RESEARCH ARTICLE

RUNNING HEAD: Local muscle fatigue in running

Submaximal running energetics are maintained despite local muscle fatigue

Key Nahan[1,2,3], Harrison Finn[2,4], John Kerr[1,2], Martin Héroux[2,5], Kirsty A. McDonald[1,2,6]

[1]School of Health Sciences, University of New South Wales, Sydney, NSW, Australia

[2]Neuroscience Research Australia, Sydney, NSW, Australia

[3]School of Public Health and Health Sciences, University of Massachusetts Amherst, Amherst, MA, USA

[4]Department of Anesthesiology, University of Utah, Salt Lake City, Utah, USA

[5]School of Biomedical Sciences, University of New South Wales, Sydney, NSW, Australia

[6]School of Medical & Health Sciences, Edith Cowan University, Perth, WA, Australia

Correspondence: *Key Nahan (keynahan6@gmail.com).*

ABSTRACT

When running, metabolic cost increases as muscles are simultaneously fatigued. However, the contribution of an individual muscle group to fatigue-related increase in metabolic costs remains unclear. We investigated the metabolic consequence of running with local plantar flexor or knee extensor fatigue and associated neuromuscular control strategies. *Recreational* and *experienced* male runners (N=20) completed two sessions (one per muscle group), with each including two 10 min running bouts: without and with local fatigue (~20% reduction in peak joint torque). Net metabolic power and muscle activity (initial and final minutes) were determined. Metabolic power was unaffected by plantar flexor (p=0.367) or knee extensor (p=0.607) fatigue in both cohorts. Plantar flexor fatigue recovered during the *fatigued run* (p=0.033), while knee extensor fatigue only recovered for the *recreational* cohort (p=0.009; *experienced*: p=0.826). With plantar flexor fatigue, plantar flexor muscle activity was unchanged between runs (p≥0.312), however initial soleus activity was greater in the *unfatigued* than *fatigued run* for *experienced* runners (p=0.022), and initial medial gastrocnemius activity was greater in the *unfatigued* than *fatigued run* for the combined cohort (p=0.009). With knee extensor fatigue, knee extensor muscle activity was mostly lower in the *unfatigued* than *fatigued run* (p≤0.009), except for final vastus lateralis activity, which was unchanged between runs (p=0.061). Therefore, muscle groups respond with different activation strategies when fatigued. Running with plantar flexor or knee extensor fatigue, at levels like those induced by prolonged running (10-42 km), does not increase metabolic power and thus, submaximal running energetics may be maintained despite local muscle fatigue.

NEW & NOTEWORTHY

While muscle fatigue is suggested to increase the metabolic cost of running, the individual contributions of key lower limb muscle groups have not been explored. We examined responses after fatigue of only the plantar flexors or the knee extensors. Results indicate that local fatigue did not affect the metabolic

power of male runners for either fatigued muscle group. These findings enhance our understanding of running performance and the interaction between fundamental criteria dictating human locomotion.

Keywords: Endurance; Energetics; Force; Locomotion; Performance.

INTRODUCTION

The metabolic cost of running, as represented by metabolic power or cost of transport, is a comprehensive measure of submaximal energy consumption and a primary determinant of running performance (1–3). Neuromuscular fatigue (i.e., reduced maximal force production of a given muscle (4)), a secondary determinant, may increase metabolic cost (5, 6), reduce running speed (5, 7, 8) and subsequently influence running performance. For example, a fatiguing squat protocol increases the metabolic cost of running (9), while a fatiguing drop jump protocol increases metabolic cost (10) and time to exhaustion (11) in cycling. Moreover, lower fatigability of the knee extensors has been associated with preserved running economy when measured before and after a fatiguing run (12).

Physiological and biomechanical mechanisms underpin the inflated metabolic cost of running with neuromuscular fatigue. Physiologically, an increased recruitment of larger, type II muscle fibers during fatiguing contractions (13, 14) may contribute to the metabolic penalty as they require more energy to contract (15–18). A change in the substrate used when muscles are fatigued may also contribute, as reliance on glycogen decreases and free fatty acid increases (19, 20). During aerobic exercise, adenosine triphosphate (ATP) produced from fat is approximately 7% less efficient than that from carbohydrates (21); thus, the metabolic cost of running may be affected by changing fuel sources. Similarly, neuromuscular fatigue is associated with increased metabolite (i.e., hydrogen ion, inorganic phosphate) concentrations; this may decrease intracellular pH and result in a reduced rate of ATP production and increased metabolic cost (22, 23). Biomechanically, changes in tissue mechanics as a result of neuromuscular fatigue (e.g., increased tendon compliance (24, 25)) may increase the metabolic cost of running (26, 27). Reduced stride frequency (28–30) and gait alterations to offload the fatigued muscle (31) may also contribute to a less metabolically optimal gait strategy and impaired running performance (32, 33).

Running-induced neuromuscular fatigue is difficult to quantify. A run induces fatigue across many muscles simultaneously (i.e., global fatigue) and to varying extents. Functional strength tests, such as drop or countermovement jump tests, do not measure neuromuscular fatigue in a single muscle group (34, 35). Alternatively, muscle activity, measured via electromyography (EMG), increases with fatigue (36) due to increased motor unit firing rate, additional recruitment of type II muscle fibers and/or synchronization of motor unit firing (36). Although EMG provides insight into neuromuscular responses to fatigue, it remains an inaccurate measure of fatigue (37). A maximum voluntary contraction (MVC) is typically used to measure neuromuscular fatigue (38). However, because partial fatigue recovery occurs almost immediately after exercise is stopped, with substantial recovery occurring in the first 1-2 min (39, 40), only one muscle group is often able to be measured after running. Therefore, assessing fatigue in a single muscle group (i.e., local fatigue) via an MVC provides the most accurate measurement of neuromuscular fatigue, effectively circumventing measurement barriers.

The plantar flexors and knee extensors are the main contributors to center of mass acceleration (i.e., positive work) and deceleration (i.e., negative work) in running (41). Considering that muscle work explains ~76% of the metabolic cost of running (42), accumulation of fatigue in these muscle groups likely inflicts a metabolic penalty. After a prolonged run (10-42 km), peak torque decreases by 9-29% in the plantar flexors (6, 43–47) and 12-30% in the knee extensors (6–8, 35, 48–51). However, it is not possible to determine the metabolic cost of running with such levels of fatigue because i) running-induced fatigue protocols cause neuromuscular fatigue in several lower limb muscle groups and ii) metabolic cost increases following a prolonged run can result from several factors in addition to neuromuscular fatigue (e.g., heat dissipation (52), pulmonary ventilation (53), and heart rate (54)). A local neuromuscular fatigue protocol that consists of a repeated single joint movement, e.g., calf raise or knee extension, may be better suited to explore the metabolic cost of neuromuscular fatigue in specific lower limb muscle groups. Indeed, this type of protocol has been used to explore the effect of local neuromuscular fatigue on running biomechanics (55, 56). While biomechanical changes were observed, it remains unclear whether this fatigue also incurs a metabolic penalty. To address this knowledge gap, we aimed to quantify the effect of local i) plantar flexor and ii) knee extensor fatigue on metabolic cost and fatigued-group muscle activity in running. First, we hypothesized that the metabolic cost of running would increase with local fatigue of either muscle groups. Second, because muscle activity of the plantar flexors and knee extensors increases with running-induced fatigue (5, 57), we hypothesized that local fatigue would also increase activity in fatigued muscles when running.

