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Interactions between perceptions of fatigue, effort, and affect decrease knee extensor endurance performance following upper body motor activity, independent of changes in neuromuscular function

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Abstract

Prior exercise has previously been shown to impair subsequent endurance performance in non-activated muscles. Declines in the neuromuscular function and altered perceptual/affective responses offer possible mechanisms through which endurance performance may be limited in these remote muscle groups. We thus conducted two experiments to better understand these performance-limiting mechanisms. In the first experiment, we examined the effect of prior handgrip exercise on the behavioral, perceptual, and affective responses to a sustained, sub-maximal contraction of the knee extensors. In the second experiment, transcranial magnetic stimulation was used to assess the neuromuscular function of the knee extensors before and after the handgrip exercise. The results of the first experiment demonstrated prior handgrip exercise increased the perceptions of effort and reduced affective valence during the subsequent knee extensor endurance exercise. Both effort and affect were associated with endurance performance. Subjective ratings of fatigue were also increased by the preceding handgrip exercise but were not directly related to knee extensor endurance performance. However, perceptions of fatigue were correlated with heightened effort perception and reduced affect during the knee extensor contraction. In the second experiment, prior handgrip exercise did not significantly alter the neuromuscular function of the knee extensors. The findings of the present study indicate that motor performance in the lower limbs following demanding exercise in the upper body appears to be regulated by complex, cognitive-emotional interactions, which may emerge independent of altered neuromuscular function. Subjective fatigue states are implicated in the control of perceptual and affective processes responsible for the regulation of endurance performance.

KEYWORDS

affect, exercise tolerance, fatigue, perception of effort, TMS, voluntary activation

1 | INTRODUCTION

For more than a century it has been recognized that sustained cognitive and physical work impairs physical performance and/or increases the subjective feelings of fatigue (Mosso, 1891). Though related (e.g., Loy, Taylor, Fling, & Horak, 2017), disassociation of these physiological and perceptual factors may provide critical insight into the nature and principal mechanisms of fatigue. For example, under certain neurological conditions, heightened perceptions of fatigue may be recorded independent of discernible motor dysfunction (de Lima et al., 2018; Dunaway Young et al., 2019; Prak, van der Naalt, & Zijdewind, 2019). In exercise, perceptual changes may similarly hold particular interest, since endurance performance has been shown, ultimately, to be limited by the attainment of maximal perceived effort rather than an inability of the muscles to meet the power or force requirements of the task (Marcora & Staiano, 2010; Staiano, Bosio, de Morree, Rampinini, & Marcora, 2018). Further investigation of the interactions between perceptual factors and motor changes during exercise may therefore aid the understanding of the fundamental basis of fatigue.

Emerging experimental paradigms including, for example, prior cognitive and remote physical tasks, have proved successful in manipulating perceptual responses during subsequent physical endurance exercise without directly challenging the neuromuscular system's capacity to produce force (Amann et al., 2013; Pageaux, Marcora, & Lepers, 2013). These paradigms may thus offer a means of investigating the perceptual regulation of exercise in isolation. For example, prior motor activity has been shown to reduce endurance performance in remote non-activated muscles (Amann et al., 2013; Bangsbo, Madsen, Kiens, & Richter, 1996; Johnson, Sharpe, Williams, & Hannah, 2015; Morgan et al., 2019; Nordsborg et al., 2003), increasing the perception of exertion or effort during the endurance task independent of observable changes in the neuromuscular function (Amann et al., 2013; Johnson et al., 2015; Morgan et al., 2019).

The perception of effort (i.e., the conscious sensation of how hard, heavy or strenuous exercise is, Marcora, 2010) is proposed as the cardinal limiter of endurance performance (Staiano et al., 2018). Effort perception is widely accepted to originate centrally, emerging from the corollary discharge of volitional motor commands from premotor or motor regions to sensory areas of the brain (de Morree, Klein, & Marcora, 2012; Zénon, Sidibé, & Olivier, 2015). Activation of small-diameter afferent fibers have also been posited to contribute to effort perception (Broxterman et al., 2017, 2018), though this remains controversial and is highly disputed by some (Barbosa et al., 2016; Mitchell, Reeves, Rogers, & Secher, 1989; Smith et al., 2003; see Marcora, 2009; Pageaux & Gaveau, 2016). Homeostatic afferent feedback is, however, considered the basis of our emotional (affective) experiences (Craig, 2002; Damasio & Carvalho, 2013) and as such, affective responses have also been associated with the physical endurance performance (Hartman, Ekkekakis, Dicks, & Pettitt, 2019; Jones et al., 2015). While effort rather than affect has dominated the study of the limits of endurance performance to date, an ability to disassociate effort and affect, that is, the *what* from *how* one feels (Hardy & Rejeski, 1989), may indicate disparate neurophysiological and behavioral functions. The interplay between the perception of effort and affect requires further investigation.

Furthermore, though the perception of effort is a central tenant of many behavioral models of fatigue (Hockey, 2011; Kuppuswamy, 2017; Marcora, 2008; Noakes, 2012), perceptions of fatigue and effort are distinct constructs (Borg, 1986; Halperin & Emanuel, 2020). Micklewright, St Clair Gibson, Gladwell, and Al Salman (2017) recently demonstrated that the perception of fatigue and effort could be disassociated during recovery following exhaustive exercise. In this study, the perception of fatigue was defined as a "feeling of diminishing capacity to cope with physical or mental stressors, either imagined or real" (Micklewright et al., 2017). While the association between perceived effort and volitional exercise behaviors is relatively well established (e.g., Christian, Bishop, Billaut, & Girard, 2014), understanding of the behavioral correlates of fatigue perceptions are less so. Recently, heightened perceptions of (mental) fatigue, evoked through demanding cognitive activity, were unrelated to subsequent self-selected cycling intensities but were correlated with the level of effort perceived during the cycling bout (Harris & Bray, 2019). This may suggest that the subjective experience of fatigue does not directly influence behavior, however, may function indirectly, ultimately limiting exercise by making it feel more effortful. Interactive relationships between perceptions of fatigue and effort have previously been postulated, but the nature of such a relationship (and similarly between fatigue and core affective responses) is not entirely clear (Kuppuswamy, 2017).

Finally, though previous assertions indicate a separation between perceptual responses to exercise and neuromuscular function following prior, remote exercise, the effect of prior exercise on the neuromuscular function in **non-active**, remote muscles remains ambiguous (see Halperin, Chapman, & Behm, 2015). Evidence of impaired maximal force production in non-active muscle groups following remote exercise is currently equivocal (Doix et al., 2018; Doix, Lefèvre, & Colson, 2013; Rattey, Martin, Kay, Cannon, & Marino, 2006; Šambaher, Aboodarda, & Behm, 2016; Sidhu et al., 2014; Triscott et al., 2008). Moreover, transcranial magnetic stimulation (TMS) studies have reported both excitatory and inhibitory effects on the excitability of the corticospinal tract of remote muscle groups (Aboodarda, Šambaher, Millet, & Behm, 2017; Šambaher et al., 2016). As reductions in the neuromuscular function may modulate the perceptual consequences of action, for example, increase the perception of

effort (Lampropoulou & Nowicky, 2014; Marcora, Bosio, & de Morree, 2008), and therefore underpin endurance performance impairments, further investigation of the disassociation of neuromuscular and perceptual responses in non-active muscle groups is required to fully contextualize any study of endurance performance regulation.

Here, we used prior remote exercise in the upper limbs (handgrip; HG) to examine the behavioral, perceptual/affective, and neuromuscular responses to a sustained submaximal contraction of the knee extensors (KE). We first hypothesized that prior HG exercise would increase the perception of fatigue, perception of effort, and negative affect, resulting in impaired endurance performance during subsequent KE exercise. Relationships between perceptual/affective constructs were subsequently explored. In a second experiment, we quantified changes in the neuromuscular function of the KE following prior HG exercise. It was hypothesized that force production and cortical voluntary activation of the KE would be unchanged by the prior HG task.

