

# Neuromuscular fatigue and gait responses to running at and above critical speed

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## Research Article

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# Abstract

Despite extensive research on running-induced neuromuscular fatigue and gait strategies independently, no studies have examined their interplay these measures during constant-pace running above or at critical speed.

**Purpose.** This study examined whether knee extensor (KE) neuromuscular fatigue was associated with alterations in gait in recreational runners.

**Methods.** Fifteen recreational runners (6 female, 9 male) completed two constant-paced runs on a flat non-motorized treadmill at 10% above and at critical speed (CS + 10 & CS, respectively) until volitional exhaustion. Maximal voluntary isometric KE contractions (MVC) with peripheral nerve stimulation and spatiotemporal gait parameters were collected pre- and post-run.

**Results.** At both running speeds, participants exhibited reductions in MVC force, voluntary activation, as well as potentiated twitch force and twitch rate of force development ( $P_{tw_{RFD}}$ ) (all  $p < 0.001$ ). No significant changes were observed in MVC rate of force development ( $MVC_{RFD}$ ). Runners also demonstrated decreased stride frequency and contact time, alongside increased stride length, flight time, and duty factor (i.e., the relative duration of flight time to step time) at both speeds (all  $p < 0.001$ ). Linear mixed-effects models demonstrated speed-dependent relationships between changes in stride frequency and stride length with MVC force (marginal  $R^2=0.38-0.46$ , conditional  $R^2=0.49-0.51$ ,  $p < 0.001$ ). Weaker relationships were observed between flight time, contact time, and duty factor with decreased muscle contractile function,  $MVC_{RFD}$ , and  $P_{tw_{RFD}}$  (marginal  $R^2=0.16-0.31$ , conditional  $R^2=0.22-0.40$ ,  $p \leq 0.05$ ).

**Conclusion.** These findings suggest that running-induced neuromuscular fatigue modulates gait strategies during running above and at critical speed in a speed-dependent manner.

## INTRODUCTION

Running-induced fatigue encompasses transient impairments in neuromuscular function and alterations in running biomechanics (Giandolini et al. 2016b). Neuromuscular responses manifest as a diminished capacity to generate force due to a decrease in central motor drive and muscle contractile function (Brownstein et al. 2021). These neuromuscular alterations and the associated inflammation are hypothesized to drive compensatory gait strategies – such as an increase in step frequency (SF) and decrease in flight time ( $t_f$ ) – to maintain running performance or attenuate pain due to muscle damage (Millet et al. 2009; Giandolini et al. 2016a, b). Although neuromuscular and gait responses to prolonged running have been extensively studied independently (Morin et al. 2011; Tomazin et al. 2012), the relationship between these measures following fatiguing running tasks remains poorly understood. Quantifying the association between alterations in neuromuscular function and gait may clarify the mechanisms underlying individual variability in responses to running-induced fatigue.

The critical speed (CS) framework provides a robust physiological model to explore fatigue-related responses to running in different exercise intensity domains (Poole et al. 2016). Critical speed represents the

boundary demarcating the heavy and severe exercise intensity domains and corresponds to the highest running speed at which a metabolic steady state can be achieved (Poole et al. 2016). Running at or below CS is often associated with attaining a metabolic steady state with a gradual development of central and peripheral fatigue, characterized by a reduction in central motor output and muscle contractile function impairment, respectively (Thomas et al. 2016). In contrast, running above CS prevents the attainment of a metabolic steady state, leading to an accelerated development of peripheral fatigue (Thomas et al. 2016). This observation is primarily attributed to interference in excitation-contraction coupling due to the accumulation of metabolites, such as inorganic phosphate and  $H^+$  ions, as well as disturbances in calcium handling (Allen et al. 2007).

Neuromuscular responses and spatiotemporal parameters also appear to change as a function of exercise intensity and duration. Short-duration, high-intensity running-induced fatigue is often attributed to metabolic disturbances within the exercising muscles (Brownstein et al. 2021), including the accumulation of metabolites such as  $H^+$ ,  $K^+$ , and lactate (Allen et al. 2007). These metabolites can interfere with excitation-contraction coupling which can explain reports of a longer contact time and shorter flight time (Hayes and Caplan 2014; Patoz et al. 2023). In turn, runners exhibit a decrease in SF and increase in step length (SL) (Avogadro et al. 2003) in an attempt to maintain running velocity. While endurance running performed at or below CS over distances up to 10 km has been reported to have minimal change in fatigue-induced gait strategies (Finni et al. 2002; Riazati et al. 2020). The general maintenance of gait strategies may be attributed to the attainment of a metabolic steady state and lack of significant muscle damage and its associated pain. However, following prolonged running tasks, such as a marathon or ultramarathon, researchers often report an increase in SF and a decrease in  $t_f$  (Millet et al. 2009). Investigators have postulated that these alterations might be due to a protective strategy to mitigate the pain associated with muscle damage resulting from the negative work performed during each footfall (Millet et al. 2009; Morin et al. 2012). In turn, it appears that running intensity and duration can mediate gait strategies.

To date, only two studies have quantified the relationship between running-induced neuromuscular fatigue and gait parameters following prolonged running. Giandolini et al., (2016a) reported a moderate negative association between the change in plantar flexors twitch force (i.e., an index of muscle contractile function) and SF following a mountainous ultramarathon (North-Face® Ultra-Trail du Mont-Blanc® 2012). These investigators demonstrated that a greater decline in twitch force output was accompanied by an increase in SF. Morin et al. (2011), however, found no association between neuromuscular fatigue and alterations in gait parameters following a 24-hour treadmill protocol. Regardless of the discrepancy in these results, both studies have explored the effect of ultra-endurance tasks. In relation to shorter, higher-intensity tasks, Morin et al. (2012) and Tomazin et al. (2012) reported no relationship between changes in neuromuscular and gait parameters following sprint protocols. It is also worth noting that the associations reported by Giandolini et al. (2016a) were quantified between the percent change in twitch force and SF, whereas the studies that reported no association (Morin et al. 2011, 2012; Tomazin et al. 2012) quantified the relationship between the absolute change in any neuromuscular and gait variables. This distinction must be emphasized since relative change normalizes outcomes to the baseline values for each individual, which is not necessarily captured when using the magnitude of change. As such, there remains a paucity of empirical evidence of the

interconnectedness of neuromuscular and gait alterations following fatiguing running performed at and above CS.

Thus, the present exploratory study examines the association between the percent changes in running-induced neuromuscular alterations and spatiotemporal gait parameters following exhaustive running at and above CS in healthy, active individuals. The primary analysis investigates the association between relative changes in knee extensors (KE) maximal voluntary contraction (MVC) force – as an index of global neuromuscular fatigue – with SF following running at CS. Secondary analyses were conducted to explore the association between KE MVC rate of force development ( $MVC_{RFD}$ ), central fatigue (quantified by estimating voluntary activation, VA), and peripheral fatigue (quantified by assessing twitch force amplitude, Ptw, and rate of twitch force development,  $Ptw_{RFD}$ ) and other spatiotemporal parameters (e.g., contact time,  $t_f$ , and duty factor). Due to the novelty of this study design in exploring neuromuscular and spatiotemporal responses to tethered running at and above CS (see *Methods*), running trials were repeated to assess measurement reliability. Elucidating these relationships at distinct running intensities provides insight into whether running-induced neuromuscular alterations are associated with changes in gait strategies, and whether these alterations are consistent across runners.

## METHODS

An *a-priori* sample size calculation was not performed due to the lack of relevant effect size estimates reported in the previous literature following repeated running tasks. Instead, a *post-hoc* sensitivity analysis was conducted (see *Statistical Analysis*). Fifteen healthy adults (6 females, 9 males, age:  $26.5 \pm 5.4$  years, body mass:  $71.3 \pm 11.6$  kg, height:  $169.0 \pm 20.7$  cm) were recruited for this study. Upon enrollment, participants completed and signed an informed consent form and a Physical Activity Readiness Questionnaire (Warburton et al. 2014). Participants were free of neurological, musculoskeletal, and cardiorespiratory conditions that would prevent them from performing high-intensity running. Participants were instructed to avoid strenuous physical activity for 24 hours, as well as ingesting caffeine and alcohol 12 hours before testing sessions. This study was approved by the Conjoint Research Ethics Board at the University of Calgary (REB23-0783) and conformed to the latest version of the Declaration of Helsinki.

## Experimental Design

Participants attended the laboratory on seven occasions at approximately the same time of the day, separated by 3–7 days to mitigate the carryover effects of fatigue from the previous sessions on performance (Fig. 1). All running tasks were performed on a modified flat non-motorized treadmill (Woodway Desmo Pro Evo 2015, Woodway, Waukesha, WI) with the motor removed to minimize friction applied to the treadmill belt. In order to propel themselves, participants wore a leather belt placed at the center of mass and were tethered by a non-extensible steel cable bound to a metal pole so that the cable was parallel to the ground while the participant was stationary.

During the familiarization session, participants were introduced to the neuromuscular assessments, as well as the flat non-motorized treadmill and tether system (Fig. 2a-c). A computer monitor was placed in front of the treadmill providing participants with feedback on the instantaneous treadmill belt speed. During the

warm-up, participants were instructed to walk and progress to a run on the treadmill at a self-selected speed. Participants then performed two 90 s all-out sprints separated by approximately 10 minutes to mitigate any learning effect or pacing strategies adopted during the 3-minute all-out critical speed assessment (3MAO) performed during visits 2 and 3 (Gama et al. 2017, 2018). While performing the all-out sprints, participants were given a 10 s countdown and instructed to begin walking at 5 s, progressively increasing their speed until a maximal effort sprint at 0 s. Participants received strong verbal encouragement and were provided feedback on the time elapsed every 20 s. Participants were then informed that feedback would not be provided throughout the 3MAO during visits 2 and 3.

## **The 3-Minute All-Out Critical Speed Assessment (3MAO)**

During visits 2 and 3, participants performed a tethered 3MAO on a flat non-motorized treadmill, which was previously validated by Gama et al. (2017; 2018). Participants completed a self-directed warm-up on the treadmill for at least 6 minutes. Participants were then instructed to increase their speed from a walk to an all-out sprint over 10 s. Participants received strong verbal encouragement throughout each 3MAO. Critical speed was calculated as the mean speed during the final 30 s of each attempt as previously suggested (Gama et al. 2018). If there was a difference in critical speed greater than 5% between both trials, participants returned for a subsequent 3MAO (Fig. 2c).