MATERIALS AND METHODS

Participants

All study procedures were approved by the University of New South Wales Human Research Ethics Committee (HC220753). Healthy male participants (N=20; age: 27.2 ± 5.7 years; body mass: 74.6 ± 9.0 kg; height: 1.80 ± 0.07 m; mean ± SD) gave their written informed consent to participate in the study after clear explanations of study procedures were provided. Females have less fatiguability than males (58), and effort and fatiguability are influenced by the specific phase of the menstrual cycle (59), with these effects often being unique to the individual (60). Therefore, we recruited only male participants to limit confounding factors.

Participants were grouped as *recreational* (N=11; age: 26.9 ± 4.9 years; body mass: 78.1 ± 8.8 kg; height: 1.81 ± 0.08 m) or *experienced* (N=9; age: 27.6 ± 6.7 years; body mass: 70.4 ± 7.5 kg; height: 1.79 ± 0.05 m) according to their 10 km running performance and training habits. *Recreational* participants were required to have a 10 km run time between 50-60 min and were also required to have run 10-20 km/week, 2-4 times per week over the past six months. *Experienced* participants were required to have at least three years of running experience, a 10 km run time of 43 min or less and were also required to have run at least 40 km/week, at least three times per week, over the past six months. All participants were free of respiratory, cardiovascular, neurological, or other conditions that could affect gait. Additional criteria required participants not to have experienced any lower limb injuries over the past six months and to have no history of rhabdomyolysis. Details for individual participants are listed in Supplementary Table 1.

Experimental preparation

The study protocol was part of a two-day analysis of running performance. Plantar flexor and knee extensor fatigue were assessed on separate non-consecutive days, randomly ordered, with an average

between-session duration of 23 ± 16 days (mean ± SD; range 6-62 days). On the day before both data collection sessions, participants were asked to refrain from their weekly long run and high-intensity exercise. On the day of data collection, participants were asked to refrain from caffeine and exercise, and to fast for the two hours immediately preceding their laboratory visit (water was permitted). Upon arrival, they completed a rating of fatigue scale to reflect their overall fatigue (61). Next, anthropometric measurements were taken (e.g., body mass, height) and limb dominance was determined by asking the participant "which foot would you kick a soccer ball with?" (62). Surface EMG (Trigno Avanti, Delsys, Natick, MA, USA) sites were prepared for seven muscles on the dominant limb according to the SENIEM guidelines (63): gluteus maximus, biceps femoris, rectus femoris (RF), vastus lateralis (VL), medial gastrocnemius (MG), soleus (SOL), and tibialis anterior. Force-sensing resistor pads (Trigno 4 Contact, Delsys, Natick, MA, USA) were placed under the insole of standardized ASICS GEL-CUMULUS 24™ footwear, in line with the mid-calcaneus and first metatarsophalangeal joint (31). The ASICS GEL-CUMULUS 24™ has a 8 mm drop and 16/24 mm (forefoot/rearfoot) midsole stack of ethylene vinyl acetate (64). Foot strike was not classified.

Experimental protocol

Participants completed a 5 min seated resting metabolic rate trial where breath-by-breath $\dot{V}_{O_2}$ (L s^{-1}) and $\dot{V}_{CO_2}$ (L s^{-1}) were collected using a portable metabolic system (K5, COSMED, Rome, Italy). They then performed a 5 min warm-up run on a treadmill (TMX428CP, Trackmaster, Full Vision, Inc, Newton, KS, USA) at 8 km h^{-1} [2.22 m s^{-1}], 0° incline. Next, participants completed four 3-5 s isometric MVCs on an isokinetic dynamometer (10 kHz, HUMAC NORM, CSMi, Stoughton, MA, USA) for the muscle group of interest (either plantar flexor or knee extensor, depending on the session) with a 1 min rest between contractions (43, 50). Verbal encouragement was given during the contractions (65). Due to the unilateral nature of the dynamometer configuration, only dominant limb MVCs were recorded. However, participants also performed concurrent maximal contractions against manual resistance with the nondominant limb. The highest torque produced by participants across their four attempts was identified as their peak baseline measurement (*MVC #1*). When testing the plantar flexors, participants were seated with their lower limb near-maximally extended, their talocrural joint positioned at 0° and their foot strapped to a footplate, against which they maximally plantarflexed. When testing the knee extensors, participants were seated with their knee flexed at 90° and the distal shank strapped to a pad attached to a lever arm, against which they maximally extended. For both muscle groups, the dynamometer axis of rotation was aligned with the relevant joint center of rotation. All torque data were collected using HUMAC software (CSMi, Stoughton, MA, USA).

After *MVC #1*, participants completed an *unfatigued run* on the treadmill for 10 min at either 10 km h^{-1} [2.77 m s^{-1}] (*recreational* group) or 12 km h^{-1} [3.33 m s^{-1}] (*experienced* group). These speeds correspond to an easy pace and have been used when collecting steady-state metabolic data from runners of varying experience levels (66, 67). Breath-by-breath gaseous exchange was recorded by the portable metabolic system attached to a harness worn by participants (total mass: 0.9 kg). All metabolic data were collected using OMNIA software (COSMED, Rome, Italy). Electromyography data were collected continuously for all seven muscles at 2000 Hz (LabChart 8, ADInstruments, Dunedin, New Zealand). After the run, participants immediately transitioned to the dynamometer for another MVC (*MVC #2*).