2 | METHOD

2.1 | Participants

The study was approved by the University of Brighton Research Ethics Committee (SSCREC18-09) with experimental procedures conducted in accordance with the *Declaration of Helsinki,* except for prior registration in a database. Twenty healthy male participants (mean $\pm$ *SD*; age: 25 $\pm$ 4 years; weight: 81.2 $\pm$ 9.0 kg; height: 1.82 $\pm$ 0.07 m) were recruited for the first experiment. All were medication-free and had no history of cardiovascular, neurological or musculoskeletal disorders. Hand (16 Right) and leg (15 Right) dominance was determined using the Edinburgh Handedness Inventory (EHI) (Oldfield, 1971). A sub-sample (*N* = 15; 25 $\pm$ 4 years; weight: 81.1 $\pm$ 9.9 kg; height: 1.82 $\pm$ 0.07 m; 13 right-handed, 12 right-legged) volunteered to take part in the second experiment. All screened negative for contraindications to TMS (Rossi, Hallett, Rossini, & Pascual-Leone, 2011). All participants were instructed to refrain from caffeine, alcohol, and strenuous exercise for 24 hr prior to each testing session.
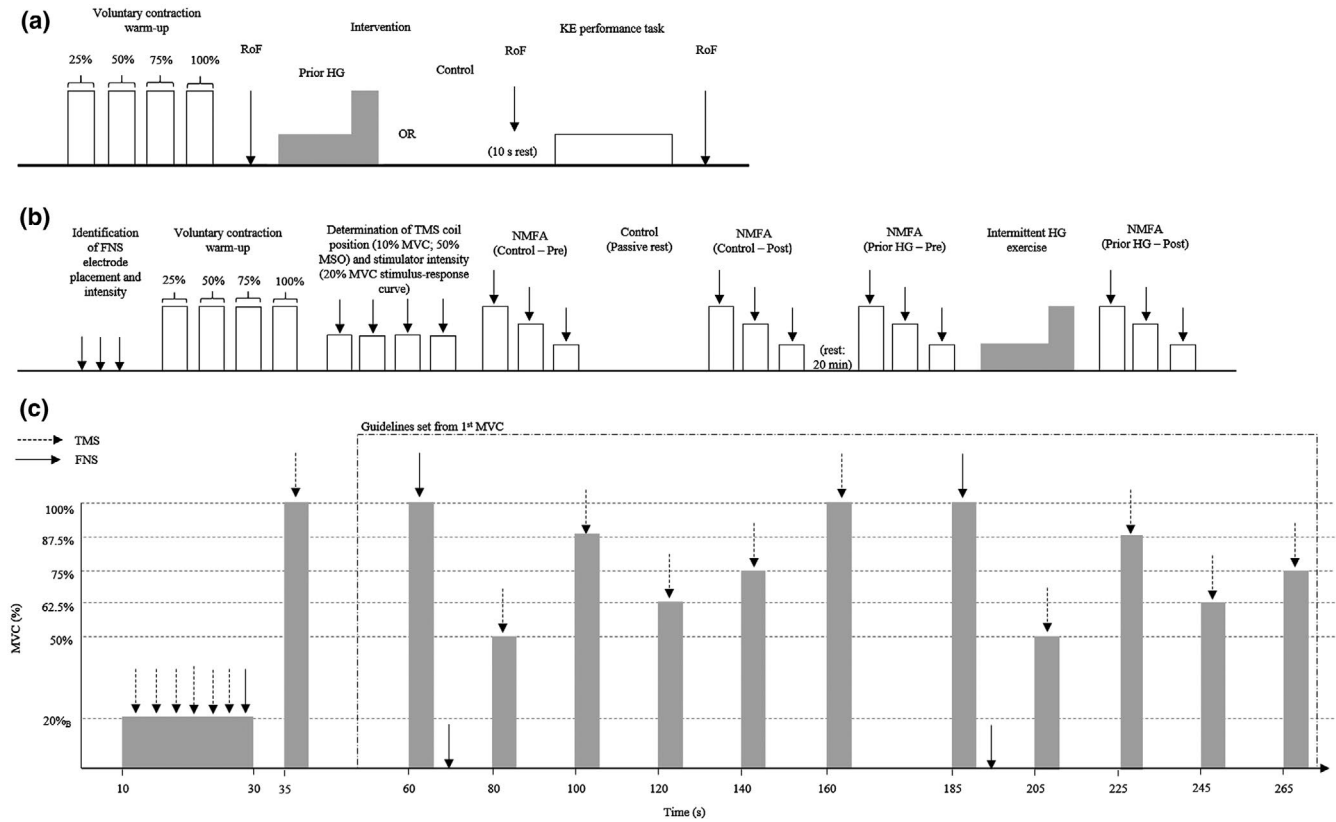
2.2 | Experiment one

Participants attended three separate sessions, conducted at the same time of day ($\pm$2 hr) with sessions separated by a minimum of 48 hr. In the preliminary session, participants were familiarised with all measures and maximal HG and KE force was determined. In the subsequent two experimental sessions, participants undertook a bilateral, intermittent HG

exercise task and time-matched control task (passive rest). KE endurance performance was evaluated after (10 s) each task (Figure 1a). The KE endurance exercise task was a sustained isometric contraction of the dominant KE at 20% maximal voluntary contraction (MVC) performed until task failure. Task failure was defined as an inability to maintain the target force for >3 s. The session order was randomized and counterbalanced across participants.

The HG exercise, based on the fatiguing protocol described by Gruet et al. (2014), consisted of repeated bilateral, sustained isometric contractions at 30% MVC for 15 s, followed immediately by a 5 s MVC. Each contraction was separated by 10 s rest. During the preliminary session, the sequence was performed until task failure (voluntary force below 30% MVC for >2 s) in the dominant hand. To standardize task duration across conditions, participants performed only the number of successfully completed contraction sequences achieved during the preliminary session (mean duration: 308.0 $\pm$ 95.6 s; range: 140–470s; 11 $\pm$ 3 repetitions). Strong verbal encouragement was provided throughout the HG, but not the KE task to prevent potential experimenter bias from influencing performance on the endurance task. Participants were instructed to relax their legs during the HG task (average VL EMG < 0.03 mV). Target submaximal forces were determined for both tasks based on the highest values recorded during the preliminary session (maximal force production did not differ from the preliminary session during experimental trials; $p > .05$, data not shown). Visual feedback of force production was presented on a monitor, with participants naïve to both elapsed time and task failure criteria.

Electromyographic (EMG) activity of the quadriceps (*vastus lateralis*: VL) was recorded throughout the KE endurance task, while perceived effort and affective state were assessed every 30 s in pseudorandomized order. Perception of effort, defined as "the conscious sensation of how hard, heavy and strenuous exercise is" (Marcora, 2010), was measured using the Borg CR-10 scale (Borg, 1982). Participants were instructed to disassociate feelings of pain and discomfort from the perception of effort, with effort representing how strenuous the exercise felt at a given point in time. Experiential anchors were set with 0 representing no effort and 10 the degree of effort felt during the strongest contraction they had previously experienced (max effort). Changes in participants' affect during the KE contraction were assessed using the Feeling Scale (FS; range +5 to −5), through which participants were asked to rate their current mood state during the KE contraction, with positive integers representing pleasurable affective states and negative integers unpleasurable affective states (Hardy & Rejeski, 1989). The extremes of the scale were anchored based on experiential factors related to prior exercise experiences, with +5 representing individuals' most pleasant experience during previous physical activity and −5 their most unpleasant experience. Subjective ratings

FIGURE 1 Schematic overview of experimental design. (a) Experiment one, (b) experiment two, and (c) overview of the neuromuscular assessment protocol for experiment two. FNS, Femoral nerve stimulation; KE, Knee extensor; MSO, Maximal stimulator output; MVC, Maximal voluntary contraction; NMFA, Neuromuscular fatigue assessment; Prior HG, Intermittent handgrip task; RoF, Rating of fatigue; TMS, Transcranial magnetic stimulation

of fatigue (RoF) were captured before the HG task and immediately after both the HG task and the KE task using an 11-point scale (Micklewright et al., 2017). The perception of fatigue was defined as a "feeling of diminishing capacity to cope with physical or mental stressors, either imagined or real" (Micklewright et al., 2017). Instructions and anchoring procedures presented to participants conformed to the authors' description, except for examples referencing the propensity to sleep or the feelings experienced upon waking. These examples were excluded based on recommendations to clearly distinguish feelings of fatigue from those of sleepiness (Pigeon, Sateia, & Ferguson, 2003).

