 60% (muscle biopsy from vastus lateralis) and the number of individuals possessing less than 50% of slow-twitch fibers were small[16–18]. Muscle fibers are recruited according to the size principle[28,29], where motor neurons innervating slow muscle fibers are activated first, and only when muscle force demand is high enough, larger motor neurons activating faster muscle fibers are additionally activated. Although speculative, it is plausible that a high proportion of slow muscle fibers (i.e. >60%) may sufficiently cover the majority of muscle force demand during running at submaximal speeds. Consequently, having even larger proportions of slow muscle fibers may yield only negligible metabolic benefits. Previous research has indeed demonstrated that muscle fiber type distribution could not distinguish between good (<1050 IAAF points) and excellent (>1050 IAAF points) endurance runners[30] further suggesting that an extremely slow muscle fiber type distribution does not provide an additional benefit. While more research is needed to either confirm or refute this hypothesis, it could explain the conflicting findings in previous studies.

Although some interaction effects were observed between muscle fiber type groups and running speed, habitual running gait was not strongly affected by one’s muscle fiber typology at submaximal running speeds. Humans demonstrate a remarkable ability to self-optimize their gait pattern by instinctively adopting the most efficient locomotion pattern[23]. Despite the distinct mechanical and metabolic properties of fast and slow muscle fibers, leading to potential variations in running gaits between muscle fiber type groups, our study found that running kinematics, kinetics, and muscle activity patterns were nearly identical across these groups at submaximal running speeds. Yet, we did find a group × speed interaction effect for stride frequency. Running faster can be achieved by increasing stride frequency, taking longer strides or a combination of both. The observed interaction effect indicates that the FT-group relied more on increasing stride frequency to run faster than the ST-group. Our selected speeds were far from maximal speeds, yet, these results potentially indicate that the FT-group may demonstrate higher stride frequencies than the ST-group at speeds close to their maximum (or can attain higher maximal running speeds). However, it is important to note that some of the p-values for the spatiotemporal variables during running were close to 0.05. This suggests that we should be cautious in drawing strong conclusions, especially considering the limited number of individuals in each group. Furthermore, we found a group × speed interaction effect for average positive knee joint power and the contribution of positive knee joint power to the total lower limb positive joint power. The vastus lateralis muscle has been previously demonstrated to reduce its contraction velocity with increasing running speed[9]. At slower contraction velocities, the metabolic benefit of slow over fast muscle fibers is larger and hence the greater increase in average positive knee joint power in the ST- compared to the FT-group may present different optimal strategies to increase running speed. Alternatively, as fast fibers are more susceptible to muscle damage than slow fibers and the vastus lateralis demonstrates eccentric muscle contractions when running fast[9] the reduced positive (as well as negative) average knee joint power in the FT-group may be a protective mechanism to avoid damage of fast muscle fibers. Lastly, the relative contribution of positive hip joint power increased with running speed, but none of the muscles assessed for muscle activation crossed the hip joint, implying that difference between muscle fiber type groups could still have occurred for these muscles. Future research directly assessing muscle fiber kinematics, including muscle activation of muscles crossing the hip joint and/or investigating faster running speeds will likely provide more in-depth information.