## **Running Above Critical Speed (CS + 10)**

During visits 4 and 5, participants performed a high-speed run at 10% above CS to volitional exhaustion. Upon arrival, participants were instructed to warm up on the treadmill at a self-selected speed for at least 6 minutes, followed by a run at CS and 10% above CS for a minimum of 1 minute each. Following the warm-up, an interval of approximately 10 minutes was allocated to perform neuromuscular assessments as well as to provide participants with instructions for the upcoming running task. Participants returned to the treadmill and were allowed to walk at a self-selected speed and progressively increase their speed until reaching CS. Following running at CS for 4 minutes, participants were instructed to increase their speed to 10% above CS until they could not maintain the speed for at least 5 s. Then, participants immediately decreased their speed to CS for a subsequent 4 minutes. Participants received strong verbal encouragement throughout the CS + 10% and final 4-minute run at CS. They were allowed to drink water *ad-libitum* during each trial (Fig. 1).

## **Running at Critical Speed (CS)**

Visits 6 and 7 were performed similarly to visits 4 and 5. However, participants maintained a constant speed pace at CS to volitional exhaustion and did not change speed (Fig. 1).

## **Neuromuscular Assessments**

Neuromuscular function of the right knee extensors was assessed using the interpolated twitch technique (ITT) during which a 100 Hz doublet ( $Db_{100}$ ) was delivered during the MVC force plateau, and at rest,

followed by a 10 Hz doublet ( $Db_{10}$ ) and a single twitch (Ptw) evoked at 2 s intervals (Fig. 2a). Upon arrival to the laboratory, participants were positioned in an isometric dynamometer (Kin-Com, Chattecx Corporation, TN, USA) with their hips and knees flexed at  $90^\circ$  and a cuff was placed around the right ankle. A circular 4 cm diameter self-adhesive foam cathodal electrode (Medi-trace, Kendall, Cardinal Health, Dublin, OH) was placed superficially on the femoral nerve within the inguinal triangle on the right leg of the participant. A  $5.1 \times 8.9$  cm self-adhesive rectangular anodal electrode (Dura-stick plus, DJO Global, Vista, CA) was placed on the right hip between the greater trochanter and the iliac crest. To determine the stimulation intensity required to elicit a supramaximal twitch response from the knee extensors, an electric stimulator (DS7A, Digitimer, Welwyn Garden City, UK) delivered a single square-wave pulse (duration: 1000  $\mu$ s, voltage: 400 V) to the femoral nerve at rest, starting at 20 mA and increasing in 10 to 20 mA increments. This procedure was repeated until no further increase was observed in Ptw force. Once a plateau in twitch force was observed, the stimulation intensity was increased by an additional 30% to ensure supramaximal stimulation (stimulation intensity:  $168.74 \pm 74.17$  mA) and was used for the remainder of the visit.

During baseline testing, participants performed three contractions for 5 s each to elicit 10%, 30%, 50%, and 75% MVC force with approximately 1 minute before each contraction. Participants then performed one repetition at 90% and two MVCs separated by approximately 2 minutes. Participants then performed MVCs coupled with peripheral nerve stimuli (Fig. 2a) separated by approximately 2 minutes, until two contractions were within 5%. Voluntary activation was calculated using the corrected formula (Eq. 1) to account for the superimposed twitch not elicited during the MVC plateau (Strojnik and Komi 1998). Voluntary activation was calculated as:

$$Voluntary\ Activation\ (\%) = 100 - \left[ \left( \frac{(SIT - F_b) \times (1 - \frac{F_b}{F_{max}})}{Db_{100}} \right) \times 100 \right] \quad [1]$$

Where SIT is the force elicited by the 100 Hz doublet superimposed twitch during the force plateau,  $F_b$  is the force immediately before the superimposed twitch,  $F_{max}$  is the maximal MVC force elicited, and  $Db_{100}$  is the force elicited by the 100 Hz doublet applied at rest. Rate of force development (RFD) during the MVC ( $MVC_{RFD}$ ) and Ptw ( $Ptw_{RFD}$ ) was quantified as the first derivate of the force-time signal during the ascending phase of each contraction. Rate of force development values were retained from the trial with the highest peak force during the MVC and Ptw, respectively.

## Gait Assessments

Before each running task, a Movella DOT (Xsens DOT, Movella, Henderson, NV) inertial measurement unit (IMU) was secured using a strap provided by the manufacturer on the posterior aspect of each ankle and positioned as suggested by the manufacturer (Movella, Henderson, NV). Each IMU recorded three axial acceleration of the foot at 120 Hz (range:  $\pm 16$  g). Data were visually inspected, and gait data for the final 5 s to 10 s of each running trial were omitted to account for participants terminating the run and transferring from the treadmill to the isometric dynamometer. Gait analysis was performed manually using data retained from the final 20 s of the 4th minute (Play et al. 2022) and final 20 s while running at CS as suggested by Strohrmann et al. (2012). Briefly, data were visually inspected for both feet, and 20 strides (40 steps) were

selected from both feet (Riazati et al. 2019). Step frequency was calculated as the number of steps divided by the total duration from the first peak in the magnitude of the resultant acceleration ( $a_{\text{resultant}}$ ) from the IMU x, y, and z coordinates to the final peak of the last step (Fig. 2d; Eq. 2). Step length was then calculated by dividing the mean treadmill speed by SF.

$$a_{\text{resultant}} = \sqrt{a_x^2 + a_y^2 + a_z^2} \quad [2]$$

Where  $a_x$ ,  $a_y$ , and  $a_z$  are the acceleration components. To calculate contact time ( $t_c$ ), initial foot contact was identified as the peak in  $a_{\text{resultant}}$  and toe off when  $a_{\text{resultant}}$  increased beyond 2 g (Fig. 2d) (Strohrmann et al. 2012). Flight time ( $t_f$ ) was then calculated by rearranging Eq. 3.

$$SF = \frac{1}{t_c + t_f} \quad [3]$$

Duty factor (DF), representing the relative duration of flight time to step time, was then calculated as:

$$\text{Duty Factor (\%)} = \left[ \frac{t_f}{t_c + t_f} \right] \times 100 \quad [4]$$

## Perceptual Responses

Perceptual responses were recorded every 4 minutes throughout each running task and running termination. Participants rated their perceived leg pain (0–10 visual analogue scale; Campbell and Lewis 1990), breathlessness (0–10 modified Borg scale; Kendrick et al. 2000), general fatigue (0–10 rating of fatigue scale; Micklewright et al. 2017), and overall effort (0–10 Borg CR10 scale; Borg 1982). For pain, participants were asked to rate their global leg pain as related to muscle aching or burning. For dyspnea, participants were asked to rate their breathlessness. For fatigue, participants were asked to provide a global rating of their sensation of fatigue or exhaustion due to the running task. For overall effort, participants were asked to rate how hard they were working. Scales were thoroughly explained during the familiarization session, and participants were briefly reminded following the neurophysiological assessments and before starting the running task.

## Data Analysis

Knee extensor force data were recorded at 2000 Hz in the Powerlab system (16/30-ML880/P, ADInstruments, Dunedin, New Zealand), amplified (ML138, ADInstruments), bandpass filtered (5-500 Hz), and analyzed offline using LabChart 8 software (ADInstruments). Changes in neuromuscular and spatiotemporal gait parameters were quantified as the relative change from pre- to post-intervention ( $\% \Delta$ ; Eq. 5):

$$\Delta X (\%) = \left( \frac{X_{\text{POST}} - X_{\text{PRE}}}{X_{\text{PRE}}} \right) \times 100 \quad [5]$$

Where  $X$  is the measured variable, and  $X_{\text{POST}}$  and  $X_{\text{PRE}}$  are the values recorded during post- and pre-intervention assessments, respectively.

## Statistical Analysis

All analyses were performed in R (Version 4.4.2, R Core Team, 2024). The data are presented as mean  $\pm$  SD. In healthy adults, KE VA assessed by electrical nerve stimulation is typically  $\geq 85\%$ , with values below reflecting incomplete neural drive (Kooistra et al. 2007; Nuzzo et al. 2021). Therefore, baseline MVC and MVC<sub>RFD</sub> with VA values  $< 85\%$  were not considered as maximal effort and were omitted from the analysis.

Reliability was quantified by the Intraclass Correlation Coefficient (ICC3,k) for the critical speed value derived from the 3MAO, as well as pre- and post-intervention outcomes for neuromuscular and gait parameters of interest. ICC was classified as poor ( $< 0.50$ ), moderate ( $0.50-0.75$ ), good ( $0.76-0.90$ ), and excellent ( $\geq 0.91$ ) (Koo and Li 2016). Values are reported as ICC [95% confidence interval].

To explore the effect of time (baselines and post-test), intervention (CS + 10 and CS), and visit (first and second attempt per intervention) on central and peripheral fatigue measures (i.e., MVC, MVC<sub>RFD</sub>, VA, Ptw, Ptw<sub>RFD</sub>, and Db10:100), gait responses (i.e., SF, SL,  $t_c$ ,  $t_f$ , and DF) and perceptual factors (i.e., leg pain, breathlessness, fatigue, and overall effort), separate mixed-effects ANOVAs were performed. A *post-hoc* Bonferroni correction was performed when significant results were returned.

To assess the association between the above-mentioned neuromuscular and gait alterations and to account for the repeated measures, separate linear mixed-effects models were used. For each model, the gait parameters were the outcome measures, whereas fixed effects and their interaction included the neuromuscular response (e.g.,  $\%\Delta\text{MVC}$ ), interventions (CS + 10 and CS), and visit. The random effect was participant to account for within-subject repeated measures. Models were fit using maximum likelihood estimation. Nested models were fit using likelihood ratio tests to determine whether the inclusion of a fixed effect and its interaction term improved model fit. If the higher-order interaction terms did not significantly improve model fit, the fixed effect term was removed from the model to preserve parsimony. Model assumptions were completed through visual inspection of residual distribution (Q-Q plots) and residual against fitted values, and models were checked for singularity. Fixed effect confidence intervals were calculated using the Wald approximation. T-tests for coefficient significance were calculated using Satterthwaite's method. When significant interaction effects were returned, *post-hoc* slope analyses were performed within each intervention. Linear mixed models were fit using the lme4 R package (Bates et al. 2015) and coefficient significance was assessed using the lmerTest R package (Kuznetsova et al. 2017). P-values were adjusted for multiple comparisons using the Benjamini-Hochberg False Discovery Rate within groups of related analyses (i.e., by outcome). Significance was set at  $p < 0.05$ .