2.3 | Experiment two

The single session was conducted at the same time of day as individual sessions performed in *experiment one*. Neuromuscular assessments were performed before and after the control and HG tasks (described above), which were presented in a constant order (Figure 1b). The neuromuscular assessment began with a 30 s KE contraction performed at 20% of baseline MVC (20%$_B$). Six TMS pulses were delivered during the sustained contraction (one every 4 s), with femoral

nerve stimulation (FNS) applied prior to the end of the contraction. Following a brief rest (5 s), two series of six contractions were then performed each comprising: (a) an MVC with superimposed TMS; (b) an MVC with FNS superimposed and applied immediately after the contraction (~2 s delay); (c) four submaximal contractions performed sequentially at 50%, 87.5%, 62.5%, and 75% of MVC each with superimposed TMS (Dekerle, Greenhouse-Tucknott, Wrightson, Schäfer, & Ansdell, 2019). MVCs were separated by 20 s, with each submaximal contraction separated by 15 s. The two contraction series were also separated by 15 s (Figure 1c). Target force levels were derived from the first MVC and displayed as visual guidelines, with participants asked to attempt to surpass the guideline during each subsequent MVC. All contractions were 5 s in duration. The post-HG exercise evaluation protocol was initiated 10 s after completing the fatiguing task.

All experimental sessions (across both experiments) started with a standardized warm-up, consisting of four bilateral handgrip contractions at 25%, 50%, and 75% of perceived maximal force (Kennedy, Hug, Sveistrup, & Guével, 2013). Participants then performed MVCs, alternating between hands (1 min separating each contraction) until the coefficient of variation across three successive trials for the same hand was <5%. The same procedure was replicated in the KE.

2.3.1 | Femoral nerve stimulation

Single percutaneous electrical stimuli (duration: 200 μs) were delivered to the right femoral nerve via a pair of square (5 × 5 cm) self-adhesive neuro-stimulation electrodes (Valutrode CF5050; Axelgaard Manufacturing Co., Ltd., California, USA), attached to a high-voltage (maximal voltage: 400 V) constant-current stimulator (Model DS7AH, Digitimer Ltd., Hertfordshire, UK). The cathode was placed high in the femoral triangle with the anode positioned midway between the ipsilateral greater trochanter and iliac crest (Sidhu, Bentley, & Carroll, 2009). The precise location of cathode placement was determined through the systematic adjustments of the electrode until the greatest amplitude for twitch force (Q_{tw}) and M-wave amplitude for a given sub-maximal current (~70–90 mA) was attained (Johnson et al., 2015). Optimal stimulation intensity was defined as the intensity at which a plateau in both Q_{tw} and M-wave was exhibited. Optimal stimulation intensity was determined through progressive increments in stimulator current (+20 mA) from 10 mA, with two stimuli delivered at each intensity. Stimulation intensity was increased by a further 30% in order to ensure full spatial recruitment of KE motor units (140 ± 40 mA).

2.3.2 | Transcranial magnetic stimulation

Single, monophasic magnetic stimuli (duration: 1 ms) were manually delivered over the contralateral primary motor cortex, powered by a magnetic stimulator (Magstim[200], The Magstim Company Ltd., Whitland, UK), using a concave (110 mm) double-cone coil. The orientation of the coil was positioned to induce a posterior–anterior intracranial current flow within the cortex. The optimal coil position for the activation of the KE was determined through marking vertex, 1, and 2 cm posterior to vertex and 1 cm contralateral to each mark along the midline (i.e., 6 marks) (Souron, Besson, Mcneil, Lapole, & Millet, 2018). The site eliciting the largest motor evoked potential (MEP) amplitude in the quadriceps and superimposed twitch (SIT) force, whilst minimizing MEP amplitude in the antagonist BF, during a 10% MVC KE contraction at 50% maximal stimulator output (MSO) was chosen. If peak amplitude and SIT force were not evoked at the same site, MEP amplitude was prioritized due to the influence of co-activation on SIT responses (Todd, Taylor, & Gandevia, 2016). Optimal stimulus intensity (65 ± 13% MSO) was determined through SIT and MEP stimulus–response curves during brief (3 s) contractions of the KE at 20% MVC (Temesi, Gruet, Rupp, Verges, & Millet, 2014). Stimulator intensities of 20%, 30%, 40%, 50%, 60%, 70%, and 80% MSO were each applied during four contractions, performed at 10 s intervals. Stimulator intensities were presented in a randomized order with 10 s between each

intensity set. If plateaus in SIT and MEP amplitudes were not evident, higher stimulator intensities were investigated (e.g., 90% MSO). A plateau in the stimulator–response curve was defined as the lowest intensity resulting in an increase of <5% of MEP amplitude with an increase in intensity (Temesi et al., 2014). The antagonist MEP amplitude was monitored in order to ensure co-activation was minimized.

2.4 | Force and electromyography recordings

Participants were seated, upright on a custom high-backed chair with hip and knee angles set at 90° (0° = full extension). The upper torso was secured to the back of the chair via two noncompliant cross-over shoulder straps, minimizing extraneous movement of the upper body. A cervical neck brace was used to constrain movements of the head. Contraction force of the KE was measured via a calibrated load cell (Model 615, Vishay Precision Group, Basingstoke, UK), secured to the lower leg via a cuff fastened slightly superior (2–4 cm) of the lateral malleoli, which attached to a custom-built bridge amplifier (Type 132-C, Datum Electronics, Isle of Wight, UK). Participants' forearms were strapped across the forearm and wrist, in a supinated position (elbow angle set at approximately 70°; 0° = full extension), to a custom table positioned in front of the rig. In each hand, participants held a handgrip transducer (MLT003/D; ADInstruments, Colorado Springs, CO). Participants held each transducer with a standardized grip posture. Force was digitized (4 kHz) and analyzed using LabChart v7.0 software (ADInstruments, Oxfordshire, UK). Surface EMG activity was recorded from the dominant VL and *bicep femoris* (BF) with pairs of self-adhesive electrodes (Kendall[TM] H59P, Coviden, Massachusettes, USA), positioned in accordance to *SENIAM* guidelines (Hermens, Freriks, Disselhorst-Klug, & Rau, 2000). The reference electrode was placed on the ipsilateral patella. The skin-electrode interface was prepared by shaving the area, lightly abrading, and cleansing with isopropyl alcohol to minimize electrical resistance. EMG signals were amplified (gain ×1000) (PowerLab 26T; ADInstruments, Oxfordshire, UK), digital band-pass filtered (20–2,000 Hz), digitized (4 kHz), recorded, and later analyzed offline (LabChart v7.0).

2.5 | Data analysis

2.5.1 | Force

Maximal and sub-maximal voluntary contraction force was defined as the greatest 500 ms average prior to stimulation. MVC force represented the highest voluntary force recorded at each assessment period. The percentage change in HG

MVC force was quantified from the initial MVC (following the warm-up) to the last MVC of the task. In *experiment two*, the amplitude of evoked mechanical variables (i.e., SIT, Q_{tw}) was analyzed for each stimulation at a given force level and then averaged across the two contraction sequences.

2.5.2 | Voluntary activation (VA_{TMS})

Following the principles of twitch interpolation, VA_{TMS} was quantified using the equation: $VA_{TMS} = 1 - (SIT/ERT) \times 100$. Estimated resting twitch (ERT) was derived through the linear regression of TMS-evoked SIT amplitude and voluntary torque. Ten points were added to each linear model (Dekerle et al., 2019). All regression analyses were statistically significant ($p < .01$) and showed a strong linear relationship: (r^2) $.89 \pm .04$, $.89 \pm .07$, $.90 \pm .06$ and $.89 \pm .08$ pre and post control and pre and post the HG task, respectively.

## 2.5.3 | EMG

Maximal root mean square (RMS_{Max}) and mean power frequency (MPF_{Max}) were obtained from a 500 ms interval centered on the highest recorded KE force value prior to

stimulation. VL RMS and MPF were calculated over consecutive 15 s sampling intervals during the KE performance task and normalized to values recorded during MVCs. In *experiment two*, MEP and M_{max} were analyzed for peak-to-peak amplitudes. MEP and M_{max} responses from one representative participant are presented in Figure 2. VL MEPs were normalized to the nearest M-wave evoked during a maximal contraction (M_{max}). MEPs recorded during $20\%_B$ were normalized to the M_{max} at the end of the same contraction (M_{max} $_{20\%B}$). Absolute antagonist MEP amplitudes were recorded at each force level. For each level of contraction from 50% to 100% MVC, MEP responses were the average of the two responses evoked in the two contraction sequences. Across conditions, MEPs during $20\%_B$ demonstrated an effect of time, with the first two responses significantly lower than the successive stimulations ($p < .05$). The first two MEPs were subsequently removed, with analysis performed on an average of the last four stimulations.