While the difference in running volume between the ST- and FT-group did not reach statistical significance (p = 0.24; Table 1), the numerical higher running volume of the ST- compared to FT-group (29 vs. 20 km/week on average) may be considered as a potential limitation of the study. There is indeed ample scientific evidence that increasing general aerobic fitness and running in particular improves running economy[31–34], and hence one could argue that the better running economy in the ST-group may be attributed to their higher average distance ran on a weekly basis. To ensure a large spread in muscle fiber type distribution among groups, we recruited physically active individuals, yet regularly running was not a prerequisite. Analyzing the data revealed that two participants in the ST-group were well-trained runners (75 and 50 km/week, respectively). When these individuals were excluded from our analysis average running volume was almost equal between groups (21 vs. 20 km/week for the ST- and FT-group respectively), yet the significantly better running economy in the ST- compared to the FT-group persisted (p = 0.03). Additionally, while there is large variability in the relative distribution of slow and fast muscle fibers among individuals, each muscle still contains a mix of both fiber types. Moreover, the use of ^{1}H-MRS to estimate a muscle fiber type distribution non-invasively, does not directly assess the myosin heavy chain isoform typically obtained through muscle biopsies. Consequently, this method does not allow for precise quantification of muscle fiber type distribution as a percentage, complicating direct comparisons with studies using muscle biopsies. Furthermore, our assessment of muscle fiber type was limited to the two major plantar flexor muscles – the gastrocnemius medialis and soleus muscle. Although this muscle group is a major energy consumer during running, accounting for up to 32% of the total whole-body metabolic rate[35], there are many other active muscles whose fiber type distribution was not assessed. While there is some intermuscular correlation in muscle fiber type within an individual[36], we should be cautious with extrapolating the muscle fiber type distributions of one muscle to another. Our study design ensured distinct groups with predominantly slow or fast muscle fiber distributions, providing meaningful insights despite these methodological considerations. As we excluded the intermediate group, we deemed the comparison between groups as the most appropriate way to evaluate our hypothesis rather than investigating correlations. Importantly, when conducting correlations analyses, our conclusions were generally consistent with the exception that no correlation between running economy and z-score was observed at 4 m/s, which is at least partially explained by the limited sample size at this running speed. Finally, while we focused on the effect of muscle fiber typology on running economy including lower body gait biomechanics as a potential confounding factor, the mechanisms underlying running economy are multifactorial, and other factors (e.g. anthropometry[37]) could have potentially confounded our results.

In summary, our study revealed that individuals with a substantially higher proportion of slow muscle fibers exhibit better running economy than individuals with higher proportions of fast muscle fibers, within a range of submaximal running speeds (2-4 m/s). Importantly, the similarities in adopted running gait and the related muscle activations suggest that the difference in running economy between these groups is likely linked to the distinct metabolic characteristics of fast and slow muscle fibers and not to differences in running gait. Furthermore, while large variability in individual running gaits exists, it appears that muscle fiber type distribution does not drive these differences at submaximal running speeds.

Perspective

The superior running economy of individuals with a large proportion of slow muscle fibers has implications for talent detection and performance. Running economy contributes to endurance running performance[2,38] and to compete with the best in the world a runner should have exceptional running economy[39]. In this study, the ST-group was 7.8% more economical than the FT-group, a difference in running economy which is almost twice as large as the benefit of advanced footwear technology (i.e. ~4%[40]). Moreover, while $\dot{V}O_2peak$ was not significantly different between muscle fiber typology groups, the maximal speed reached during the $\dot{V}O_2peak$ test was greater in the ST- than in the FT-group highlighting the importance of a rather slow muscle fiber type distribution as one element for endurance running performance.