To evaluate the minimum detectable effect (MDE) of fixed effects and interaction terms, *post-hoc* sensitivity analysis was performed using a Wald-type approximation with significance set at  $\alpha \leq 0.05$ . Minimum detectable effect was calculated as the product of each coefficient's standard error and the critical  $t$  value. If a term exceeded the MDE, it indicated that there was sufficient sensitivity to detect a difference in the outcome variable.

# RESULTS

## 3-Minute All-Out Critical Speed Assessment (3MAO)

There were no significant differences between critical speed values derived from the 3MAO assessments (attempt 1:  $2.23 \pm 0.58$  m/s, attempt 2:  $2.24 \pm 0.58$  m/s, ICC = 0.94 [0.89–0.98]). One participant was asked to return to the laboratory for a third 3MAO assessment because the difference in the derived critical speed between the first and second trials was greater than 5%. A representative response to the 3MAO from one participant is found in Fig. 2c.

## Reliability

There was good to excellent reliability for all neuromuscular and gait variables across all visits at baseline (e.g., MVC CS + 10: ICC = 0.98, 95% CI [0.96–1.00]; CS: 0.98, 95% CI [0.93–0.99]) and post-intervention (e.g., MVC CS + 10: ICC = 0.97, 95% CI [0.92–0.99]; CS: 0.98, 95% CI [0.94–0.99]). There was no significant effect of visit on any of the neuromuscular and gait outcomes in the mixed-effect ANOVAs, indicating that there were consistent neuromuscular and gait responses across interventions.

## Time to Task Failure and Perceptual Responses

Time to task failure was significantly shorter during CS + 10 than CS trials (CS + 10:  $463.5 \text{ s} \pm 443.8 \text{ s}$ , CS:  $1644.1 \text{ s} \pm 1118.8 \text{ s}$ ,  $p < 0.001$ ). There were no significant differences between CS + 10 and CS for end-exercise effort (CS + 10:  $9.03 \pm 0.94$ , CS:  $8.34 \pm 2.07$ ,  $p = 0.08$ ), fatigue (CS + 10:  $8.90 \pm 1.29$ , CS:  $8.36 \pm 1.96$ ,  $p = 0.18$ ), leg pain (CS + 10:  $7.69 \pm 2.38$ , CS:  $7.76 \pm 1.66$ ,  $p = 0.90$ ), or breathlessness (CS + 10:  $8.21 \pm 1.29$ , CS:  $7.54 \pm 1.95$ ,  $p = 0.08$ ).

## Neuromuscular Responses

Participants performed the post-intervention assessment at  $38.7 \text{ s} \pm 6.85 \text{ s}$ . The mixed-effects ANOVA returned a significant time effect for MVC (CS + 10:  $-6.97\% \pm 10.57\%$ , CS:  $-4.67\% \pm 10.44\%$ ,  $p < 0.001$ ), VA (CS + 10:  $-1.69\% \pm 6.46\%$ , CS:  $-3.50\% \pm 6.23\%$ ,  $p = 0.02$ ), Ptw (CS + 10:  $-12.01\% \pm 10.75\%$ , CS:  $-8.49 \pm 13.17$ ,  $p < 0.001$ ), Ptw<sub>RFD</sub> (CS + 10:  $-18.36\% \pm 19.01\%$ , CS:  $-12.59\% \pm 15.72\%$ ,  $p < 0.001$ ), and Db10:Db100 (CS + 10:  $-9.21\% \pm 13.54\%$ , CS:  $-8.75\% \pm 8.31\%$ ,  $p < 0.001$ ) (Fig. 3).

## Spatiotemporal Gait Responses

The mixed-effects ANOVA returned a significant time effect for  $t_f$  ( $p = 0.007$ ) and DF ( $p = 0.04$ ), and significant intervention effects for SF (CS + 10:  $-0.10\% \pm 6.77\%$ , CS:  $-2.06\% \pm 2.90\%$ ,  $p < 0.001$ ), SL (CS + 10:  $2.27\% \pm 7.78\%$ , CS:  $1.82\% \pm 2.82\%$ ,  $p < 0.001$ ),  $t_c$  (CS + 10:  $-2.17\% \pm 16.37\%$ , CS:  $-0.11\% \pm 15.78\%$ ,  $p < 0.001$ ),  $t_f$  (CS + 10:  $9.19 \pm 20.10$ , CS:  $10.99 \pm 18.86$ ,  $p < 0.001$ ), and DF (CS + 10:  $6.60\% \pm 16.55\%$ , CS:  $8.43\% \pm 19.09$ ,  $p < 0.001$ ) (Fig. 4).

## Linear Mixed-Effects Models

Inclusion of visit as a fixed effect and its interaction with neuromuscular response (e.g., % $\Delta$ MVC) and intervention (CS + 10 and CS) did not significantly improve any of the model fits (likelihood ratio test,  $p = 0.21-0.89$ ), nor did it change fixed effect estimates and their interaction. Accordingly, the visit was excluded from the final model to preserve parsimony. The results herein are presented from the simplified model.

## Step Frequency and Step Length

There was a significant % $\Delta$ MVC  $\times$  intervention interaction on % $\Delta$ SF ( $\beta = 0.56$ , 95% CI [0.34, 0.77],  $p < 0.001$ ). The random intercept SD was 0.96 and the residual SD was 3.47. The fixed effects (% $\Delta$ MVC, intervention, and their interaction) in the model explained 46% of the variance in % $\Delta$ SF (marginal  $R^2 = 0.46$ ) and 49% of the variance in % $\Delta$ SF (conditional  $R^2 = 0.49$ ) when including participant-level random effects, indicating modest between-participant variability. *Post-hoc* analysis of the estimated marginal means (slope) revealed that % $\Delta$ SF was positively associated with % $\Delta$ MVC following CS + 10 ( $\beta = 0.39$ , 95% CI [0.21, 0.57]) and negatively associated following CS ( $\beta = -0.17$ , 95% CI [-0.33, -0.01]), indicating the relationship between % $\Delta$ MVC and % $\Delta$ SF was stronger following CS + 10 (Fig. 5a).

There was a significant % $\Delta$ MVC  $\times$  intervention interaction on % $\Delta$ SL ( $\beta = -0.52$ , 95% CI [-0.71, -0.32],  $p < 0.001$ ). The random intercept SD was 1.61 and the residual SD was 3.21. The fixed effects (% $\Delta$ MVC, intervention, and their interaction) model explained 38% of the variance in % $\Delta$ SL (marginal  $R^2 = 0.38$ ) and 51% of the variance in % $\Delta$ SL (conditional  $R^2 = 0.51$ ) when including participant-level random effects, indicating large between-participant variability. *Post-hoc* analysis of the estimated marginal means (slope) revealed that % $\Delta$ SL was negatively associated with % $\Delta$ MVC following CS + 10 ( $\beta = -0.36$ , 95% CI [-0.54, -0.19]) and positively associated following CS ( $\beta = 0.15$ , 95% CI [-0.01, 0.31]), indicating the relationship between % $\Delta$ MVC and % $\Delta$ SL was stronger following CS + 10.

Linear mixed-effects models for  $t_c$ ,  $t_a$ , and DF are found in Table 1–3. There were no significant fixed effects or interactions for VA and Db10:Db100 with any spatiotemporal gait outcome.

Table 1  
Fixed-effects estimates and model fits from linear mixed-effects models for secondary outcomes

| Outcome                                                                                                                                                                                                                                                                                                                                                              | Predictor            | Neuromuscular effect    |                   | Intervention effect       |      | Interaction             |                   | $R^2m$ | $R^2c$ |
|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------|-------------------------|-------------------|---------------------------|------|-------------------------|-------------------|--------|--------|
|                                                                                                                                                                                                                                                                                                                                                                      |                      | $\beta$ [95% CI]        | $p$               | $\beta$ [95% CI]          | $p$  | $\beta$ [95% CI]        | $p$               |        |        |
| % $\Delta t_f$                                                                                                                                                                                                                                                                                                                                                       | % $\Delta MVC_{RFD}$ | -0.19<br>[-0.33, -0.04] | <b>0.05</b>       | 3.19<br>[-7.40, 13.62]    | 0.69 | 0.04<br>[-0.21, 0.28]   | 0.80              | 0.18   | 0.39   |
|                                                                                                                                                                                                                                                                                                                                                                      | % $\Delta Ptw$       | 0.92<br>[0.40, 1.45]    | <b>0.009</b>      | -1.50<br>[-14.55, 11.55]  | 0.82 | -1.26<br>[-1.35, 0.31]  | 0.36              | 0.20   | NA*    |
|                                                                                                                                                                                                                                                                                                                                                                      | % $\Delta Ptw_{RFD}$ | 0.73<br>[0.28, 1.18]    | <b>0.009</b>      | -7.86<br>[-21.10, 5.38]   | 0.36 | -0.74<br>[-1.33, -0.15] | <b>0.03</b>       | 0.16   | NA*    |
| % $\Delta t_c$                                                                                                                                                                                                                                                                                                                                                       | % $\Delta Ptw$       | -0.66<br>[-1.11, -0.22] | <b>0.01</b>       | -4.26<br>[-14.75, 6.39]   | 0.50 | -0.01<br>[-0.69, 0.67]  | 0.97              | 0.23   | 0.30   |
|                                                                                                                                                                                                                                                                                                                                                                      | % $\Delta Ptw_{RFD}$ | -0.60<br>[-0.99, -0.22] | <b>0.01</b>       | 4.61<br>[-6.14, 15.57]    | 0.50 | 0.54<br>[0.06, 1.03]    | 0.06              | 0.16   | 0.22   |
| % $\Delta DF$                                                                                                                                                                                                                                                                                                                                                        | % $\Delta MVC_{RFD}$ | -0.18<br>[-0.32, -0.03] | <b>0.02</b>       | 2.05<br>[-7.81, 11.83]    | 0.75 | 0.03<br>[-0.21, 0.25]   | 0.78              | 0.18   | 0.40   |
|                                                                                                                                                                                                                                                                                                                                                                      | % $\Delta Ptw$       | 1.24<br>[0.67, 1.81]    | <b>&lt; 0.001</b> | -4.41<br>[-18.37, 9.55]   | 0.68 | -0.65<br>[-1.53, 0.23]  | 0.23              | 0.29   | NA*    |
|                                                                                                                                                                                                                                                                                                                                                                      | % $\Delta Ptw_{RFD}$ | 1.15<br>[0.68, 1.62]    | <b>&lt; 0.001</b> | -14.47<br>[-28.08, -0.85] | 0.07 | -1.10<br>[-1.70, -0.50] | <b>&lt; 0.001</b> | 0.31   | NA*    |
| Note: Bolded text indicates significant outcomes. $t_f$ : flight time, $t_c$ : contact time, DF: duty factor, $MVC_{RFD}$ : maximal voluntary contraction rate of force development, Ptw: potentiated twitch, $Ptw_{RFD}$ : potentiated twitch force rate of force development, $R^2m$ : marginal $R^2$ , $R^2c$ : conditional $R^2$ , % $\Delta$ : relative change. |                      |                         |                   |                           |      |                         |                   |        |        |

\*Models are singular when random intercept SD is 0 resulting in no conditional  $R^2$ . Models that were singular were retained to account for the repeated measures.