2.5.4 | Effort and affect

The rate of change was calculated as the change in effort and affect from the first to the last response provided, as a function of time.
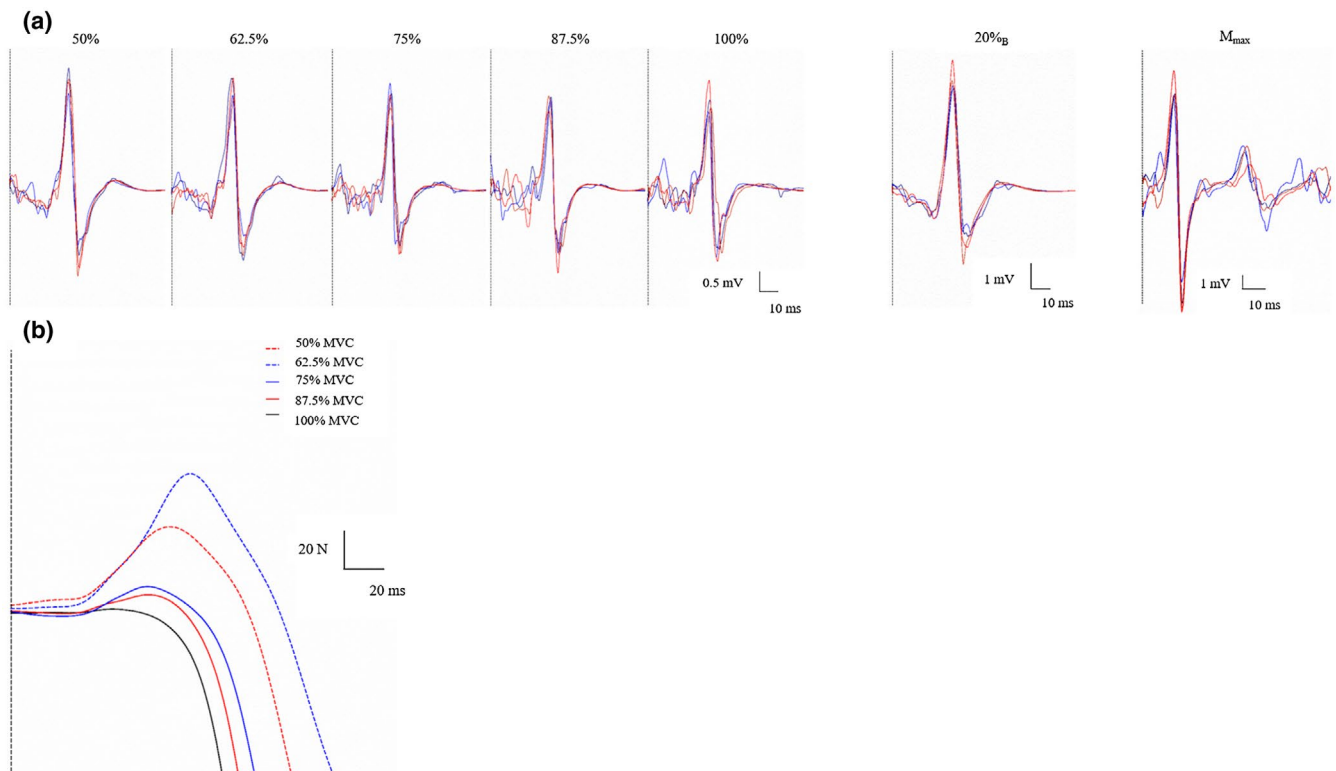
FIGURE 2 Representative traces of motor evoked potential (MEP) at each voluntary force level and M_{max} (a). Blue line: control—preintervention. Dark blue line: control—postintervention. Red line: prior HG—preintervention. Dark red line: Prior HG—postintervention. Raw traces of example superimposed twitches evoked during maximal voluntary contraction (100% MVC) and submaximal forces (50%, 62.5%, 75%, and 87.5% MVC) (b). Dotted black line represents the point of magnetic or electrical stimulation

2.6 | Statistical analysis

Statistical procedures were performed using Statistical Package for the Social Sciences (SPSS Inc., v25, Chicago, IL) unless stated otherwise. Gaussian distributions were verified using a combination of normal Q–Q plots and Shapiro–Wilk tests. Sphericity was assessed using Maulchy's test, with Greenhouse-Geisser correction applied as appropriate ($\varepsilon < 0.75$). In *experiment one*, time to task failure (TTF) violated the assumptions of normality and was thus analyzed using a Wilcoxon signed-rank test. Effort and affective responses were analyzed at each time point up to sample iso-time (i.e., time from the beginning of the KE endurance task to the penultimate measurement before task failure in the shortest performance). In this instance, responses at 30 and 60 s were compared across conditions using a two-way (2×2) repeated measures ANOVA. Effort and affective responses at task failure were not included in this general linear model due to observed ceiling and floor effects, respectively. Instead, effort and affect at task failure were assessed using Wilcoxon signed-rank tests, due to the violations of the assumptions of normality. RoF was assessed using a two-way, repeated measures (2×3) ANOVA. The effect of prior HG exercise on EMG RMS and MPF of the VL were analyzed with a two-way (2×7) repeated measures ANOVA up to sample iso-time, with values at task failure analyzed using paired-sample t tests. The analysis was performed on $N = 19$, as one participant was removed from the analysis due to the loss of EMG signal during the endurance task in one trial. Exploratory Spearman's rank correlation coefficients assessed the relationships between TTF and select perceptual and affective variables within each condition separately, with the false discovery (FDR) rate adjusted for multiple comparisons (Benjamini & Yosef, 2000; Pike, 2011). Within-participant, repeated measures correlations were used to assess the relationships between perceptual and affective responses using the *rmcorr* package (Bakdash & Marusich, 2017) in R (R Core Team, 2018). This was performed to assess relationships across a larger range of subjective fatigue responses.

In e*xperiment two*, mechanical and EMG responses were analyzed with a two-way (2×2) repeated-measures ANOVA. Significant main effects of time and interaction effects were followed up with Bonferroni adjusted pairwise comparisons. Data that violated the assumption of normality (i.e., M_{max}, BF MEPS) were *log*(10) transformed. Tests of equivalence were also performed to test the null hypotheses of *experiment two* in jamovi (v1.0, The jamovi project, 2019) using the TOSTER package for R (Lakens, 2017). Tests of equivalence were performed between conditions on the pre-to-post change in the mechanical and EMG variables.

Data for parametric analyses were reported as mean $\pm$ *SD*, while non-parametric analyses were reported as median

(*Mdn*) plus interquartile range (*IQR*), unless otherwise stated. Effect sizes for main effects are presented as partial eta squared (η_p^2), while the pairwise comparison of mean differences are presented as Cohen's d_{av} (Lakens, 2013) for parametric data, and coefficients of correlation ($r = z/\sqrt{N}$) for non-parametric analyses. The null hypothesis was rejected at an α-level of .05.

3 | RESULTS

3.1 | Experiment one

#### 3.1.1 | Handgrip task and knee extension endurance performance: TTF

The HG task induced substantial reductions in maximal force production in both the dominant ($-47.0 \pm 10.1\%$; range: -28.0 to -68.1%) and non-dominant hand ($-45.2 \pm 10.4\%$; range: -23.3 to -63.2%), with no difference between hands ($t_{(19)} = -1.17$, $p = .258$, $d_{av} = 0.18$). Importantly, prior HG activity significantly impaired KE endurance performance (prior HG: Mdn: 230.5 s [191–332 s], control: Mdn: 257.0 s [197.25–363 s]; $Z = -2.24$, $p = .025$, $r = .35$). Reductions were evidenced in 15 of 20 participants and resulted in a mean reduction of $11.1 \pm 20.8\%$ (Figure 3).