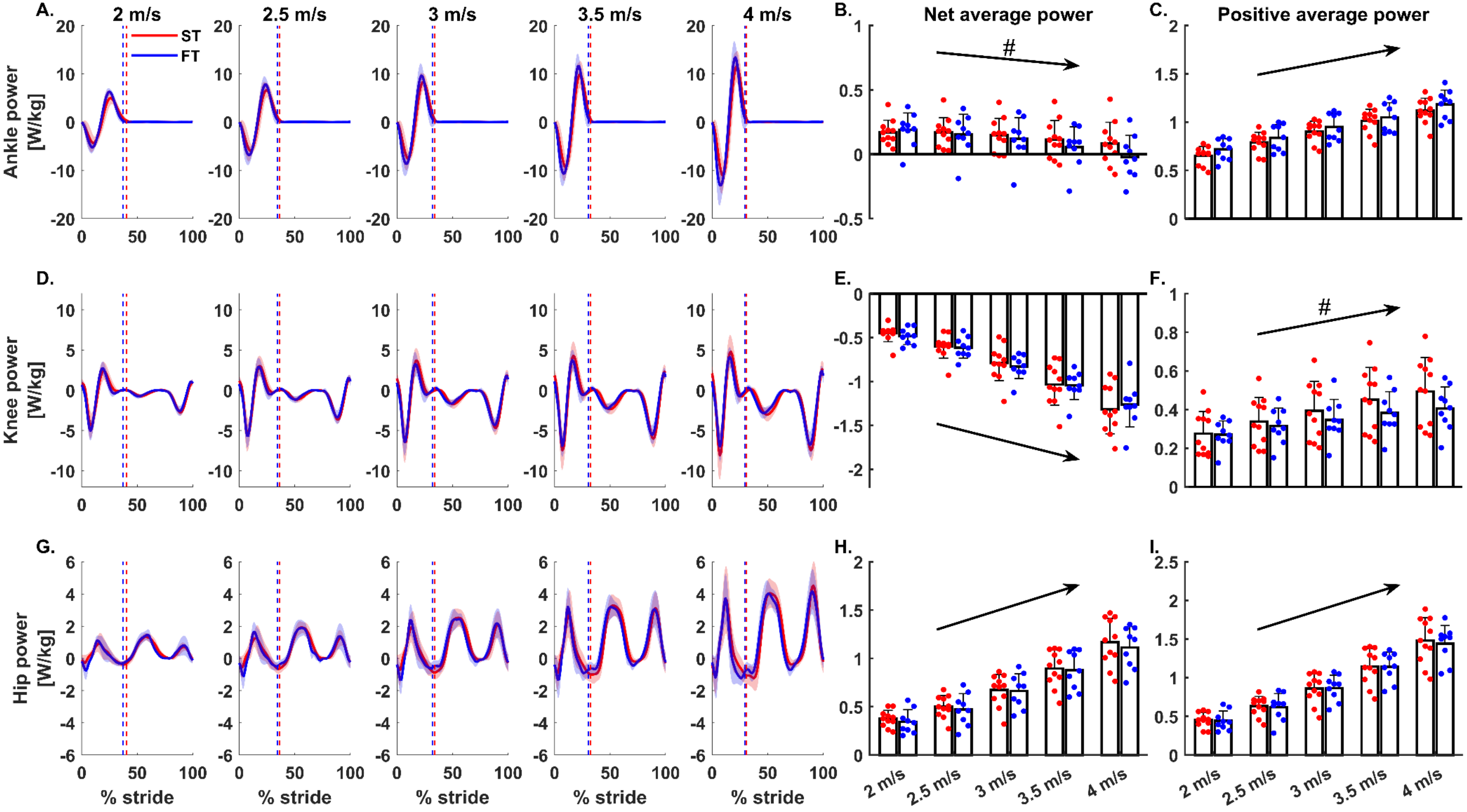

Figure 2. Lower limb joint power for the slow (red, ST-group, n = 11) and fast (blue, FT-group, n = 9) muscle fiber type groups across a range of running speeds. Solid line present the group mean data with shaded area the standard deviation. Right: net and positive average joint power across a range of

running speeds. Dots present the individual data with mean and standard deviation represented by the bar graphs. Arrows indicate significant main effect for running speed ($p < 0.05$). # indicates a significant group × speed interaction effect ($p < 0.05$).