Table 2

Post-hoc comparisons of the estimated marginal means for significant interaction effects (presented in Table 1)

| Outcome                                                                                                                                                                                                                                                                                                                                                                               | Predictor            | Intervention | $\beta$ [95% CI]    |
|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------|--------------|---------------------|
| % $\Delta t_f$                                                                                                                                                                                                                                                                                                                                                                        | % $\Delta Ptw_{RFD}$ | CS + 10      | -0.01 [-0.41, 0.39] |
|                                                                                                                                                                                                                                                                                                                                                                                       |                      | CS           | 0.73 [0.25, 1.22]   |
| % $\Delta DF$                                                                                                                                                                                                                                                                                                                                                                         | % $\Delta Ptw_{RFD}$ | CS + 10      | 0.05 [-0.36, 0.47]  |
|                                                                                                                                                                                                                                                                                                                                                                                       |                      | CS           | 1.15 [0.65, 1.65]   |
| t <sub>f</sub> : flight time, t <sub>c</sub> : contact time, DF: duty factor, MVC <sub>RFD</sub> : maximal voluntary contraction rate of force development, Ptw: potentiated twitch, Ptw <sub>RFD</sub> : potentiated twitch force rate of force development, R <sup>2</sup> m: marginal R <sup>2</sup> , R <sup>2</sup> c: conditional R <sup>2</sup> , % $\Delta$ : relative change |                      |              |                     |

Table 3

Random-effects and residual standard deviations from the linear mixed-effects models (presented in Table 1)

| Outcome                                                                                                                                                                                                                                                                                                                                     | Predictor            | Random Intercept SD | Residual SD |
|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------------|---------------------|-------------|
| % $\Delta t_f$                                                                                                                                                                                                                                                                                                                              | % $\Delta MVC_{RFD}$ | 8.76                | 16.98       |
|                                                                                                                                                                                                                                                                                                                                             | % $\Delta Ptw$       | NA*                 | 17.81       |
|                                                                                                                                                                                                                                                                                                                                             | % $\Delta Ptw_{RFD}$ | NA*                 | 18.27       |
| % $\Delta t_c$                                                                                                                                                                                                                                                                                                                              | % $\Delta Ptw$       | 4.45                | 14.07       |
|                                                                                                                                                                                                                                                                                                                                             | % $\Delta Ptw_{RFD}$ | 3.88                | 14.69       |
| % $\Delta DF$                                                                                                                                                                                                                                                                                                                               | % $\Delta MVC_{RFD}$ | 3.80                | 16.92       |
|                                                                                                                                                                                                                                                                                                                                             | % $\Delta Ptw$       | NA*                 | 19.95       |
|                                                                                                                                                                                                                                                                                                                                             | % $\Delta Ptw_{RFD}$ | NA*                 | 18.78       |
| SD: standard deviation, $t_f$ : flight time, $t_c$ : contact time, DF: duty factor, $MVC_{RFD}$ : maximal voluntary contraction rate of force development, Ptw: potentiated twitch, $Ptw_{RFD}$ : potentiated twitch force rate of force development, $R^2_m$ : marginal $R^2$ , $R^2_c$ : conditional $R^2$ , % $\Delta$ : relative change |                      |                     |             |

\*Models are singular when random intercept SD is 0 resulting in no conditional  $R^2$ . Models that were singular were retained to account for the repeated measures.

## Sensitivity Analysis

Post-hoc sensitivity analyses revealed that all significant effects and interactions exceeded their respective MDE, indicating that the models were statistically sensitive to detect effects of the observed magnitude on the outcome measure.

## DISCUSSION

This is the first study to quantify the relationship between running-induced neuromuscular fatigue and spatiotemporal gait alterations following exhaustive runs performed at and above critical speed. Overall, the results indicate that there is an intensity-dependent association between changes in neuromuscular fatigue and gait parameters. Specifically, reductions in MVC were associated with increased SF following CS and decreased SF following CS + 10, as well as between  $\% \Delta \text{Ptw}_{\text{RFD}}$  with  $\% \Delta t_f$  and  $\% \Delta \text{DF}$ . A novel aspect of our study is the inverse relationship between  $\% \Delta \text{MVC}$  with  $\% \Delta \text{SF}$  and  $\% \Delta \text{SL}$  at CS + 10 and CS. Additionally, there were associations between  $\% \Delta \text{MVC}_{\text{RFD}}$ ,  $\% \Delta \text{Ptw}$ , and  $\% \Delta \text{Ptw}_{\text{RFD}}$  with  $\% \Delta t_c$ ,  $\% \Delta t_f$ , and  $\% \Delta \text{DF}$  that were independent of running intensity. Collectively, these findings suggest that neuromuscular fatigue can modulate gait parameters in an intensity-dependent manner.

## Neuromuscular Fatigue Following Running at Different Speeds

For the decline in MVC, VA, and Ptw, while we observed a 1–3% decline in VA and 9–12% decline in Ptw, which has been previously reported (Škof and Strojnik 2006), the MVC force showed a 5–7% decline at both running intensities. This appears to fall within the lower range reported following exhaustive running. For instance, prior researchers have reported up to a 15% decline in MVC following a prolonged run at the second metabolic threshold (Škof and Strojnik 2006; Dittrich et al. 2013). In another study, Márquez et al. (2023) explored the effect of different running intensities and reported no change in MVC following a run below CS, and an 11% reduction following maximal effort running. One plausible explanation for the modest decline in MVC observed in the present study could be premature task termination due to the physiological and metabolic demands associated with non-motorized treadmill running. Unlike motorized treadmills, the treadmill used in this study does not have a rigid deck, which increases impact absorption and may compromise the energy returned to the runner (Montgomery et al. 2016; Colino et al. 2020; Woodway, 2024). To overcome the attenuated energy restitution, runners appear to develop a compensatory gait strategy characterized by increased muscle fiber recruitment and activity (Montgomery et al. 2016). The increased muscular demands likely elevate the metabolic cost of running, promoting an earlier reliance on anaerobic metabolism, and accelerates the development of parameters such as perceived effort, ultimately leading to shorter time to exhaustion (Edwards et al. 2017; Dabbs et al. 2021). Indeed, participants experienced near-maximal to maximal values for the effort (~ 8–10), pain (~ 7–9) and fatigue (~ 8–10) (all on 0–10 scales) at the end of both CS and CS + 10 trials. The attenuated neuromuscular responses may be due to runners achieving maximal perceived effort and leg pain rather than the integration of multiple systems.

## Gait Responses to Fatiguing Running at Different Speeds

The gait changes observed in the present study contrast with the prevailing hypothesis that runners increase their SF and decrease their  $t_f$  as fatigue develops (Millet et al. 2009). These adjustments have been attributed to a diminished propulsive capacity or a protective strategy to attenuate discomfort associated with repeated eccentric loading (Giandolini et al. 2016a). However, this framework may be more applicable to prolonged running tasks that induce substantial muscle damage rather than shorter exhaustive runs at

higher intensities. Runners in the present study exhibited no change in SF and an 8–9% increase in  $t_f$ , aligning with gait alterations previously reported following exhaustive heavy- to severe-intensity running (Borrani et al. 2003; Avogadro et al. 2003). Other researchers have reported a decline in SF (~ 1.8%) which is similar to the directional changes we found in this study, although the changes in this study weren't significant. One explanation for this gait strategy is that runners adopt a more propulsive gait strategy at higher intensities and during non-motorized treadmill running which manifests as an increase in SL and  $t_f$  accompanied by a decrease in step frequency. Namely, the friction applied against the runners during tethered non-motorized treadmill running scales with speed and body mass (Lakomy 1987). To compensate, runners tend to adopt a forward lean (Lakomy 1987) and forefoot strike pattern which increases KE and plantar flexor muscle activity (Montgomery et al. 2016). This posture resembles that adopted during high-speed running (e.g., CS + 10), suggesting that fatigued running at high intensities prioritizes propulsion rather than being a protective strategy. Previous reports have demonstrated this following an exhaustive severe intensity run that elicited similar neuromuscular alterations to those in the current study (Márquez et al. 2023). In contrast, the inverse relationship observed during CS may reflect lower frictional forces due to the reduced speed and vertical forces (Jiang et al. 2024). At lower speeds, runners may not need to lean as far forward throughout the gait cycle resulting in slower fatigue development and the emergence of an alternative gait strategy.

## Associations Between Neuromuscular Fatigue and Gait Alterations

To the best of our knowledge, only two studies have quantified the association between neuromuscular fatigue and spatiotemporal gait parameters following prolonged running. Giandolini et al. (2016a) reported a moderate correlation ( $r = 0.5$ ) between indices of peripheral fatigue of the plantar flexors and an increase in SF, whereas Morin et al. (2010) observed no relationship between KE or plantar flexor fatigue and spatiotemporal parameters following an ultramarathon and a 24-hour treadmill run, respectively. The relationships observed in the current study were stronger than those previously reported, likely attributable to methodological differences between studies. Primarily, Giandolini et al. (2016a) assessed the plantar flexors, which primarily contribute to horizontal propulsion whereas the KE contribute predominantly to vertical propulsion (Kotsifaki et al. 2021). Secondly, the timing of the neuromuscular assessments differed substantially between studies. Our study assessed participants within 40 s, whereas Giandolini et al. (2016a) conducted assessments approximately 60 minutes following running completion. The 1-hour interval permits partial recovery and secondary processes (e.g., inflammatory responses) to influence neuromuscular outcomes, potentially attenuating the strength of the relationship. In contrast, Morin et al. (2011) quantified the associations between absolute rather than relative change, which might influence the strength of the relationship. Altogether, these methodological differences likely contributed to the stronger associations observed in the present study highlighting the importance of running intensity, muscle group selection, and assessment timing when examining the interaction between neuromuscular fatigue and running mechanics.