3.1.2 | Perception of effort, affect, and RoF during knee extension endurance task

Effort and affective responses are presented in Table 1. Heightened effort perception was observed in the prior HG condition ($F_{(1,19)} = 4.46$, $p = .048$, $\eta_p^2 = 0.518$) and across time ($F_{(1,19)} = 30.92$, $p < .001$, $\eta_p^2 = 0.619$), but no interaction between condition and time was observed ($F_{(1,19)} = 3.26$, $p = .087$, $\eta_p^2 = 0.146$). Effort at task failure was maximal (or near maximal) in both the prior HG and control condition ($Z = 0.56$, $p = .577$, $r = .09$). Similarly, affect was reduced by prior HG activity compared to the control condition ($F_{(1,19)} = 9.80$, $p = .006$, $\eta_p^2 = 0.340$), and declined across time ($F_{(1,19)} = 8.00$, $p = .011$, $\eta_p^2 = 0.296$). There was no interaction between condition and time ($F_{(1,19)} = 1.09$, $p = .309$, $\eta_p^2 = 0.054$) and there was no difference in affect at task failure ($Z = -0.54$, $p = .589$, $r = -.09$).

A main effect of condition ($F_{(1,19)} = 50.63$, $p < .001$, $\eta_p^2 = 0.727$), time ($F_{(1.22,23.11)} = 61.05$, $p < .001$, $\eta_p^2 = 0.763$), and interaction ($F_{(1.54,29.16)} = 72.84$, $p < .001$, $\eta_p^2 = 0.793$) was observed for RoF. Pairwise comparisons showed that RoF were elevated by the HG task ($t_{(19)} = -12.07$, $p < .001$; $d_{av} = 3.01$) and was increased further by the completion of the KE task ($t_{(19)} = -2.79$, $p = .035$; $d_{av} = 0.49$). In

FIGURE 3 Effect of prior handgrip (HG) exercise on time to task failure in the knee extensor (KE) endurance task. Connected grey points represent paired performance times for a given participant. Colored bars represent *Mdn* and *IQR*. *N* = 20
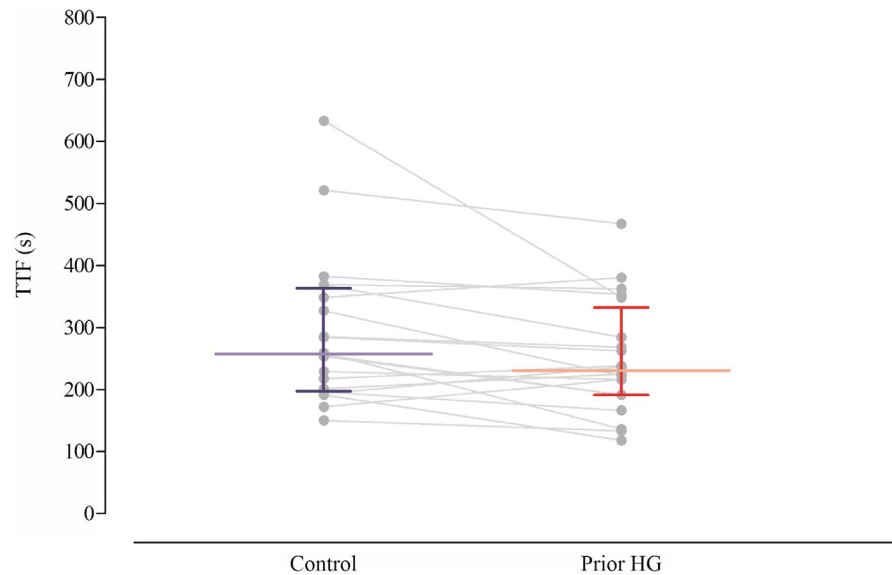
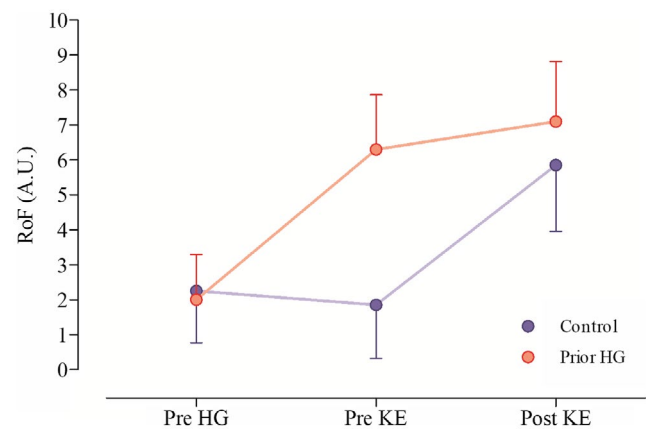**TABLE 1** Effort and affect ratings across the KE performance task

	Time		
	30 s	60 s	TTF
Effort			
Control	3 ± 1	4 ± 1	10 [9 – 10]
Prior HG	4 ± 2	5 ± 2	10 [9 – 10]
Affect			
Control	2 ± 2	1 ± 1	−4 [−5 – −2]
Prior HG	1 ± 2	0 ± 1	−4 [−5 – −3]

Note: Data presented as mean ± *SD* for variables analyzed with parametric models and *Mdn* [*IQR*] for variables assessed using non-parametric analysis. *N* = 20.


FIGURE 4 Ratings of fatigue (RoF) across stages of the experimental protocol in both the prior handgrip (HG; red circles) and a control (blue circles) conditions. Ratings were collected pre HG (i.e., immediately prior to the handgrip task), pre KE (i.e., immediately prior to the knee extensor endurance task) and post KE (i.e., immediately after the knee extensor endurance task). *N* = 20

contrast, there was a small decrease in RoF following the control intervention ($t_{(19)} = 2.99$, $p = .023$; $d_{av} = -0.27$), but RoF was elevated following the KE task ($t_{(19)} = -6.64$, $p < .001$; $d_{av} = 2.33$). There was no difference between conditions prior to the respective interventions ($t_{(19)} = 0.96$, $p = .349$; $d_{av} = -0.18$), but RoF was greater in the prior HG condition immediately after the HG task ($t_{(19)} = -9.53$, $p < .001$; $d_{av} = 2.88$) and remained greater immediately after the KE task ($t_{(19)} = -8.15$, $p < .001$; $d_{av} = 0.69$) (Figure 4).

3.1.3 | Relationships between RoF, perceived effort, affect, and task performance

Exploratory relationships between TTF and perceptual and affective variables (effort and affect at 60 s, rate of change in effort and affect, RoF post-HG task) were

consistent across conditions (Figure 5). TTF was negatively correlated with effort responses at 60 s (control: $r_s = -.72$, FDR-adjusted $p = .001$; prior HG: $r_s = -.61$, $p = .006$) and positively correlated with affective valence at 60s (control: $r_s = .68$, $p = .002$; prior HG: $r_s = .46$, $p = .042$). Rate of change in effort perception was also negatively associated with TTF (control: $r_s = -.78$, $p < .001$; prior HG: $r_s = -.59$, $p = .008$). However, both the rate of change in affect (control: $r_s = -.26$, $p = .233$; prior HG: $r_s = -.03$, $p = .535$) and RoF immediately preceding the start of the KE task (control: $r_s = .12$, $p = .439$; prior HG: $r_s = .11$, $p = .439$) were not correlated with TTF.