Next, one of two fatigue protocols was completed depending on the session. For the plantar flexors, participants completed 2-3 sets of bilateral bodyweight calf raises on the edge of a ~20 cm high step

with 1 min rest in between sets (68). Calf raises were done to a 65-bpm metronome with a beat on full plantarflexion and a beat on full dorsiflexion. For the knee extensors, participants completed 2-3 sets of bilateral knee extensions in a knee extension machine (Hammer Strength, Rosemont, IL, USA) set to 20% of their peak torque measurement (highest torque obtained across *MVC #1* and *#2*) converted to a mass, with 1 min rest in between sets. Repetitions were completed to a 60-bpm metronome with a beat on full knee extension and a beat on full knee flexion (~90°). Each set was done until failure, which could be volitional, or performance-based (e.g., incomplete range of motion, poor timing with the metronome). After two sets, participants immediately completed an MVC (*MVC #3*) to ensure fatigue had reached the target value of 75-85% of their peak baseline torque measure. This range of neuromuscular fatigue was chosen as it reflects the percentage torque decrease that occurs in these muscle groups after a prolonged run (6–8, 35, 43–49, 51). If fatigue was not within the suitable range, participants completed another set of calf raises or knee extensions, or rested, and fatigue was reassessed. One participant required a fourth set of calf raises but all other participants required 2-3 sets of calf raises and knee extensions. The number of sets and repetitions are found in Supplementary Tables 3 and 4. When the suitable range of fatigue was achieved, participants immediately transitioned to a *fatigued run* on the treadmill. Conditions between the *unfatigued* and *fatigued runs* were mirrored, and the same data were collected. Finally, after the *fatigued run*, participants immediately completed a final MVC (*MVC #4*). The dynamometer was in close proximity to the treadmill and fatigue protocol equipment, which allowed for a rapid measure of fatigue (~10-20 s transition). This was important because recovery occurs rapidly after a fatiguing activity (39, 40). A summary of the protocol is presented in Figure 1.

Data processing

All data were processed using custom Python scripts (Python Software Foundation, version 3.9). $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ and data were smoothed with a third-order, low pass digital filter with a cut-off frequency of 0.04 Hz (69). Resting metabolic rate was calculated from 1 min of $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ data selected from the minute with the lowest average magnitudes across the final two minutes of the seated trial, when the gaseous exchange data had reached a plateau.

To compute net metabolic power ($C_{met,P}$; W kg^{-1}), oxygen inspiration ($\dot{V}_{O_2}$; L s^{-1}) and carbon dioxide expiration ($\dot{V}_{CO_2}$; L s^{-1}) resting rates were subtracted from equivalent values obtained in the *unfatigued* and *fatigued run*, and entered into Equation 1 (70, 71), where M represents the participant's body mass (kg):

$$C_{met,P} = 1000\left(\frac{16.89\dot{V}_{O_2} + 4.82\dot{V}_{CO_2}}{M}\right). \quad (1)$$

$\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ data were selected from the eighth minute of the *unfatigued* and *fatigued run* to avoid the psychological effects of participants knowing the run would end soon.

An increase in metabolic power represents worsening running economy. Even small changes (e.g., 1%) can have meaningful effects on running performance (72). However, a 4% metabolic equipment error has been observed and this must be considered when interpreting the results (73). Between-day reliability of metabolic power is unclear; however, running economy (O_2 kg^{-1} km^{-1}) demonstrates high reliability, with an intraclass correlation coefficient of 0.81-0.83 and a typical error of 2.72-3.31% (74). Cost of transport (kcal kg^{-1} km^{-1}) also has good-to-high reliability, with an intraclass correlation

coefficient of 0.75-0.79 and a typical error of 3.05-3.72% (74). For two participants the fifth minute was used to calculate metabolic power in both runs because of supraphysiological magnitudes observed during the later stages of the run (confirmed to be a hardware error).

Respiratory exchange ratio (RER; $\dot{V}_{CO_2}/\dot{V}_{O_2}$) was calculated for the same time periods as metabolic cost. One participant's metabolic data from both runs for both muscle groups were excluded because their RER exceeded 1.0 during the steady-state period.

Fatigue was defined as a decline in peak torque (N m) relative to the peak torque baseline measurement taken from the highest peak measurement across *MVC #1* and *#2*. Previous research has reported high between-day reliability of peak knee extensor torque measured during isometric MVC, with intraclass correlation coefficients of 0.92-0.97 and coefficients of variation of 4-5% (75). For peak plantar flexor torque measured via isometric MVC, between-subject reliability is good but shows moderate variability, with an intraclass correlation coefficient of 0.77 and a coefficient of variation value of 16.7% (76).

For the plantar flexor fatigue, 17 participants (17/18) had their baseline peak torque measurement recorded in *MVC #1* and one participant (1/18) had it recorded in *MVC #2.* For the knee extensor fatigue, 12 participants (12/18) had their baseline peak torque measurement recorded in *MVC #1* and six participants (6/18) had it recorded in *MVC #2*. For one participant, their highest knee extensor peak torque was attained during *MVC #4*. However, their *MVC #1* and *MVC #4* values fell within an appropriate intraclass correlation range for knee extension MVCs (0.92 (75)). Thus, their *MVC #1* value was selected as their baseline.

Mean and 95% confidence intervals (CI) were calculated from the predicted values derived from the linear mixed effects models (see 'Statistical analysis' section below). However, raw data were used when addressing atypical data points in text to illustrate their impact. Additionally, raw data were used to calculate peak torque percentage changes. The baseline measure (*MVC #1* or *#2*) was set to 100%, and subsequent MVCs were expressed as percentages relative to the baseline. Percentage changes were determined by subtracting the percentage MVC values from the baseline percentage.

Mean integrated EMG ($iEMG$) from *minute 1* and *minute 10* of both runs was calculated for the SOL and MG for the plantar flexor fatigue protocol and the VL and RF for the knee extensor fatigue protocol. To our understanding, there is no published data on the between-day reliability of iEMG during running when amplitudes are normalized to peak MVC signal. However, between-day reliability of plantar flexor and knee extensor root mean square EMG, normalized to the MVC signal, is moderate to high, with intraclass correlations of 0.68-0.90 and coefficients of variation of 6-8% (77).

The raw EMG data were DC offset, band-pass filtered (20-350 Hz), full-wave rectified, and low-pass filtered (6 Hz); fourth-order dual-pass Butterworth filters were used (78). The resulting linear envelopes for the *unfatigued* and *fatigued run* trials were normalized to the linear envelope of the peak EMG signal captured during *MVC #1*. The linear envelope of the peak EMG signal captured during *MVC #2* was used for normalization for two participants who did not have EMG data for *MVC #1* because of connectivity interruptions during data collection. The normalized linear envelope data (EMG_{env}) for each muscle (i = 1-4) were then parsed into strides (j = 1, 2 …) using force-sensing resistor pad data, which were filtered with a fourth-order low-pass Butterworth filter with a 10 Hz cut-off frequency. Strides were defined from initial contact of the dominant limb (t_0) to the consecutive initial contact of the dominant

limb (t_f), and then converted to a rate using stride time (T_j) (79, 78). The processed muscle activity data for muscle i, stride j (a_{ij}) is represented by Equation 2:

$$a_{ij} \triangleq \frac{1}{T_j} \int_{t_0}^{t_f} (EMG_{env})_{ij}\, dt. \tag{2}$$

The a_{ij} data consisted of two one-minute windows and mean iEMG values were calculated for each window for the *unfatigued* and *fatigued run*.