## Secondary Analyses

During secondary analyses, we found relationships between  $\%\Delta\text{Ptw}$ ,  $\%\Delta\text{Ptw}_{\text{RFD}}$  and  $\%\Delta\text{MVC}_{\text{RFD}}$  with  $\%\Delta t_f$  and  $\%\Delta\text{DF}$ . These associations suggest that muscle contractile impairment might play a role in regulating gait responses during exhaustive running. Contractile interference due to the accumulation of inorganic phosphate,  $\text{H}^+$  ions, and changes in  $\text{Ca}^{2+}$  kinetics can slow muscle contraction, which has been observed as the decline in  $\text{Ptw}_{\text{RFD}}$  and  $\text{MVC}_{\text{RFD}}$  following running tasks (Nicol et al. 1991; Avela et al. 1999; Finni et al. 2002). To compensate for slowed muscle contraction and to produce sufficient propulsion, runners must adopt a longer contact time. The prolonged  $t_c$  allows runners to drift further back on the treadmill belt, necessitating an increase in  $t_f$  and SL to reposition themselves to their initial position. This gait strategy may also function as a protective response to the deleterious effects of pain. Namely, leg pain experienced during running at and above CS + 10 may elicit a gait strategy whereby an increase in  $t_f$  attenuates the pain associated with concentric muscle actions that occur during the stance phase (Vecchiet et al. 1999). Accordingly, the relationships observed between  $\%\Delta\text{MVC}$  with  $\%\Delta\text{SF}$  and  $\%\Delta\text{SL}$  may arise indirectly from the development of peripheral fatigue and its influence on  $t_c$  and flight time. This would suggest that fatigue-induced gait alterations emerge through the interplay between contractile interference and gait adjustments rather than directly modulating stride parameters. This mechanism would be applicable during short, high-intensity running, complimenting the hypothesis by Millet et al. (2009) that runners increase their SF and decrease their  $t_f$  following prolonged running.

## Limitations

The running strategies adopted during CS + 10 and CS may have been influenced by the constraints placed upon the runner by the treadmill used in this study. Namely, runners had to overcome opposing frictional forces which could have resulted in a different muscle recruitment strategy and body posture. However, we did not record EMG or motion capture to substantiate these claims. Additionally, we did not compare neuromuscular and gait responses during overground and treadmill running at the same intensity to non-motorized treadmill running. These limitations necessitate further research to determine whether the relationships observed here persist following high-intensity running across running modalities.

## Conclusion

This study demonstrates that running-induced neuromuscular fatigue is associated with spatiotemporal gait alterations and that these adaptations are intensity-dependent. Notably, the direction of the relationship between  $\%\Delta\text{MVC}$  and  $\%\Delta\text{SF}$  indicates intensity-dependent mechanisms. These results underscore the importance of considering intensity-specific neuromuscular constraints when interpreting compensatory gait strategies adopted during exhaustive running. Collectively, our results challenge current research by suggesting that running-induced fatigue affects compensatory gait strategies distinctly when running at and above CS.

## Abbreviations

3MAO

3-minute all-out critical speed assessment

CI  
Confidence interval  
CS  
Critical speed  
CS + 10  
10% above critical speed  
 $Db_{10}$   
10 Hz doublet  
 $Db_{100}$   
100 Hz doublet  
DF  
Duty factor  
ICC  
Intraclass correlation coefficient  
IMU  
Inertial measurement unit  
IQR  
Inter-quartile range  
ITT  
Interpolated twitch technique  
MDE  
Minimal detectable effect  
MVC  
Maximal voluntary contraction  
Ptw  
Potentiated twitch  
RFD  
Rate of force development  
SF  
Step frequency  
SL  
Step length  
 $t_c$   
Ground contact time  
 $t_f$   
Flight time  
VA  
Voluntary activation

## Declarations

The authors do not declare competing financial or non-financial interests that are directly or indirectly related to this work.

## Author Contribution

A.Z.P., S.J.A., and G.Y.M conceived the protocol, A.Z.P. wrote the main manuscript text, A.Z.P. performed all data analyses, A.Z.P. prepared all figures and tables. All authors reviewed the manuscript.

## Data Availability

All data supporting the findings of this study are presented within the paper.

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Figures

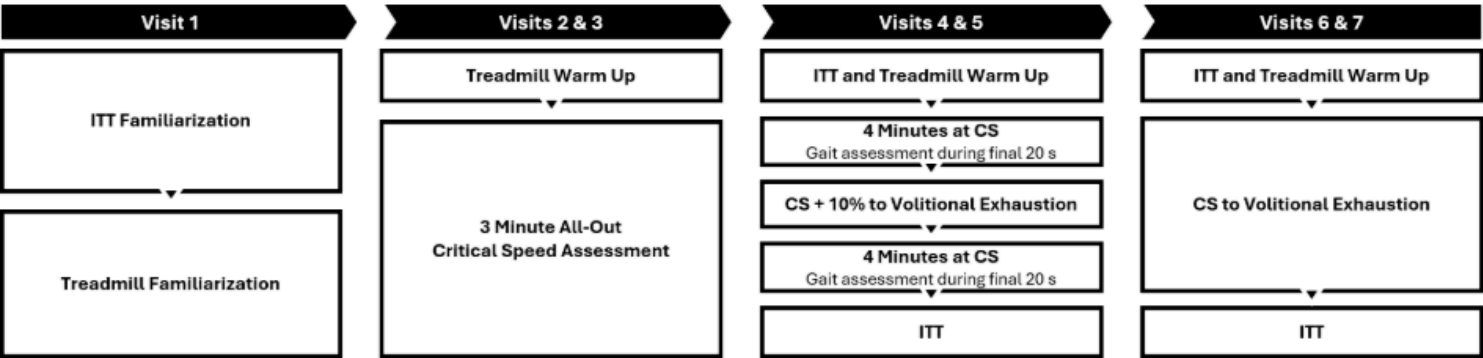


Figure 1

Study protocol with each visit performed twice

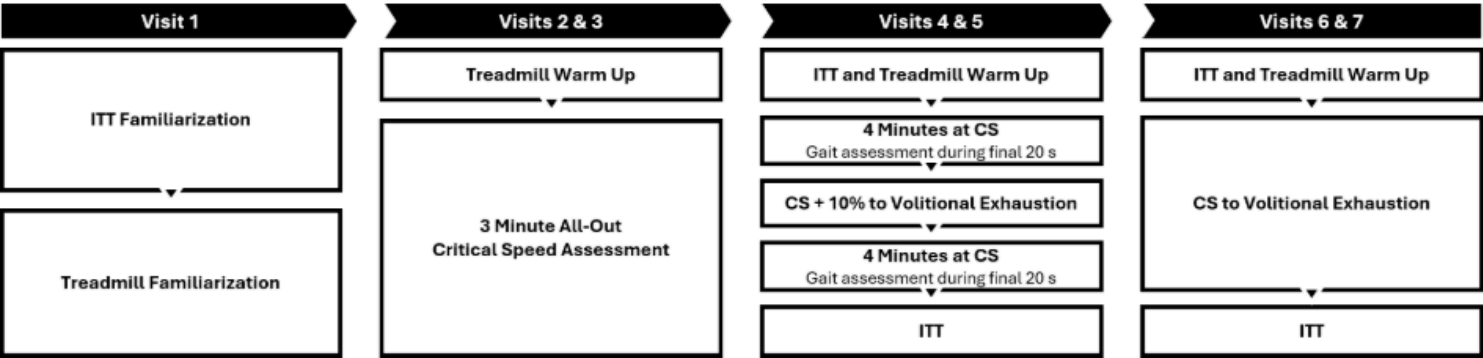


Figure 1

Study protocol with each visit performed twice

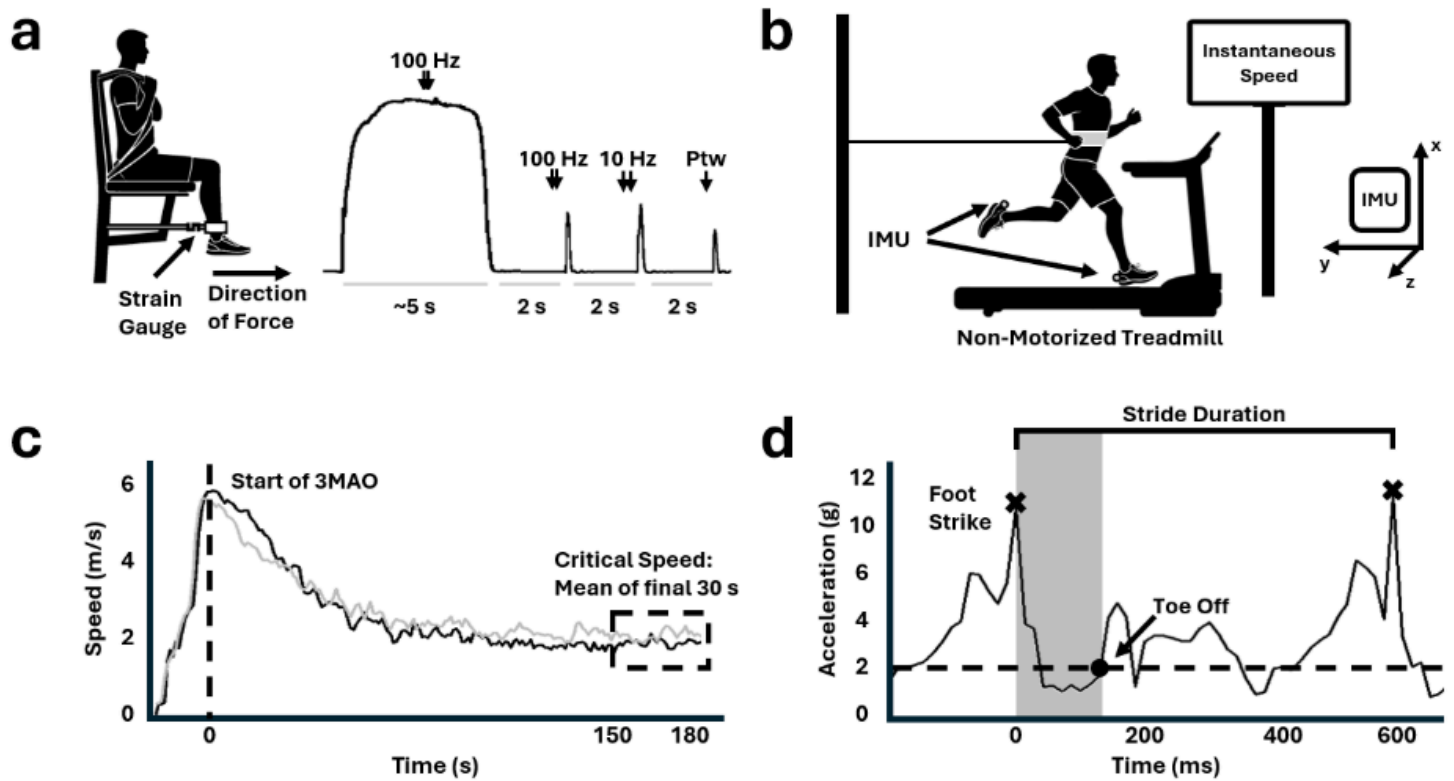


**Figure 2**

Isometric knee extension assessment and representative trace of an MVC with a superimposed Db100 during the force plateau followed at rest by Db100, Db10, and Ptw (a), tethered running setup with an IMU on each foot and the IMU coordinate system (b), a representative trace of speed over time during both 3MAO critical speed assessments (c), and a representative trace of the magnitude of acceleration while running with contact duration in grey (d). IMU: inertial measurement unit, ITT: interpolated twitch technique, Ptw: potentiated twitch (singlet)