We next explored whether perceived fatigue ratings (RoF) were related to subsequent perceptual and affective

FIGURE 5 Correlations between time to task failure (TTF) during the knee extensor (KE) endurance task and initial effort ratings (upper panel), initial affect ratings (middle panel), and the rate of change in effort perception (lower panel). Correlation coefficients are fitted for both the prior handgrip (HG; red circles) and control (blue circles) condition. $N = 20$
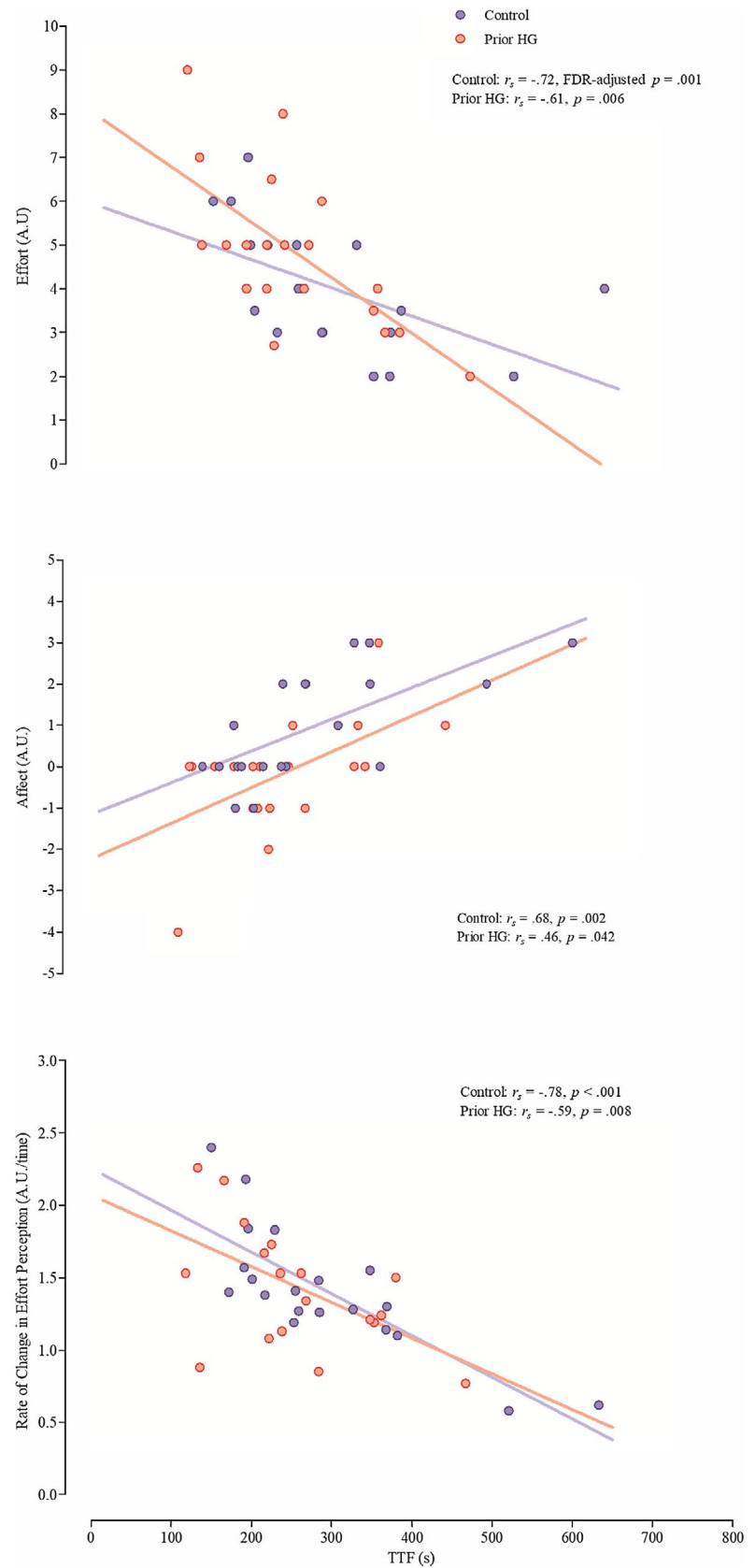
responses during (i.e., 60 s) motor activity. The repeated measures correlations demonstrated that RoF displayed a positive ($r_{rm} = .60$ [95% CI: 0.25–0.80], $p = .004$) and negative ($r_{rm} = -.68$ [95% CI: −0.51 to −0.87], $p < .001$) relationship with perceived effort and affective responses, respectively (Figure 6).

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3.1.4 | EMG responses during knee extension endurance task

RMS EMG and MPF demonstrated a main effect of time, increasing ($F_{(2.7, 48.8)} = 21.94$, $p < .001$, $\eta_p^2 = 0.549$) and decreasing ($F_{(3.5, 59.1)} = 33.82$, $p < .001$, $\eta_p^2 = 0.665$) across the KE task, respectively. However, there was no main effect of condition (RMS: $F_{(1,18)} = 2.96$, $p = .103$, $\eta_p^2 = 0.141$; MPF: $F_{(1,17)} = 0.32$, $p = .578$, $\eta_p^2 = 0.019$) or interaction across iso-time (RMS: $F_{(2.7, 48.5)} = 0.60$, $p = .603$, $\eta_p^2 = 0.032$; MPF: $F_{(3.0, 50.6)} = 0.52$, $p = .666$, $\eta_p^2 = 0.030$). RMS and MPF were not different between conditions at task termination (RMS: $t_{(18)} = 0.46$, $p = .653$, $d_{av} = -0.03$; MPF: $t_{(17)} = -1.57$, $p = .134$, $d_{av} = 0.23$) (Figure 7).

3.2 | Experiment two

Repetitions and duration of the HG task performed by the sub-sample were similar to that observed in the whole sample in the first experiment (11 ± 3 reps [range: 6–16 reps]; 310.0 ± 89.0 s [range: 170–470 s]). Within the sub-sample, no difference was observed in the percentage change in HG MVC force of either the dominant ($t_{(14)} = 1.50$, $p = .156$, $d_{av} = -0.44$) or the non-dominant ($t_{(14)} = 0.56$, $p = .582$, $d_{av} = -0.18$) hand between experiments.

3.2.1 | Neuromuscular function of the KE following prior HG exercise

Voluntary and evoked neuromuscular responses are shown in Table 2. Small reductions in voluntary force led to a main effect of time, with MVC declining across both conditions ($F_{(1,14)} = 11.82$, $p = .004$, $\eta_p^2 = 0.458$). MVC force was also significantly greater ($F_{(1,14)} = 13.47$, $p = .003$, $\eta_p^2 = 0.490$) in the control compared to the prior HG task (control: 555.5 ± 84.7 N; prior HG: 532.8 ± 79.0 N). Further investigation into this main effect of condition demonstrated that MVC force was different between the two conditions prior to the intervention ($t_{(14)} = 2.87$, $p = .012$, $d_{av} = -0.27$). There was no interaction between condition and time for MVC force ($F_{(1,14)} = 0.06$, $p = .808$, $\eta_p^2 = 0.004$). The TOST procedure indicated that the observed effect in the change in MVC force between conditions ($d_z = 0.06$) was not significantly within the prescribed bounds of equivalence ($d_z = -0.39$ and $d_z = 0.39$; $t_{(14)} = -1.26$, $p = .113$).

Q_{tw} decreased across interventions ($F_{(1,14)} = 16.43$, $p = .001$, $\eta_p^2 = 0.540$; pre: 147.3 ± 22.0 N versus. post: 142.8 ± 21.4 N) and was also greater across the control condition ($F_{(1,14)} = 18.09$, $p = .001$, $\eta_p^2 = 0.564$; control: 149.8 ± 18.8 N; prior HG: 140.2 ± 23.5 N). Again, condition effects could be attributed to differences between conditions prior to the interventions ($t_{(14)} = 3.66$, $p = .003$, $d_{av} = -0.43$). However, there was no interaction effect on Q_{tw} ($F_{(1,14)} = 0.04$, $p = .846$, $\eta_p^2 = 0.003$). The TOST procedure indicated that the observed effect ($d_z = 0.05$) was not significantly within the prescribed bounds of equivalence ($d_z = -0.05$ and $d_z = 0.05$; $t_{(14)} = -0.003$, $p = .499$). No condition, time or interaction effects were observed for M_{max} responses (Table 2). The observed effect across interventions ($d_z = -0.06$) was not within prescribed equivalence bounds ($d_z = -0.06$ and $d_z = 0.06$; $t_{(14)} = 0.008$, $p = .503$).