Due to the time-sensitive nature of fatigue recovery, we did not stop the run or restart any part of the protocol—if an EMG sensor came loose or was moved, the affected data were excluded from the analysis. Comprehensive lists of sample sizes used to calculate study outcomes can be found in Supplementary Table 2, and lost data across the participant sample can be found in Supplementary Table 5.

Statistical analysis

Separate linear mixed-effects models were performed to analyze data from the plantar flexor and knee extensor fatigue conditions. Participants were modeled as a random factor with a random intercept for all models. The model structures were as follows:

- Metabolic power, RER, and stride frequency: fixed effects included group (*recreational* or *experienced*), run (*unfatigued* or *fatigued*), and their interaction (two-way).
- Peak torque: fixed effects included group, MVC # (*1-4*), and their interaction (two-way).
- iEMG: fixed effects included group, run, minute (*1* and *10*), and their interactions (two- or three-way).

A likelihood ratio test was conducted to assess model fit with and without a group interaction. If model fit was improved by the inclusion of this interaction term ($p<0.05$), it was retained. *Pooled* group data were analyzed if the interaction was removed, while *recreational* and *experienced* group data were analyzed if the interaction was retained. Because differences between *recreational* and *experienced* runners were not relevant to the study aims, group main effects were not of interest. Differences between levels were further evaluated with post-hoc pairwise comparisons, and Bonferroni correction was applied. Custom contrasts were used for peak torque analysis (i.e., *MVC #2-1* and *MVC #4-3*) to constrain the models and investigate comparisons relevant to the study aim.

Statistical significance was set at $\alpha=0.05$ and results are reported as estimated marginal mean [95% CI] and mean differences [95% CI]. R (R Development Core Team, Vienna, Austria) was used for all statistical analyses.

RESULTS

Metabolic power

Individual participant metabolic power data and group means for the plantar flexor and knee extensor fatigue protocols are presented in Figure 2A and Figure 2B, respectively.

Plantar flexor fatigue

The interaction between group and run did not improve model fit (p=0.125) and thus was removed. There was no change in metabolic power between the *unfatigued run* (14.6 W kg^{-1} [13.9, 15.3]) and *fatigued run* (14.8 W kg^{-1} [14.1, 15.5]), with a difference of 0.2 W kg^{-1} [-0.3, 0.6] (p=0.367). Therefore, plantar flexor fatigue did not induce a change in metabolic power during running.

Knee extensor fatigue

The interaction between group and run did not improve model fit (p=0.072) and thus was removed. There was no change in metabolic power between the *unfatigued run* (13.9 W kg^{-1} [13.1, 14.7]) and *fatigued run* (14.0 W kg^{-1} [13.2, 14.8]), with a difference of 0.1 W kg^{-1} [-0.3, 0.4] (p=0.607). Therefore, knee extensor fatigue did not induce a change in metabolic power during running.

Respiratory exchange ratio (RER)

Plantar flexor fatigue

The interaction between group and run improved model fit (p=0.023) and thus was retained. For the *recreational* group, RER was greater in the *unfatigued run* (0.88 [0.84, 0.92]) than *fatigued run* (0.86 [0.81, 0.90]), with a difference of -0.02 [-0.04, 0.00] (p=0.030). Conversely, in the *experienced* group, RER was unchanged between the *unfatigued run* (0.86 [0.82, 0.91]) and the *fatigued run* (0.87 [0.83, 0.92]), with a difference of 0.01 [-0.01, 0.03] (p=0.341). Thus, compared to unfatigued running, running with plantar flexor fatigue decreased RER in *recreational* but not *experienced* runners.

Knee extensor fatigue

The interaction between group and run did not improve model fit (p=0.197) and thus was removed. RER was lower in the *unfatigued run* (0.86 [0.84, 0.88]) compared to the *fatigued run* (0.84 [0.82, 0.87]), with a difference of -0.02 [-0.03, 0.00] (p=0.015). Therefore, compared to unfatigued running, running with knee extensor fatigue increased RER.

Peak torque (fatigue)

Individual participant joint torque data and group means for the plantar flexor and knee extensor fatigue protocols are presented in Figure 2C/Table 1 and Figure 2D/Table 2, respectively.

Plantar flexor fatigue

The interaction between group and MVC # did not improve model fit (p=0.707) and thus was removed. Plantar flexor torque was greater when measured before (*MVC #1*) as compared to after (*MVC #2*) the *unfatigued run* (p<0.001). The plantar flexor fatigue protocol resulted in a 20% [19, 22] reduction in maximal torque. Plantar flexor torque increased from before (*MVC #3*) to after (*MVC #4*) the *fatigued run* (p=0.033). Therefore, plantar flexor fatigue accumulated over the *unfatigued run* and recovered over the *fatigued run*.

Knee extensor fatigue

The interaction between group and MVC # improved model fit (p=0.016) and thus was retained. For the *recreational* group, knee extensor torque was unchanged when measured before as compared to after the *unfatigued run* (p=0.578). The knee extensor fatigue protocol generated 21% [20, 23] fatigue in this cohort. Their knee extensor torque increased from before to after the *fatigued run* (p=0.009). For the *experienced* group, knee extensor torque was greater when measured before as compared to after the *unfatigued run* (p=0.003). The knee extensor fatigue protocol generated 22% [19, 24] fatigue in this

cohort. Their knee extensor torque was unchanged when measured before and after the *fatigued run* (p=0.826). Therefore, *recreational* runners maintained stable torque production during the *unfatigued run* and recovered over the *fatigued run*, while *experienced* runners accumulated knee extensor fatigue over the *unfatigued run* and did not recover over the *fatigued run*.

Muscle activity

Muscle activity data is presented in Figure 3.

Plantar flexor fatigue

For SOL activity, the interactions between group and other factors improved model fit (p=0.017) and thus were retained. For the *recreational* group, SOL iEMG in *minute 1* was unchanged between the *unfatigued run* (0.27 [0.21, 0.33]) and the *fatigued run* (0.30 [0.24, 0.36]), with a difference of 0.03 [0.02, 0.08] (p=0.312). Similarly, at *minute 10*, SOL iEMG was unchanged between the *unfatigued run* (0.26 [0.20, 0.32]) and the *fatigued run* (0.28 [0.22, 0.34]), with a difference of 0.02 [-0.03, 0.07] (p=0.350). For the *experienced* group, SOL iEMG in *minute 1* was greater in the *unfatigued run* (0.37 [0.29, 0.44]) than the *fatigued run* (0.30 [0.23, 0.37]), with a difference of -0.07 [-0.13, -0.01] (p=0.022). However, a*t minute 10*, SOL iEMG was unchanged between the *unfatigued run* (0.29 [0.22, 0.36]) and the *fatigued run* (0.29 [0.22, 0.36]), with a difference of 0.00 [-0.05, 0.06] (p=0.853). Therefore, in *recreational* runners, plantar flexor fatigue did not affect SOL iEMG during running, but for the *experienced* runners, it reduced initial SOL iEMG during running.