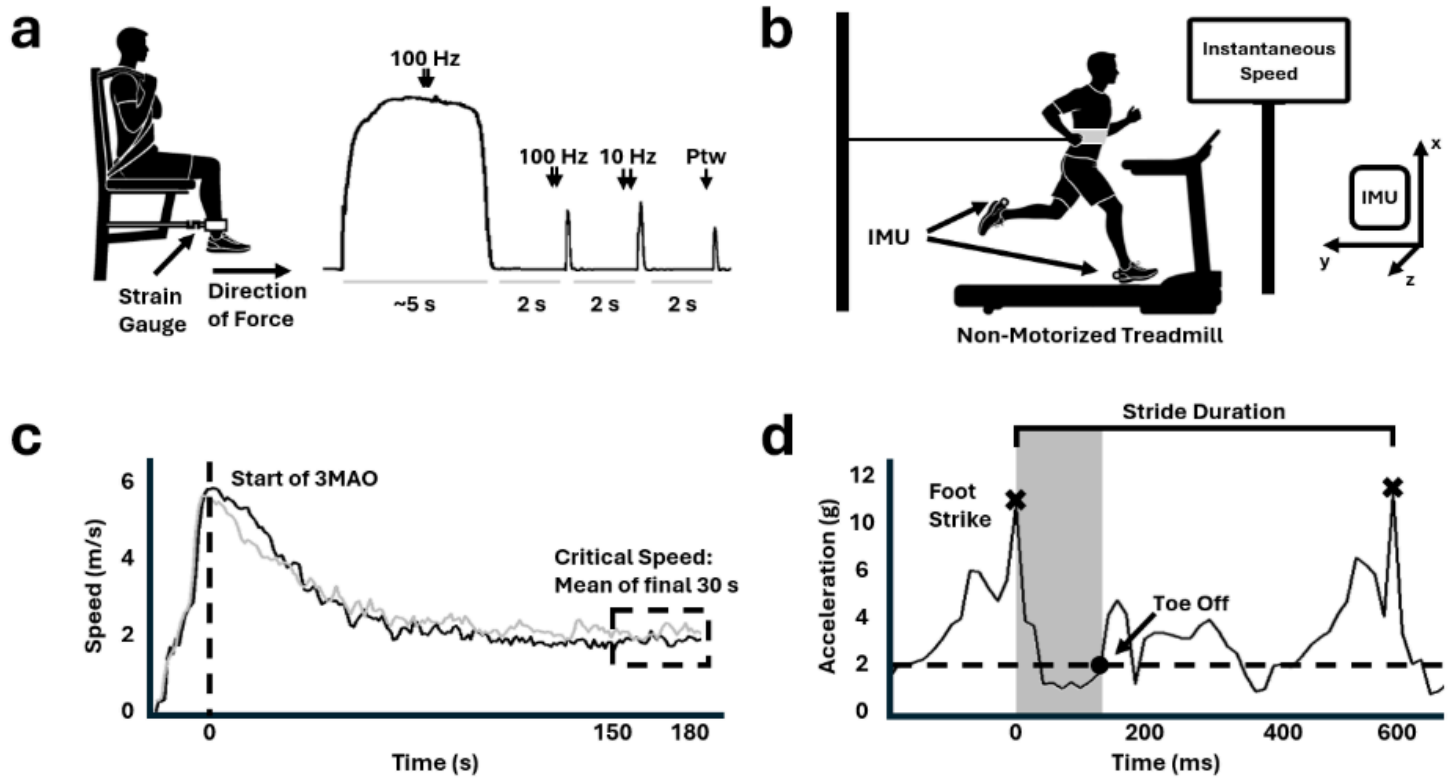


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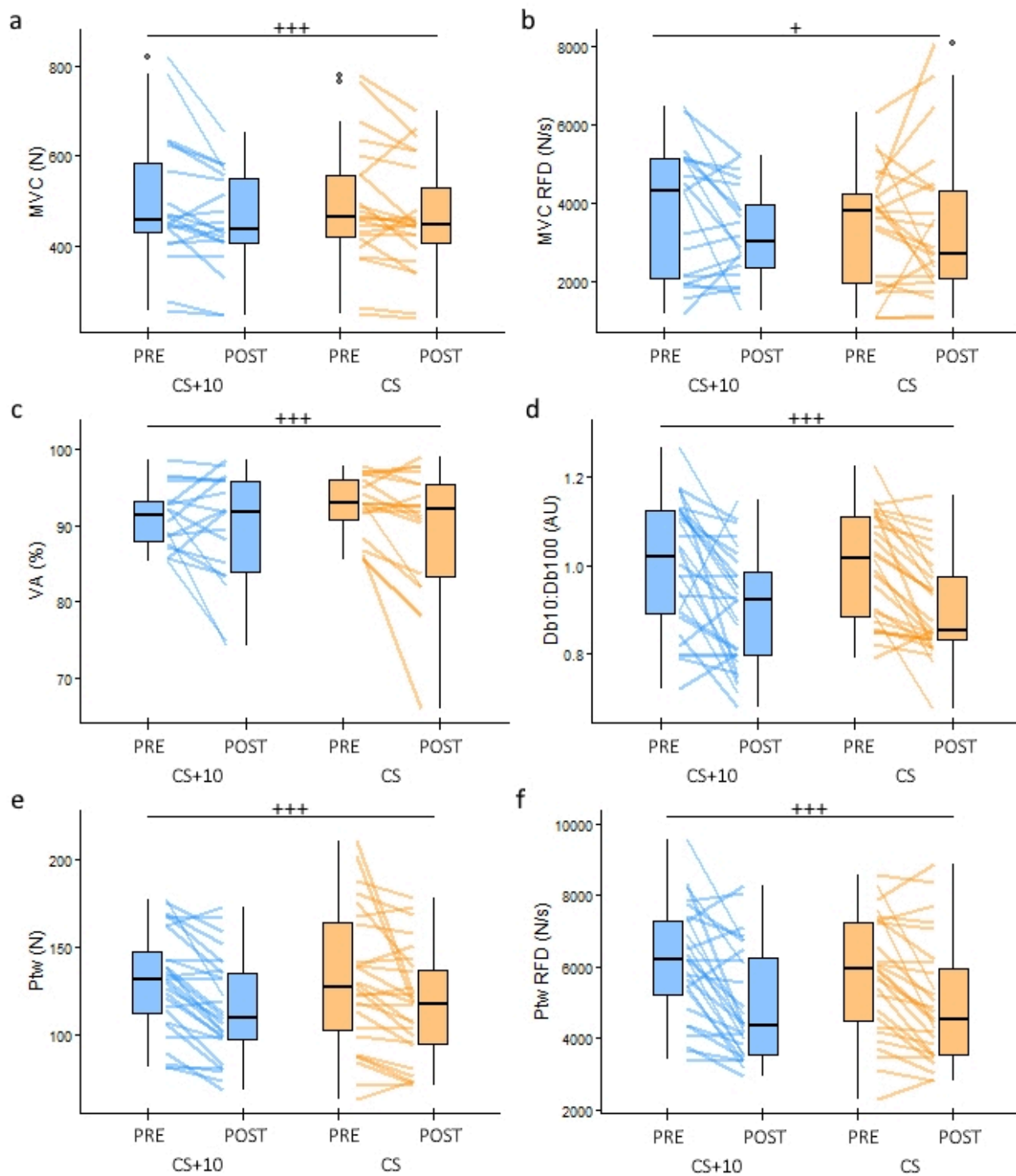


**Figure 3**

MVC (a), MVC<sub>RFD</sub> (b), VA (c), Db10:Db100 (d), Ptw (e), and Ptw<sub>RFD</sub> (f) before (pre) and after (post) the CS+10 (blue) and CS (orange) interventions. Individual participant responses are shown as lines between boxplots. Boxes represent the interquartile range (IQR) with the horizontal line indicating the median; whiskers extend to  $1.5 \times \text{IQR}$ . MVC: maximal voluntary contraction, MVC<sub>RFD</sub>: maximal voluntary contraction rate of force development VA: voluntary activation, Ptw: potentiated twitch, Ptw<sub>RFD</sub>: potentiated twitch force rate of force development. Significant time effect is indicated as +:  $p < 0.05$ , ++:  $p < 0.01$ , +++:  $p < 0.001$ .