Changes across time were not evident for VA_{TMS} ($F_{(1,14)} = 2.64$, $p = .127$, $\eta_p^2 = 0.159$) but voluntary activation was slightly lower in the prior HG condition ($F_{(1,14)} = 10.46$, $p = .006$, $\eta_p^2 = 0.428$; control: 95.9 ± 2.9%, prior HG: 94.1 ± 3.7%). No interaction effect was found for VA_{TMS}
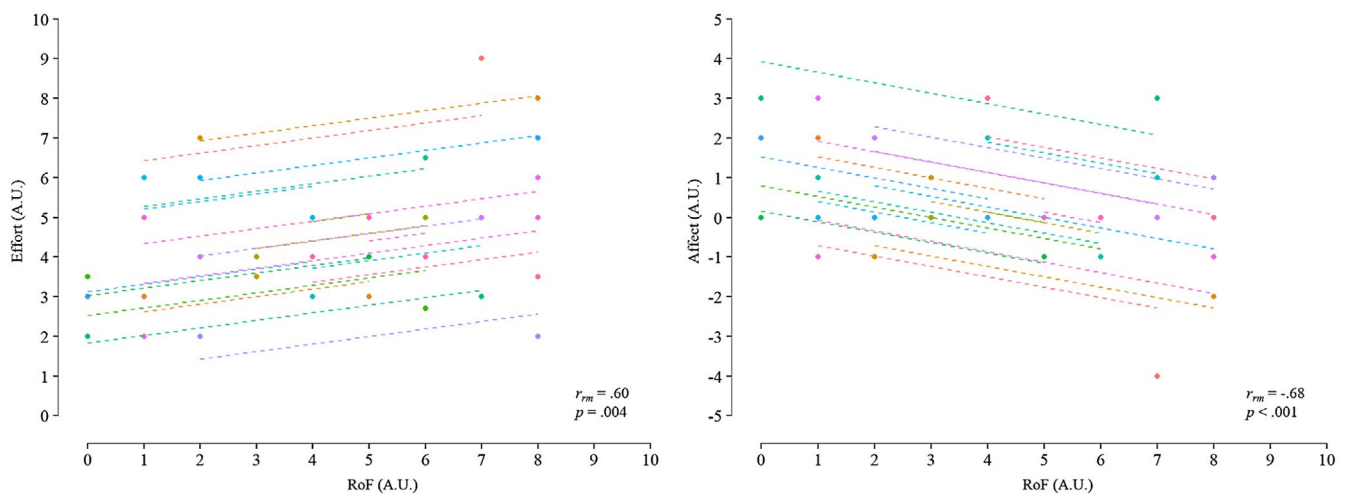
FIGURE 6 Repeated measures correlations between ratings of fatigue and initial effort (left panel) and initial affect (right panel). Observations from the same participant are represented by points of the same color. Corresponding dashed colored lines represent the repeated measures correlation fitted for each participant. $N = 20$
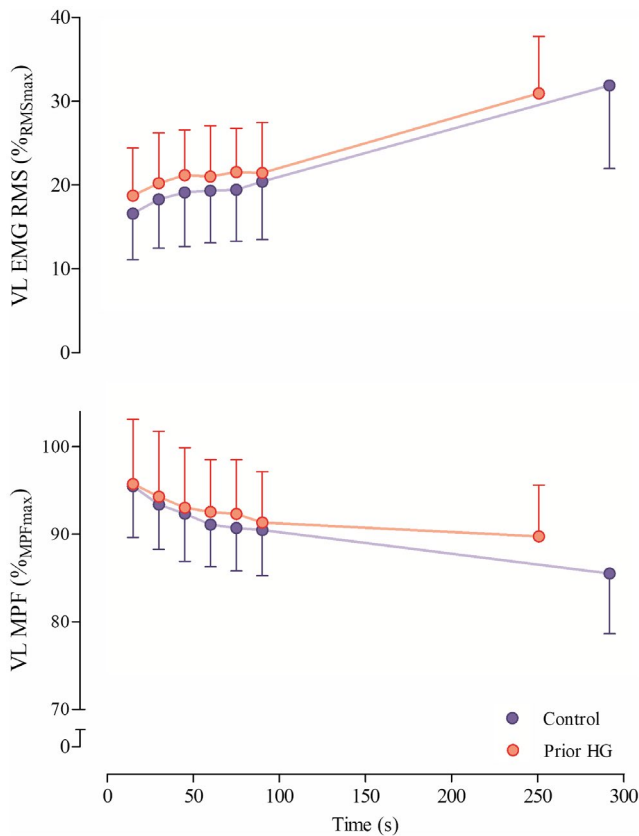
FIGURE 7 Effect of prior handgrip (HG) task on the root mean square (RMS) EMG (upper panel) and mean power frequency (MPF) (lower panel) of the *vastus lateralis* (VL) during the KE endurance task following both prior HG (red circles) and control (blue circles) conditions. Values are expressed relative to responses recorded during maximal contractions preintervention. $N = 19$

($F_{(1,14)} = 3.93$, $p = .067$, $\eta_p^2 = 0.219$). The TOST procedure demonstrated that the effect between conditions in the change in VA$_{TMS}$ ($d_z = 0.51$) was not significantly within the bounds of equivalence ($d_z = -0.26$ and $d_z = 0.26$; $t_{(14)} = 0.977$, $p = .827$). Greater SIT$_{100\%}$ force was evident in the prior HG condition ($F_{(1,14)} = 5.42$, $p = .035$, $\eta_p^2 = 0.279$; control: $1.00 \pm 0.80\%_{MVC}$; prior HG: $1.25 \pm 0.88\%_{MVC}$) but no time ($F_{(1,14)} = 1.87$, $p = .193$, $\eta_p^2 = 0.118$) or interaction effects were evident ($F_{(1,14)} = 4.44$, $p = .054$, $\eta_p^2 = 0.241$). The effect in the change in SIT$_{100\%}$ between conditions ($d_z = -0.55$) was not significantly within the bounds of equivalence ($d_z = -0.38$ and $d_z = 0.38$; $t_{(14)} = -0.636$, $p = .732$).

Agonist MEP amplitudes (%M_{max}) evoked in the KE are presented in Table 3. Irrespective of volitional contraction intensity, corticospinal excitability was unchanged by both condition ($F = 0.04$–1.36, all $p > .05$, $\eta_p^2 = 0.003$–0.089) and time ($F = 0.11$–3.21, all $p > .05$, $\eta_p^2 = 0.008$–0.187). Background EMG RMS, recorded immediately prior to stimulation, was unaffected by the experimental manipulations (all $p > .05$), while antagonist BF MEP responses were also unchanged (all $p > .05$) (Data for antagonist MEP responses and background

TABLE 2 Parameters of the neuromuscular function of the knee extensors (KE) evoked before and after prior handgrip exercise (prior HG) and time-matched passive rest (control).

	Control			Prior HG			ANOVA		
	Pre	Post	%Pre	Pre	Post	%Pre	Condition	Time	Interaction
MVC (N)	561.1 ± 84.3	549.8 ± 87.6	98.0 ± 4.8%	539.8 ± 75.7	525.9 ± 84.2	97.2 ± 4.2%	0.003	0.004	0.808
VA$_{TMS}$ (%)	95.8 ± 2.7	96.0 ± 3.3	N.A.	95.1 ± 2.8	93.0 ± 4.2	N.A.	0.006	0.127	0.067
SIT (%MVC)	1.09 ± 0.84	0.92 ± 0.78	N.A.	1.02 ± 0.60	1.49 ± 1.06	N.A.	0.035	0.193	0.054
ERT (N)	136.9 ± 38.5	118.3 ± 37.7*	86.4 ± 12.8%	110.4 ± 31.7†	107.3 ± 30.6†	98.0 ± 15.1%	0.007	<0.001	0.015
Q_{tw} (N)	152.0 ± 20.0	147.7 ± 18.0	97.4 ± 4.4%	142.6 ± 23.6	137.9 ± 24.0	96.6 ± 4.9%	0.001	0.001	0.846
M_{max} (mV)	9.20 ± 3.00 (0.95 ± 0.12)	9.14 ± 2.54 (0.95 ± 0.11)	100.7 ± 9.1% (100.4 ± 4.1%)	8.76 ± 2.80 (0.92 ± 0.13)	8.84 ± 2.85 (0.93 ± 0.12)	101.3 ± 8.7% (100.6 ± 4.1%)	0.110	0.674	0.837

Note: Data presented as mean ± *SD*. Values in parentheses represent descriptive statistics for *log*(10) transformed variables. $N = 15$.

Abbreviations: M_{max}, M-wave during 100% MVC; MVC, maximal voluntary contraction; Q_{tw}, twitch force; SIT, superimposed twitch; VA$_{TMS}$, voluntary activation.

*Significantly different from prevalues ($p < .05$);

†Significantly different from the respective control value ($p < .05$).