For MG activity, the interactions between group and other factors did not improve model fit (p=0.872) and thus were removed. MG iEMG in *minute 1* of the *unfatigued run* (0.23 [0.20, 0.26]) was greater than *minute 1* of the *fatigued run* (0.21 [0.18, 0.24]), with a difference of -0.02 [-0.04, 0.00] (p=0.009). However, at *minute 10*, MG iEMG during the *unfatigued run* (0.21 [0.18, 0.24]) was unchanged from the *fatigued run* (0.21 [0.18, 0.24]), with a difference of 0.00 [-0.02, 0.02] (p=0.969). Therefore, plantar flexor fatigue initially reduced MG iEMG during running.

Knee extensor fatigue

For VL activity, the interactions between group and other factors did not improve model fit (p=0.053) and thus were removed. VL iEMG in *minute 1* of the *unfatigued run* (0.14 [0.09, 0.18]) was lower than *minute 1* of the *fatigued run* (0.16 [0.12, 0.20]), with a difference of 0.02 [0.00, 0.04] (p=0.018). However, at *minute 10*, VL iEMG during the *unfatigued run* (0.14 [0.10, 0.18]) was unchanged from the *fatigued run* (0.16 [0.11, 0.20]), with a difference of 0.02 [0.00, 0.04] (p=0.061). Therefore, knee extensor fatigue initially increased VL iEMG during running.

For RF activity, the interactions between group and other factors did not improve model fit (p=0.964) and thus were removed. RF iEMG in *minute 1* of the *unfatigued run* (0.07 [0.05, 0.09]) was lower than *minute 1* of the *fatigued run* (0.09 [0.07, 0.11]), with a difference of 0.02 [0.00, 0.03] (p=0.009). Additionally, at *minute 10*, RF iEMG during the *unfatigued run* (0.08 [0.06, 0.10]) was lower than the *fatigued run* (0.09 [0.07, 0.12]), with a difference of 0.02 [0.00, 0.03] (p=0.010). Therefore, knee extensor fatigue increased RF iEMG during running.

Stride frequency

Plantar flexor fatigue

The interaction between group and run did not improve model fit (p=0.555) and thus was removed. There was no change in stride frequency between the *unfatigued run* (82.0 strides min^{-1} [79.6, 84.4]) and *fatigued run* (82.1 strides min^{-1} [79.7, 84.6]), with a difference of 0.2 strides min^{-1} [-0.3, 0.7] (p=0.506). Therefore, running with plantar flexor fatigue did not affect stride frequency.

Knee extensor fatigue

The interaction between group and run did not improve model fit (p=0.531) and thus was removed. There was no change in stride frequency between the *unfatigued run* (79.8 strides min^{-1} [77.7, 81.9]) and *fatigued run* (80.4 strides min^{-1} [78.7, 82.5]), with a difference of 0.6 strides min^{-1} [-0.4, 1.6] (p=0.237). Therefore, running with knee extensor fatigue did not affect stride frequency.

DISCUSSION

Neuromuscular fatigue, accumulated globally during a prolonged running bout, like a 10-42 km run, is thought to decrease running performance (8, 80–82) via an increase in the metabolic cost of running (5, 6, 29, 83–88). Yet, the contribution of individual muscle group fatigue to this increase is unclear. Our primary aim was therefore to quantify the effect of local i) plantar flexor and ii) knee extensor fatigue on the metabolic cost of running. Our fatigue protocol of repeated calf raises or knee extensions achieved respective torque reductions of 20% for the plantar flexor group and 21-22% for knee extensor group. These values are similar to torque reductions induced by a prolonged run (6–8, 35, 43–51). Interestingly, local muscle fatigue of either muscle group had no effect on metabolic power during running, therefore, our first hypothesis was not supported. The majority of participants (plantar flexors: 10/18, knee extensors: 13/18) did not demonstrate a meaningful change in metabolic cost (i.e., equal to or greater than 4%), beyond that which could be explained by metabolic equipment error (73).

Our findings contrast with much of the running literature examining the effect of global muscle fatigue on the metabolic cost of prolonged running (5, 6, 29, 83–87, 89). In our study, local fatigue of the plantar flexors and knee extensors likely resulted in only minimal changes across several key variables known to influence metabolic cost, including fiber type recruitment (15–18) and substrate use (21)—as supported by the minor differences in RER (<0.03) between the *unfatigued* and *fatigued runs*, as well as metabolite concentrations and the rate of ATP production (22, 23). We also observed no changes in stride frequency with fatigue of either muscle group, even though a reduced stride frequency is often regarded as a marker of fatigue (28–30). Moreover, while a comprehensive biomechanical analysis was beyond the scope of the current study, such an analysis would likely have revealed limited gait adaptations with the addition of fatigue because adaptations away from a habitual running pattern often incur a metabolic penalty (32, 33). To explain the absence of a metabolic penalty, it is plausible that i) the cumulative burden of fatigue across multiple muscle groups is required to elicit a metabolic penalty, ii) fatigue in a single muscle group not measured in this study (e.g., dorsi flexors (90)) is required to elicit a metabolic penalty, or iii) a metabolic penalty may only be observed to occur if the local fatiguing task replicates the joint and/or musculotendon specific requirements of running.

Running relies on the stretch-shortening cycle, which involves rapid stretching and shortening of the musculotendon unit, with the muscle contracting in a quasi-isometric manor (91). In contrast, the fatigue protocols incorporated slower, isolated concentric and eccentric contractions. The stretch-

shortening cycle enhances force production and reduces the metabolic cost of running, in part, by elastic energy storage and release from tendons (92–94). However, a review by (95) found little to no effect of stretch-shortening cycle fatiguing tasks (e.g., running) on Achilles tendon stiffness. Moreover, while Fletcher & MacIntosh (26) reported reduced Achilles tendon stiffness and increased metabolic cost following a 90-minute run, this was not associated with meaningful plantar flexor fatigue (3%). Plantarflexion and knee extension fatiguing tasks can affect tendon stiffness, however these studies (24, 25) utilized static stretching (e.g., 35° of dorsiflexion for 5 min), different contraction types (e.g., isometric), and greater levels of fatigue (e.g., 36% plantar flexion fatigue, 44% knee extension fatigue) than those of the current study. Although the fatiguing protocol and stretch-shortening cycle differ, their acute effects on tendon properties appear similar. Thus, changes in tendon properties do not seem to explain the preservation of metabolic cost despite 20-22% neuromuscular fatigue.