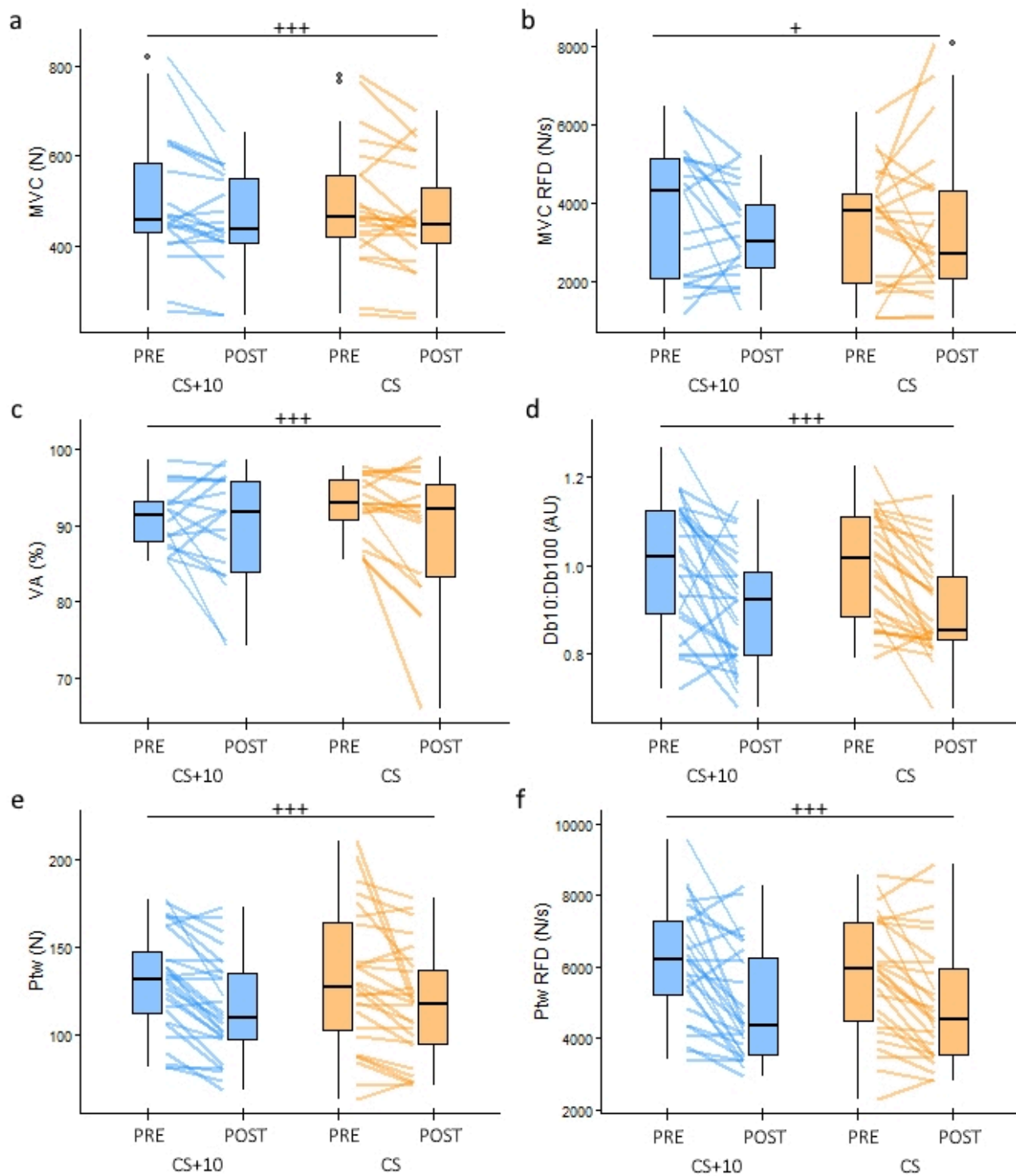


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MVC (a), MVC<sub>RFD</sub> (b), VA (c), Db10:Db100 (d), Ptw (e), and Ptw<sub>RFD</sub> (f) before (pre) and after (post) the CS+10 (blue) and CS (orange) interventions. Individual participant responses are shown as lines between boxplots. Boxes represent the interquartile range (IQR) with the horizontal line indicating the median; whiskers extend to  $1.5 \times \text{IQR}$ . MVC: maximal voluntary contraction, MVC<sub>RFD</sub>: maximal voluntary contraction rate of force development VA: voluntary activation, Ptw: potentiated twitch, Ptw<sub>RFD</sub>: potentiated twitch force rate of force development. Significant time effect is indicated as +:  $p < 0.05$ , ++:  $p < 0.01$ , +++:  $p < 0.001$ .

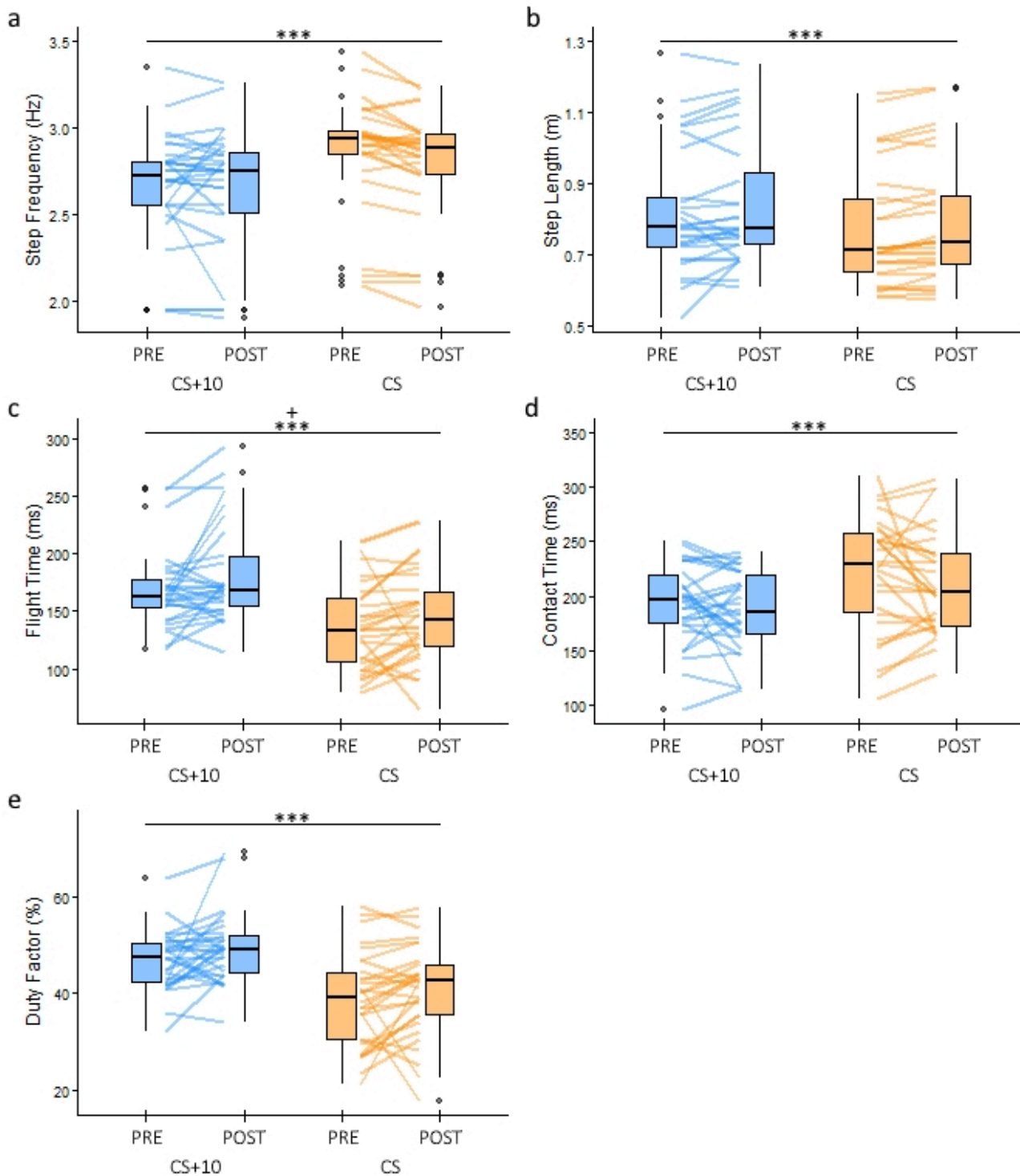


**Figure 4**

Step frequency (a), step length (b), flight time (c), contact time (d), and duty factor (e) before (pre) and after (post) the CS+10 (blue) and CS (orange) interventions. Individual participant responses are shown as lines between boxplots. Boxes represent the interquartile range (IQR) with the horizontal line indicating the median; whiskers extend to 1.5 x IQR. Outliers are identified as individual points. Significant time effect is indicated as +:  $p < 0.05$ , ++:  $p < 0.01$ , +++:  $p < 0.001$ . Significant intervention effect is indicated as \*:  $p < 0.05$ , \*\*:  $p < 0.01$ , \*\*\*:  $p < 0.001$

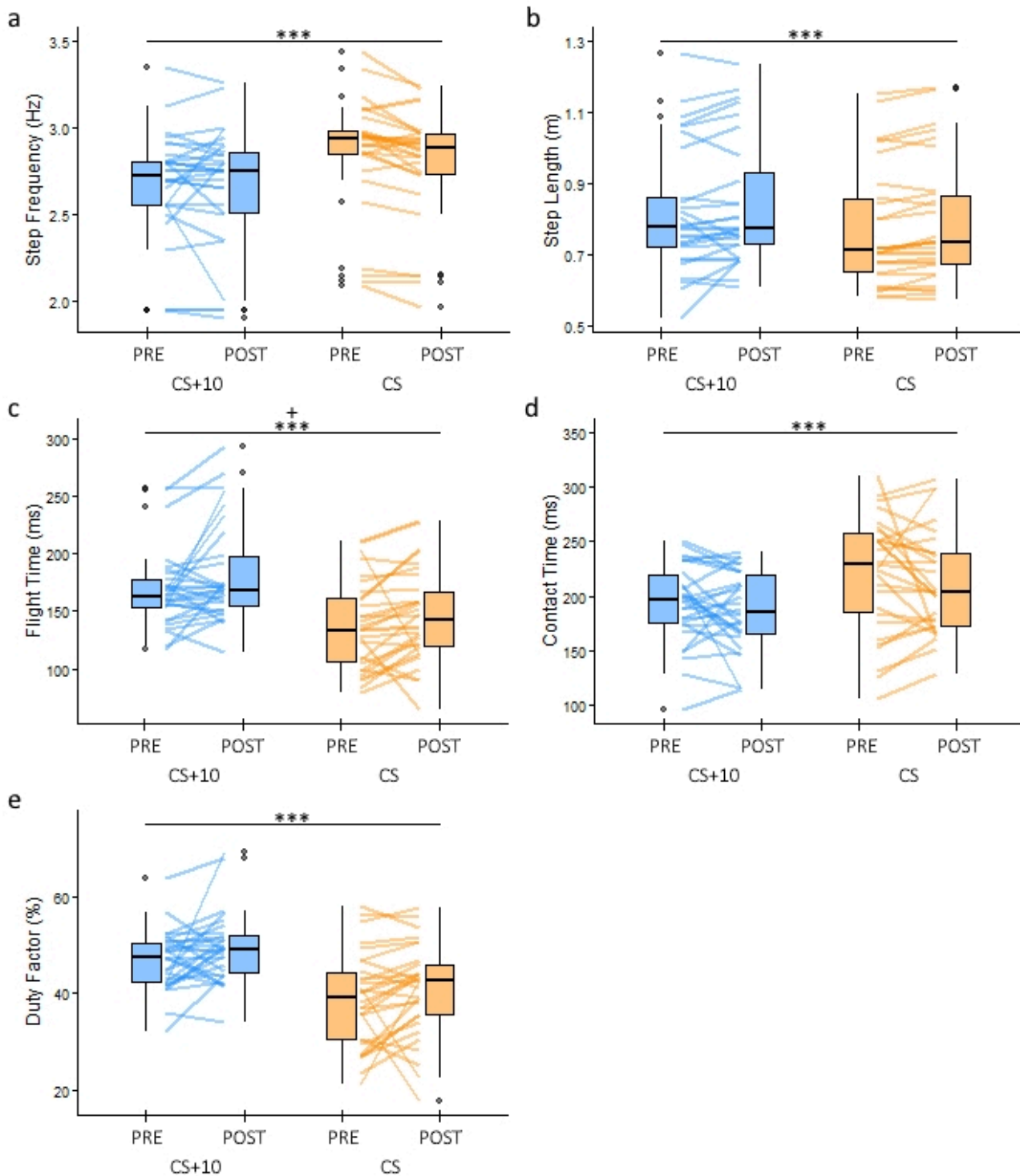


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Step frequency (a), step length (b), flight time (c), contact time (d), and duty factor (e) before (pre) and after (post) the CS+10 (blue) and CS (orange) interventions. Individual participant responses are shown as lines between boxplots. Boxes represent the interquartile range (IQR) with the horizontal line indicating the median; whiskers extend to 1.5 x IQR. Outliers are identified as individual points. Significant time effect is indicated as +:  $p < 0.05$ , ++:  $p < 0.01$ , +++:  $p < 0.001$ . Significant intervention effect is indicated as \*:  $p < 0.05$ , \*\*:  $p < 0.01$ , \*\*\*:  $p < 0.001$