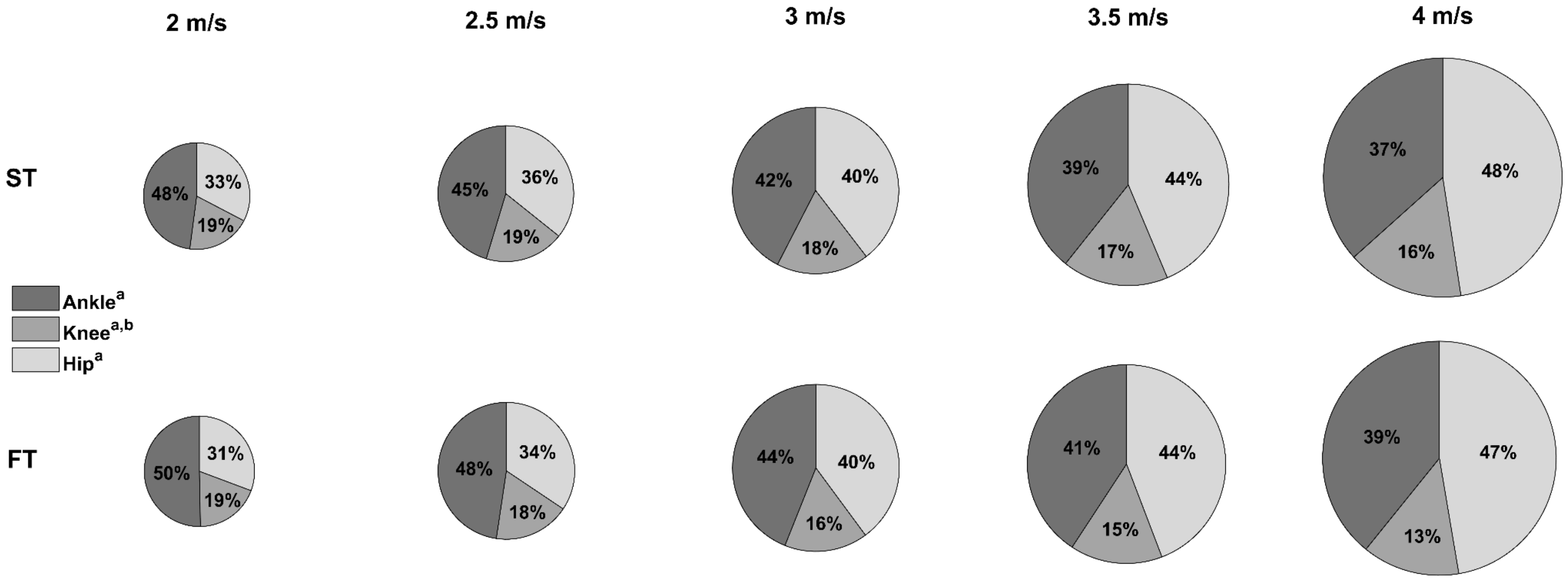

Figure 3. The relative contribution of each lower limb joint to positive average joint power (in %) across a range of speeds in two groups with either a slow (ST-group, upper) or fast (FT-group, lower) muscle fiber type distribution. Radius of the pie charts is scaled on the total positive power in each condition. [a] *significant speed effect ($p < 0.05$);* [b] *significant muscle typology × speed interaction effect ($p < 0.05$).*