Our muscle activity analyses of SOL and MG did not provide support for our hypothesis that iEMG of fatigued muscles would increase. With plantar flexor fatigue, we found initial reductions in SOL iEMG in the *experienced* group (~18%), as well as initial reductions in MG iEMG in the *pooled* group (~9%). This contrasts previous research that observed a similar magnitude of fatigue (~20%) but no change in MG iEMG following a 10 km run (45) and an increase in MG iEMG following a marathon (5). However, the current study presents the iEMG as a rate, normalized to the peak EMG signal obtained during an MVC, whereas previous research did not, so this may have contributed to the inconsistent findings. A decrease in iEMG may suggest fatigue (96), possibly via reduced neural drive, firing rate or increased inhibitory signals. However, more likely, it represents a compensatory strategy in response to fatigue. Muscle activity is redistributed between muscles of similar function during global (31, 97–99) and local (100, 101) fatigue. Thus, plantar flexor fatigue may result in a redistribution of effort to non-fatigued muscles, such as the hip or knee extensors.

Interestingly, muscle activity analyses for VL and RF during knee extensor fatigue conflicted the plantar flexor results and did provide some support for our hypothesis that iEMG of the fatigued muscles would increase. We found initial increases in VL iEMG (~18%), as well as initial (~24%) and final (~19%) increases in RF iEMG with knee extensor fatigue. This was supported by research reporting increased VL activity following a ~2 h run at 13.80 km h^{-1} [3.82 m s^{-1}] (57) and increased vastus medialis activity during running at 12.96 km h^{-1} [3.60 m s^{-1}] after a simultaneous knee extensor and flexor fatigue protocol (61). Yet, VL and RF activity did not change over a five-hour run at 10.00 km h^{-1} [2.77 m s^{-1}] (50). This discrepancy may stem from differences in run intensity, duration and participant fitness. The VL iEMG returned to *unfatigued run* levels in the final minute of the *fatigued run* but the RF iEMG did not. Differences in knee extensor muscle activity may stem from differences in muscle fiber distribution or role in the gait cycle (i.e., the RF flexes the hip and extends the knee, whereas the VL only extends the knee). The muscle activity analyses may collectively indicate that plantar flexor recovery is of greater priority, consistent with their primary role in propulsion (41).

Application to distance running

The participants in this study had ~80% torque or strength reserves after the fatigue protocols and this may have been sufficient to meet the work demands of the fatigued run (106). Our participants' maximum plantar flexor torque values were slightly lower, while knee extension torque values were much higher than the peak torque measures observed during similar-speed running (106). Our maximum torque was measured via isometric contractions, which do not capture the elastic energy

contributions available to aid joint torque during running. The Achilles tendon plays a significant role in ankle torque generation during running (95). Therefore, despite acute plantar flexor and knee extensor fatigue (~20%), the work demands of the run were adequately met with the strength reserves. Considering this, runners may choose not to slow down during periods of lower limb fatigue in submaximal conditions but instead maintain the same pace knowing that their strength reserves are sufficient to maintain task demands. Nevertheless, fatigue perception does not accurately reflect neuromuscular fatigue; rather, it encompasses a combination of physiological, psychological, and sensory factors, which could make an in-run analysis of fatigue challenging.

Considerations and limitations

The sample sizes utilized in this study are relatively low (N=20; *recreational:* 10*, experienced:* 8) therefore it is unclear whether they were sufficiently powered to detect smaller effects, and whether the effects detected were genuine or false-positive findings. Therefore, a focus on the size (estimate) and precision (95% CI) of the effects from the study could help us to better understand what results may be of interest (e.g., effects with large sizes or narrow confidence intervals), and what may be less interesting (e.g., effects with small sizes or wide confidence intervals).

For the *recreational* group, both muscle groups recovered across the *fatigued run*, which may, in part, explain the lack of metabolic penalty observed. For example, type II fibers may not have been involved during the period of metabolic cost measurement. To assess whether the use of an earlier (presumably less recovered) timepoint in the run would have impacted the results, we also analyzed metabolic cost during the fifth minute of the run; we found no effect of fatigue from either muscle on metabolic power ($p<0.05$). Thus, it is unlikely that metabolic power was different between the *unfatigued* and *fatigued running* conditions for either muscle group.

One participant achieved their highest maximum knee extensor torque after the fatigue run, despite being sufficiently fatigued (~17%) before the run (Figure 2C). This may reflect a learning effect related to the MVC task, as they had no prior experience with it. In contrast, Figure 2D highlights two participants with notable knee extensor fatigue after the *fatigued run* (~7% and ~10% torque reductions, respectively). One participant, a habitual barefoot runner, may have lower knee extensor endurance due to a plantar flexor bias and non-rearfoot strike. The other participant showed consistent fatigue accumulation throughout the protocol, potentially influenced by unconfirmed factors like psychological stress or illness. All participants were included in the analysis, as their results were deemed valid.

Conclusion

This study quantified the individual effects of local plantar flexor and knee extensor fatigue on the metabolic cost of running. Running with ~20% plantar flexor and, separately, 21-22% knee extensor neuromuscular fatigue had no effect on the metabolic cost of running for *recreational* and *experienced* runners. Therefore, optimal submaximal running performance appears to be unaffected by local fatigue of these muscle groups. However, we do not discount an indirect effect of local fatigue on subjective determinants, such as rate of perceived exertion. These findings can be applied to racing and training practices, e.g., development of pacing strategies for races and strength training programs for performance.

DATA AVAILABILITY

Source data for this study are not publicly available due to privacy or ethical restrictions. The source data are available to verified researchers upon request by contacting the corresponding author.

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AUTHOR CONTRIBUTIONS

KN: Conceived and designed the research, performed data collection, analyzed data, interpreted results, prepared figures, drafted the manuscript, edited and revised the manuscript, and approved the final version of the manuscript.

HF: Contributed to study design, interpreted results, revised the manuscript, and approved the final version of the manuscript.

JK: Contributed to data collection, revised the manuscript, and approved the final version of the manuscript.

MH: Contributed to study design, interpreted results, prepared figures, revised the manuscript, and approved the final version of the manuscript.

KM: Conceived and designed the research, analyzed data, interpreted results, prepared figures, revised the manuscript, and approved the final version of the manuscript.

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790 # FIGURE LEGENDS

791 **Figure 1** Study protocol. Conducted over two non-consecutive days, one muscle group (plantar flexors or
792 knee extensors) per day (order randomized). MVC = maximum voluntary contraction, EMG =
793 electromyography, FSR = force-sensing resistor.