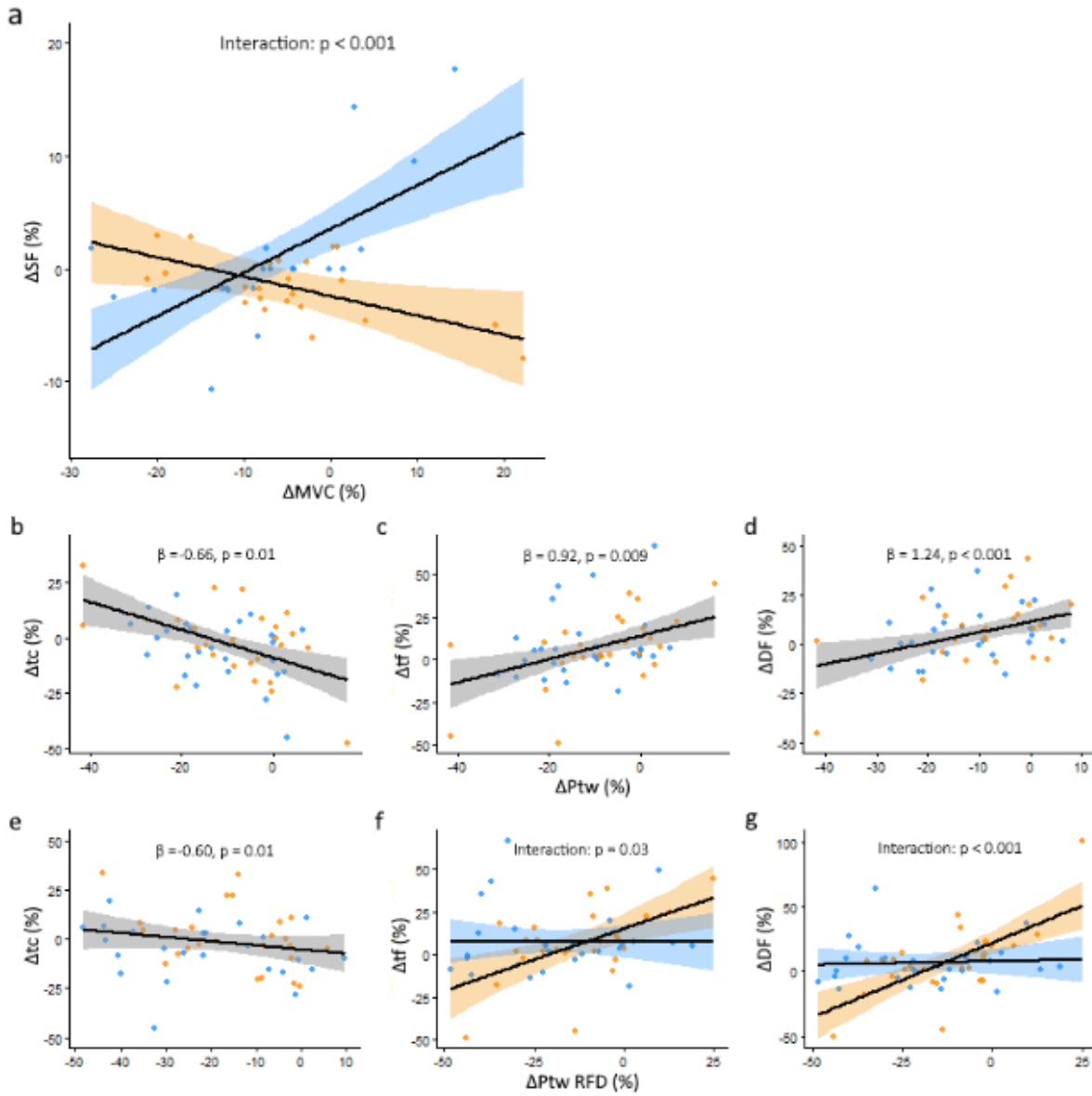


**Figure 5**

Visualization of mixed model slopes for  $\% \Delta SF$  vs  $\% \Delta MVC$  (a),  $\% \Delta t_c$  vs  $\% \Delta Ptw$  (b),  $\% \Delta t_f$  vs  $\% \Delta Ptw$  (c),  $\% \Delta DF$  vs  $\% \Delta Ptw$  (d),  $\% \Delta t_c$  vs  $\% \Delta Ptw_{RFD}$  (e),  $\% \Delta t_f$  vs  $\% \Delta Ptw_{RFD}$  (f), and  $\% \Delta DF$  vs  $\% \Delta Ptw_{RFD}$  (g) for CS+10 (blue) and CS (orange). Individual observations are included.

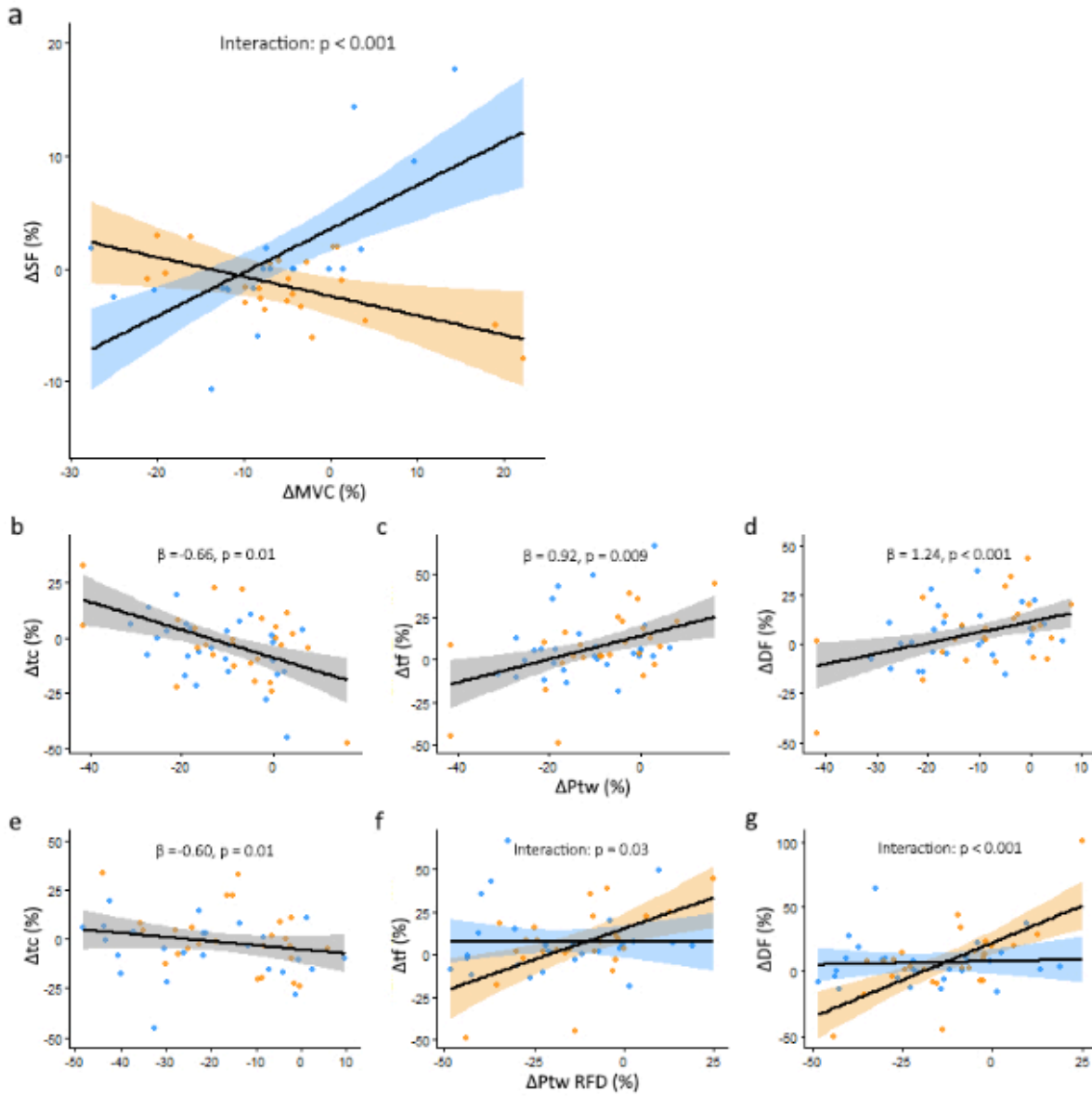


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Visualization of mixed model slopes for % $\Delta SF$  vs % $\Delta MVC$  (a), % $\Delta t_c$  vs % $\Delta Ptw$  (b), % $\Delta t_f$  vs % $\Delta Ptw$  (c), % $\Delta DF$  vs % $\Delta Ptw$  (d), % $\Delta t_c$  vs % $\Delta Ptw_{RFD}$  (e), % $\Delta t_f$  vs % $\Delta Ptw_{RFD}$  (f), and % $\Delta DF$  vs % $\Delta Ptw_{RFD}$  (g) for CS+10 (blue) and CS (orange). Individual observations are included.