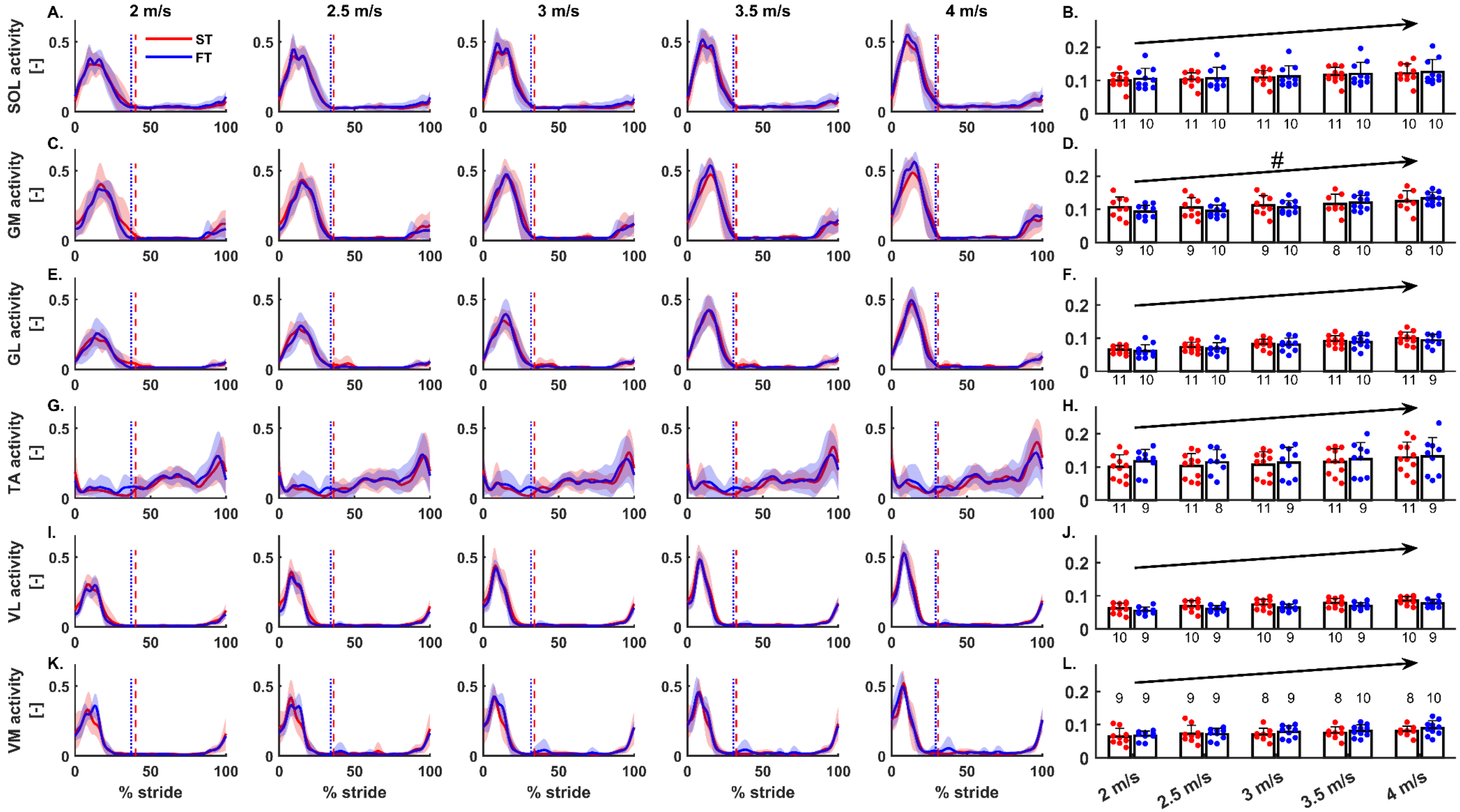

Figure 4. Mean muscle activity for the slow (red, ST-group) and fast (blue, FT-group) muscle fiber type groups across a range of running speeds. Solid lines present the group mean data with shaded area the standard deviation. Right: stride mean muscle activation across a range of running speeds. Dots present

the individual data with mean and standard deviation represented by the bar graphs. Arrows indicate significant main effect for running speed ($p < 0.05$). # indicates a significant group × speed interaction effect ($p < 0.05$). SOL: soleus; GM: gastrocnemius medialis; GL: gastrocnemius lateralis; TA: tibialis anterior; VL: vastus lateralis; VM = vastus medialis. Number under each bar graph represent number of subjects included in the analysis.

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Conflict of Interest

The authors declare no conflict of interest.

References

1. Joyner MJ. Modeling: Optimal marathon performance on the basis of physiological factors. *J Appl Physiol*. 1991;70(2):683-687. doi:10.1152/jappl.1991.70.2.683

2. Hoogkamer W, Kipp S, Spiering BA, Kram R. Altered running economy directly translates to altered distance-running performance. *Med Sci Sports Exerc*. 2016;48(11):2175-2180. doi:10.1249/MSS.0000000000001012

3. Barnes KR, Kilding AE. Running economy: measurement, norms, and determining factors. *Sport Med - Open*. 2015;1(1). doi:10.1186/s40798-015-0007-y

4. He ZH, Bottinelli R, Pellegrino MA, Ferenczi MA, Reggiani C. ATP consumption and efficiency of human single muscle fibers with different myosin isoform composition. *Biophys J*. 2000;79(2):945-961. doi:10.1016/S0006-3495(00)76349-1

5. Swinnen W, Lievens E, Hoogkamer W, De Groote F, Derave W, Vanwanseele B. Muscle fiber typology affects whole-body metabolic rate during isolated muscle contractions and human locomotion. *J Physiol*. 2024;602(7):1297-1311. doi:10.1113/JP285846

6. Barclay CJ, Constable JK, Gibbs CL. Energetics of fast- and slow-twitch muscles of the mouse. *J Physiol*. 1993;472(1):61-80. doi:10.1113/jphysiol.1993.sp019937

7. Costill DL, Daniels J, Evans W, Fink W, Krahenbuhl G, Saltin B. Skeletal muscle enzymes and fiber composition in male and female track athletes. *J Appl Physiol*. 1976;40(2):149-154.