794 **Figure 1** The metabolic cost of **A.** plantar flexor and **B.** knee extensor fatigue during the *unfatigued run*
795 and *fatigued run*. **C.** Plantar flexor and **D.** knee extensor fatigue before (*MVC #1*) and after (*MVC #2*) the
796 *unfatigued run*, as well as before (*MVC #3*) and after (*MVC #4*) the *fatigued run*. *Pooled* group (N=18)
797 mean data in black, *recreational* group (N=10) data in green, and *experienced* group (N=8) data in
798 purple. The mean 95% CI are represented by horizontal bolded lines. Individual participant data, colored
799 by group affiliation, are displayed as thin lines in the background. MVC = maximum voluntary
800 contraction.

801 **Figure 2** Maximum voluntary contraction (MVC)-normalized integrated mean electromyography (iEMG)
802 measurements of the **A.** soleus (SOL) and **B.** medial gastrocnemius (MG) muscles for plantar flexor
803 fatigue, and **C.** vastus lateralis (VL) and **D.** rectus femoris (RF) for knee extensor fatigue. The normalized
804 linear envelope was normalized to the peak baseline MVC signal, parsed into strides (foot contact to
805 foot contact of the same foot), presented as a rate, and averaged for *minute 1* and *minute 10* of the
806 *unfatigued* (circles and solid lines) and *fatigued* (triangles and dashed lines) *run*. Error bars represent the
807 95% CI. *Pooled* (black; N=18), *recreational* (green; N=10), and *experienced* (purple; N=8) group data are
808 presented for all muscles.

TABLES

Table 1 Mean peak plantar flexor torque (N m [95% CI]) for maximum voluntary contractions (MVCs) #1-4 for the pooled group (N=18), recreational group (N=10), and experienced group (N=8). Differences (N m [95% CI]) are provided for MVC #2-1 and #4-3 for the pooled group as an interaction between group and MVC # was excluded.

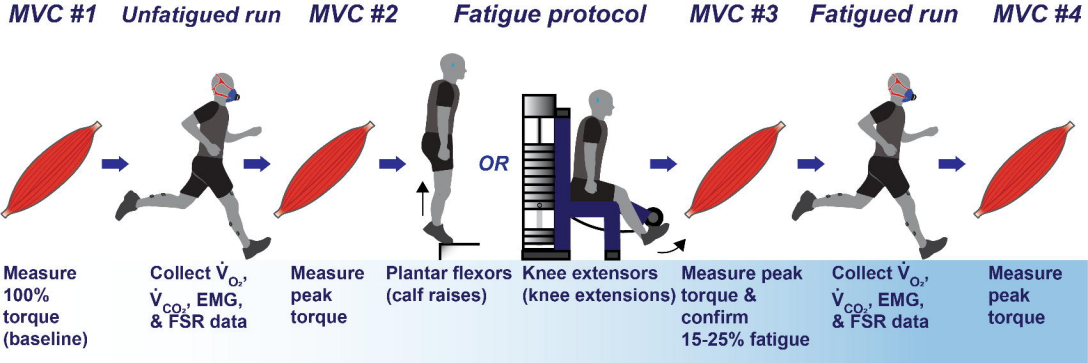
Group	*MVC #1*	*MVC #2*	*MVC #3*	*MVC #4*	Difference (*MVC #2-1*)	p-value (*MVC #2-1*)	Difference (*MVC #4-3*)	p-value (MVC *#4*-3)
Pooled	178 [158, 197]	161 [142, 181]	143 [124, 163]	150 [130, 170]	-16* [-24, -8]	p<0.001*	7* [-1, 15]	p=0.033*
Recreational	176 [150, 202]	160 [134, 186]	142 [116, 168]	149 [123, 175]				
Experienced	179 [150, 208]	163 [134, 192]	145 [116, 174]	152 [120, 179]				

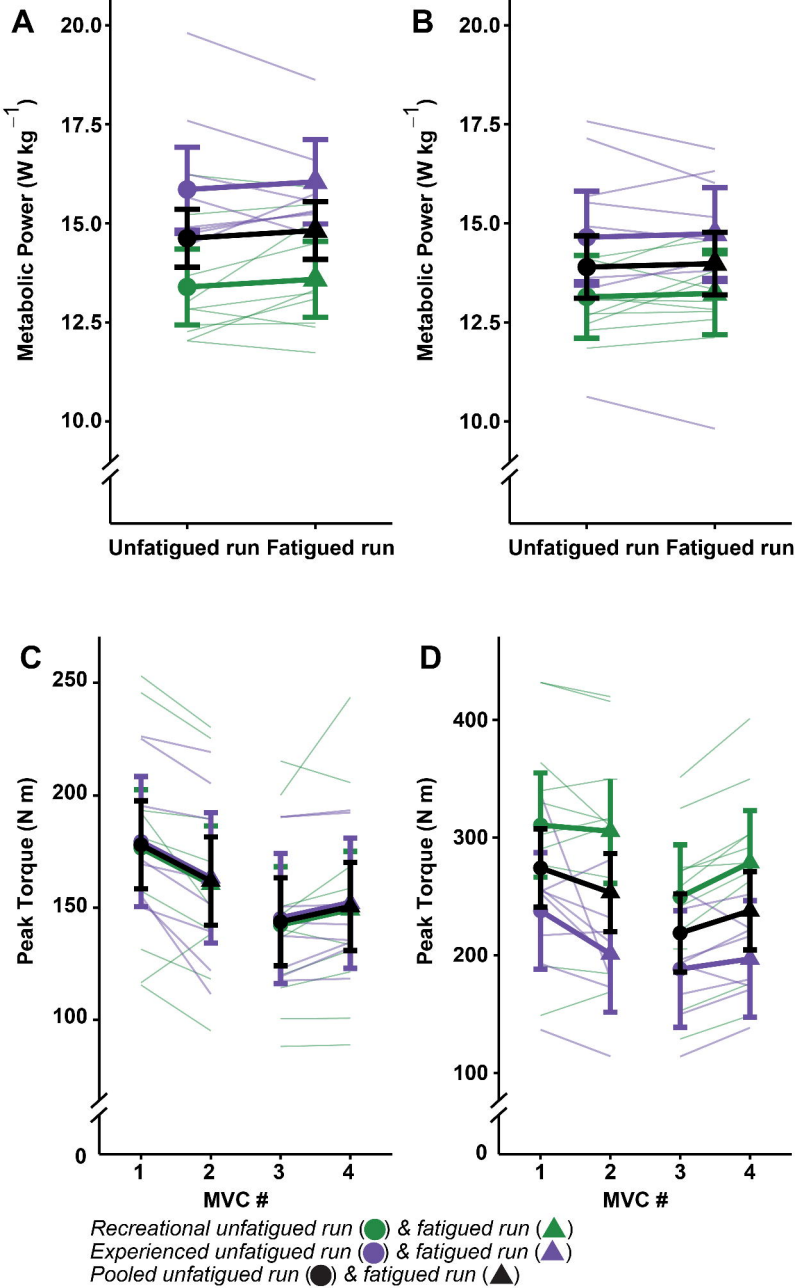
*Indicates statistical significance (p<0.05).

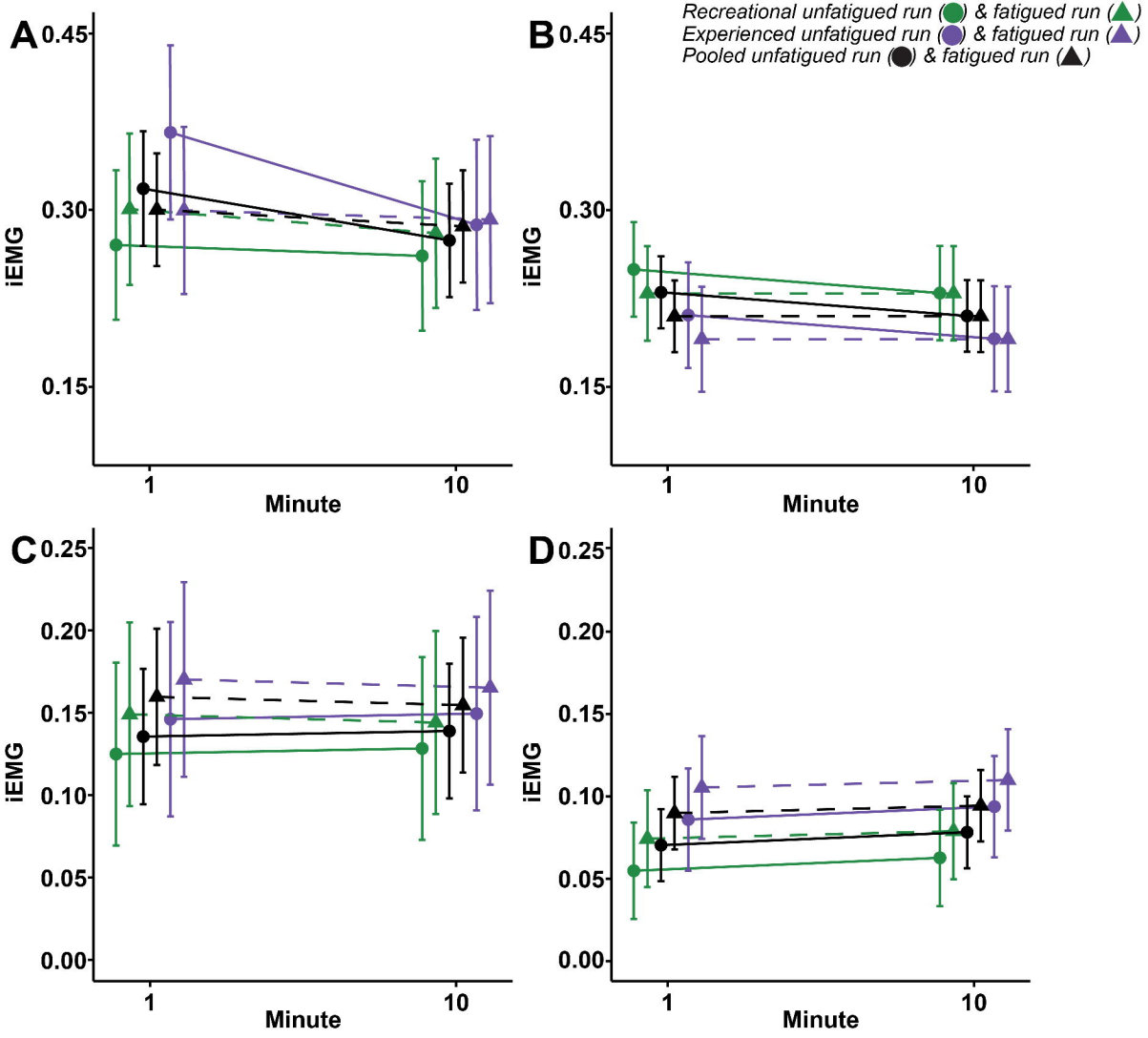
Table 2 Mean peak knee extensor torque (N m [95% CI]) for maximum voluntary contractions (MVCs) *#1-4* for the *pooled* group (N=18), recreational group (N=10), and experienced group (N=8). Differences (N m [95% CI]) are provided for MVC #2-1 and #4-3 for the *recreational and experienced* group as an interaction between group and MVC # was excluded.

Group	*MVC #1*	*MVC #2*	*MVC #3*	*MVC #4*	Difference (*MVC #2-1*)	p-value (*MVC #2-1*)	Difference (*MVC #4-3*)	p-value (MVC *#4*-3)
Pooled	273 [240, 307]	252 [219, 286]	218 [185, 251]	237 [204, 270]				
Recreational	310 [266, 354]	305 [260, 349]	249 [204, 293]	278 [234, 322]	-5 [-28, 18]	p=0.578	29* [6, 52]	p=0.009*
Experienced	237 [187, 286]	200 [151, 250]	187 [138, 237]	196 [147, 246]	37* [-62, -11]	p=0.003*	9 [-17, 34]	p=0.826

*Indicates statistical significance (p<0.05).


MVC #1
Unfatigued run
MVC #2
Fatigue protocol
MVC #3
Fatigued run
MVC #4
OR
Measure 100% torque (baseline)
Collect $\dot{V}_{O_2}$, $\dot{V}_{CO_2}$, EMG, & FSR data
Measure peak torque
Plantar flexors (calf raises)
Knee extensors (knee extensions)
Measure peak torque & confirm 15-25% fatigue
Collect $\dot{V}_{O_2}$, $\dot{V}_{CO_2}$, EMG, & FSR data
Measure peak torque


A
B
C
D
Metabolic Power (W kg^{-1})
20.0
17.5
15.0
12.5
10.0
Unfatigued run
Fatigued run
Peak Torque (N m)
250
200
150
100
0
400
300
1
2
3
4
MVC #
Recreational unfatigued run ( ) & fatigued run ( )
Experienced unfatigued run ( ) & fatigued run ( )
Pooled unfatigued run ( ) & fatigued run ( )


Recreational unfatigued run (●) & fatigued run (▲)
Experienced unfatigued run (●) & fatigued run (▲)
Pooled unfatigued run (●) & fatigued run (▲)
A
B
C
D
iEMG
Minute
0.45
0.30
0.15
0.25
0.20
0.15
0.10
0.05
0.00
1
10