doi:10.1152/jappl.1976.40.2.149

8. Saltin B, Henriksson J, Nygaard E, Andersen P, Jansson E. Fiber types and metabolic potentials of skeletal muscles in sedentary man and endurance runners. *Ann N Y Acad Sci*. 1977;301(1):3-29. doi:10.1111/j.1749-6632.1977.tb38182.x

9. Monte A, Baltzopoulos V, Maganaris CN, Zamparo P. Gastrocnemius Medialis and Vastus Lateralis in vivo muscle-tendon behavior during running at increasing speeds. *Scand J Med Sci Sport*. 2020;30(7):1163-1176. doi:10.1111/sms.13662

10. Bohm S, Marzilger R, Mersmann F, Santuz A, Arampatzis A. Operating length and velocity of human vastus lateralis muscle during walking and running. *Sci Rep*. 2018;8(1). doi:10.1038/s41598-018-23376-5

11. Swinnen W, Hoogkamer W, Delabastita T, Aeles J, De Groote F, Vanwanseele B. Effect of habitual foot-strike pattern on the gastrocnemius medialis muscle-tendon interaction and muscle force production during running. *J Appl Physiol*. 2019;126(3):708-716. doi:10.1152/japplphysiol.00768.2018

12. Lai A, Lichtwark GA, Schache AG, Lin Y-C, Brown NAT, Pandy MG. In vivo behavior of the human soleus muscle with increasing walking and running speeds. *J Appl Physiol*. 2015;118(10):1266-1275. doi:10.1152/japplphysiol.00128.2015

13. Bosco C, Montanari G, Ribacchi R, et al. Relationship between the efficiency of muscular work during jumping and the energetics of running. *Eur J Appl Physiol Occup Physiol*. 1987;56(2):138-143. doi:10.1007/BF00640636

14. Bellinger P, Derave W, Lievens E, et al. Determinants of last lap speed in paced and maximal 1500-m time trials. *Eur J Appl Physiol*. 2021;121(2):525-537. doi:10.1007/s00421-020-04543-x

15. Franch J, Madsen K, Djurhuus MS, Pedersen PK. Improved running economy following intensified training correlates with reduced ventilatory demands. *Med Sci Sports Exerc*.

1998;30(8):1250-1256. doi:10.1097/00005768-199808000-00011

16. Williams KR, Cavanagh PR. Relationship between distance running mechanics, running economy, and performance. *J Appl Physiol*. 1987;63(3):1236-1245. doi:10.1152/jappl.1987.63.3.1236

17. Kyröläinen H, Kivelä R, Koskinen S, et al. Interrelationships between muscle structure, muscle strength, and running economy. *Med Sci Sports Exerc*. 2003;35(1):45-49. doi:10.1097/00005768-200301000-00008

18. Lundby C, Montero D, Gehrig S, et al. Physiological, biochemical, anthropometric, and biomechanical influences on exercise economy in humans. *Scand J Med Sci Sport*. 2017;27(12):1627-1637. doi:10.1111/sms.12849

19. Hunter GR, Mccarthy JP, Carter SJ, et al. Muscle fiber type, achilles tendon length, potentiation, and running economy. *J Strength Cond Res*. 2015;29(5):1302-1309. doi:10.1519/JSC.0000000000000760

20. Pellegrino J, Ruby BC, Dumke CL. Effect of plyometrics on the energy cost of running and MHC and titin isoforms. *Med Sci Sports Exerc*. 2016;48(1):49-56. doi:10.1249/MSS.0000000000000747

21. Reggiani C, Bottinelli R, Stienen GJM. Sarcomeric myosin isoforms: Fine tuning of a molecular motor. *News Physiol Sci*. 2000;15(1):26-33. doi:10.1152/physiologyonline.2000.15.1.26

22. Widrick JJ, Trappe SW, Costill DL, Fitts RH. Force-velocity and force-power properties of single muscle fibers from elite master runners and sedentary men. *Am J Physiol - Cell Physiol*. 1996;271(2-1):C676-83. doi:10.1152/ajpcell.1996.271.2.c676

23. Swinnen W, Mylle I, Hoogkamer W, De Groote F, Vanwanseele B. Changing Stride Frequency Alters Average Joint Power and Power Distributions during Ground Contact and Leg Swing in Running. *Med Sci Sport Exerc*. 2021;53(11):2111-2118. doi:10.1249/mss.0000000000002692

24. Lievens E, Van Vossel K, Van De Casteele F, et al. CORP: Quantification of human skeletal muscle carnosine concentration by proton magnetic resonance spectroscopy. *J Appl Physiol*. 2021;131(1):250-264. doi:10.1152/japplphysiol.00056.2021

25. Van Vossel K, Hardeel J, Van de Casteele F, et al. Can muscle typology explain the inter-individual variability in resistance training adaptations? *J Physiol*. 2023;601(12):2307-2327. doi:10.1113/JP284442

26. Delp SL, Anderson FC, Arnold AS, et al. OpenSim: Open source to create and analyze dynamic simulations of movement. *IEEE Trans Biomed Eng*. 2007;54(11):1940-1950. doi:10.1109/TBME.2007.901024

27. Péronnet F, Massicotte D. Table of nonprotein respiratory quotient: an update. *Can J Sport Sci*. 1991;16(1):23-29.

28. Henneman E, Somjen G, Carpenter DO. Functional significance of cell size in spinal motoneurons. *J Neurophysiol*. 1965;28:560-580. doi:10.1152/jn.1965.28.3.560

29. Henneman E, Somjen G, Carpenter DO. Excitability and inhibitability of motoneurons of different sizes. *J Neurophysiol*. 1965;28(3):599-620. doi:10.1152/jn.1965.28.3.599

30. Bex T, Baguet A, Achten E, Aerts P, De Clercq D, Derave W. Cyclic movement frequency is associated with muscle typology in athletes. *Scand J Med Sci Sport*. 2017;27(2). doi:10.1111/sms.12648

31. Jones AM. A five year physiological case study of an Olympic runner. *Br J Sports Med*. 1998;32(1):39-43. doi:10.1136/bjsm.32.1.39

32. Beneke R, Hütler M. The effect of training on running economy and performance in recreational athletes. *Med Sci Sports Exerc*. 2005;37(10):1794-1799. doi:10.1249/01.mss.0000176399.67121.02

33. Swinnen W, Kipp S, Kram R. Comparison of running and cycling economy in runners, cyclists, and triathletes. *Eur J Appl Physiol*. 2018;118(7). doi:10.1007/s00421-018-3865-4

34. Jones AM, Carter H. The effect of endurance training on parameters of aerobic fitness. *Sport Med*. 2000;29(6):373-386. doi:10.2165/00007256-200029060-00001

35. Swinnen W, Hoogkamer W, De Groote F, Vanwanseele B. Habitual foot strike pattern does not affect simulated triceps surae muscle metabolic energy consumption during running. *J Exp Biol*. 2019;22(23). doi:10.1242/jeb.212449

36. Vikne H, Gundersen K, Liestøl K, Mælen J, Vøllestad N. Intermuscular relationship of human muscle fiber type proportions: Slow leg muscles predict slow neck muscles. *Muscle and Nerve*. 2012;45(4):527-535. doi:10.1002/mus.22315

37. Black MI, Allen SJ, Forrester SE, Folland JP. The Anthropometry of Economical Running. *Med Sci Sports Exerc*. 2020;52(3). doi:10.1249/MSS.0000000000002158

38. Conley DL, Krahenbuhl GS. Running economy and distance running performance of highly trained athletes. *Med Sci Sport Exerc*. 1980;12(5):357-360. doi:10.1249/00005768-198012050-00010

39. Jones AM, Kirby BS, Clark IE, et al. Physiological demands of running at 2-hour marathon race pace. *J Appl Physiol*. 2021;130(2). doi:10.1152/JAPPLPHYSIOL.00647.2020

40. Hoogkamer W, Kipp S, Frank JH, Farina EM, Luo G, Kram R. A Comparison of the Energetic Cost of Running in Marathon Racing Shoes. *Sport Med*. Published online 2017:1-11. doi:10.1007/s40279-017-0811-2