TABLE 3 Motor evoked potentials (MEPs; $\%M_{max}$) recorded in the *vastus lateralis* (VL) at both relative and absolute force levels

Force	Control		Prior HG		ANOVA		
	Pre	Post	Pre	Post	Condition	Time	Interaction
100%	40.9 ± 7.8	38.0 ± 11.3	38.9 ± 9.5	39.2 ± 13.7	0.811	0.512	0.255
87.5%	40.7 ± 12.8	40.5 ± 10.3	39.8 ± 10.6	41.9 ± 10.4	0.853	0.611	0.546
75%	43.7 ± 10.2	42.5 ± 11.6	40.9 ± 11.1	40.2 ± 10.5	0.263	0.656	0.860
62.5%	45.0 ± 10.5	43.5 ± 11.3	42.4 ± 10.2	45.2 ± 9.7	0.747	0.750	0.110
50%	46.1 ± 10.9	40.8 ± 10.0	42.5 ± 11.2	42.8 ± 12.0	0.479	0.095	0.068
20%$_B$	49.6 ± 13.2	44.3 ± 14.8	46.4 ± 11.8	49.3 ± 14.2	0.549	0.208	0.060

Note: Data presented as mean ± SD. 20%$_B$: Absolute force value (126.5 ± 18.6 N) equating to 20% of preliminary maximal force production. $N = 15$.

RMS EMG are not shown). At an absolute force level (20%$_B$: 126.5 ± 18.6 N), corticospinal excitability was unchanged (Table 3). Evoked antagonist responses at 20%$_B$ were also unaffected (interaction: $F_{(1,14)} = 0.68$, $p = .425$, $\eta_p^2 = 0.046$; condition: $F_{(1,14)} = 0.73$, $p = .408$, $\eta_p^2 = 0.049$; time: $F_{(1,14)} < 0.01$, $p = .979$, $\eta_p^2 < 0.001$). All observed effects in the change in MEP response between conditions were not deemed equivalent (all $p > .05$).

4 | DISCUSSION

In the first experiment, we used prior remote exercise in the upper body to study the interactions between perceptions of fatigue, effort, and affect during a sustained, sub-maximal contraction of the KE. As hypothesized, impaired KE endurance performance was associated with increased perceptions of effort and reduced affect. Perceptions of fatigue were also increased by the HG exercise, but perceptions of fatigue were not correlated with KE endurance performance. Perceptions of fatigue were, however, correlated with effort and affective ratings during the endurance exercise. In the second experiment, the absence of interaction effects suggests that maximal force production, voluntary activation, and corticospinal responses of the KE were not influenced directly by the performance of prior HG exercise. We cautiously interpret our findings to indicate no difference in recorded neuromuscular function between conditions. These results indicate that cognitive–emotional interactions limit endurance performance, independent of acute alterations to neuromuscular function.

Termination of endurance performance is limited by the attainment of maximal perceived effort, which has been associated with either homeostatic threat (Noakes, 2012) or more general motivational processes (Marcora, 2008). In the present study, effort perception was increased following the HG exercise compared to the control condition. The correlations between TTF and the rate of change in effort perception across both conditions suggest that this increased effort perception induced by the HG exercise caused faster attainment of maximal effort. Our results support previous observations in both single limb and whole-body exercise, demonstrating

increased effort perception following prior remote exercise independent of concomitant changes in the neuromuscular function (Amann et al., 2013; Johnson et al., 2015; Morgan et al., 2019). The results of the present study also parallel those observed following prior cognitive tasks (Pageaux et al., 2013; Pageaux, Marcora, Rozand, & Lepers, 2015) which may support the proposal that prior cognitive activity and remote motor exercise increase effort and limit subsequent motor performance through shared processes within the brain (Pageaux & Lepers, 2016). The absence of neuromuscular impairment suggests that heightened effort perception was unlikely a response to compensatory increases in motor output (and thus corollary discharge) from motor centers (de Morree et al., 2012; Marcora et al., 2008). An alternative explanation may be that prior neural activity during the HG exercise elicited changes in sensorimotor regions and the processing of corollary discharges during the KE endurance task (Pageaux & Lepers, 2016). However, the present study was not equipped to investigate this hypothesis.

Affective valence was also reduced by prior HG exercise and affective responses were related to task performance across conditions. Our data, therefore, indicate both effort perception and affective valence are important for behavioral regulation during motor activity. Challenges to homeostasis are sensed within interoceptive circuits and are intrinsically valenced (Lindquist, Satpute, Wager, Weber, & Barrett, 2016). Homeostatic challenges thus evoke affective changes, which may disrupt current goal-related actions and influence decision making in favor of more biologically significant behaviors, that is, the preservation of homeostasis (Damasio & Carvalho, 2013). Unsurprisingly then, affect has previously been associated with endurance performance (Hartman et al., 2019; Jones et al., 2015; Renfree, West, Corbett, Rhoden, & Gibson, 2012). Hartman et al. (2019) proposed that during intense exercise, the perception of effort is intrinsically affective, such that the two constructs merge, with the experience of intense displeasure enabling the sense of effort to enter consciousness and ultimately lead to the termination of the activity. This may explain why both effort and affect were related to endurance performance within the present study. However, unlike effort, the rate of change of affect was not associated

with task termination which may question the validity of this proposition. Further studies are required not only to further distinguish the behavioral influence of both effort and affective valence, but also clearly differentiate the two constructs.

Prior motor activity also led to greater subjective RoF. Though not correlated with the performance itself, perceptions of fatigue were associated with initial effort and affective responses during the KE endurance task. Our findings support recent observations following prior cognitive activity (Harris & Bray, 2019) and are also in line within findings within clinical populations (Prak et al., 2019). Disassociation of perceptions of fatigue, effort, and affect may be inherently difficult since all may reflect outcomes of the same integrated control process (Hockey, 2011). However, we appear to have been able to, at least partially, disassociate fatigue from perceptual/affective regulatory responses to endurance exercise, evidenced not only through different behavioral correlates but also the intensity of the responses. While effort and affect were (or close to) maximal and minimal, at task failure in both conditions, respectively, perceptions of fatigue were distinctly sub-maximal and differed between conditions.

Recent metacognitive theories of fatigue may provide a framework to understand the observed relationships between the studied perceptual and affective responses. Within these theories, fatigue reflects a concern (or negative belief) in one's ability to control (or predict) bodily states (Manjaly et al., 2019; Stephan et al., 2016). The perception of effort (Kuppuswamy, 2017) and core affect (Barrett, 2017) have been proposed to emerge through a mismatch (i.e., prediction error) between the predicted proprioceptive/interoceptive sensory consequences of action and the actual sensory feedback received. Prediction error increases attention towards ascending sensory information and conscious awareness of perceptual and affective changes, which may undermine belief in held internal models generating control predictions (Stephan et al., 2016). Declines in confidence (or precision) in issued proprioceptive/interoceptive predictions (that is, fatigue) may, therefore, lead to greater prediction errors and attention towards ascending sensory information in lower parts of the system, which further influence perceptual responses to action (i.e., increasing perceived effort and reducing affect). Our findings appear to support the structure of these metacognitive theories and implicate fatigue within an overarching control of the psychophysiological regulation of endurance performance. As the RoF does not capture the hedonic properties of fatigue (Micklewright et al., 2017), it is possible that the association between affect and fatigue simply reflects the emotional component of the fatigue perceptions (St Clair Gibson et al., 2003). However, that the two constructs could be at least partially disassociated would appear to suggest otherwise. In line with metacognitive propositions, we suggest that the perception of fatigue sits above lower-level perceptual (e.g., effort) and affective responses and modulates the attention afforded to ascending prediction

errors within proprioceptive/interoceptive systems (i.e., how much effort is required and/or the affective responses evoked through physiological perturbations), which in turn influence action. Further, larger-scale investigations analyzing the mediating effect of the perception of fatigue may enable the assessment of this hypothesis.

In *experiment two*, the prior HG exercise did not significantly alter neuromuscular responses of the rested dominant KE. All interaction effects between condition and time were non-significant. Though changes in parameters fell outside the estimated bounds of equivalence, we cautiously interpret our findings to demonstrate no significant effect of prior HG exercise on KE neuromuscular function. The findings add to a growing number of observations describing no functional effects (i.e., loss of force) across the upper and lower body within non-activated, heterologous muscle groups following both whole-body (Decorte, Lafaix, Millet, Wuyam, & Verges, 2012; Ross, Middleton, Shave, George, & Nowicky, 2007) and single-limb exercise (Aboodarda, Copithorne, Power, Drinkwater, & Behm, 2015; Aboodarda et al., 2017). It appears that, following prior remote exercise, cortical motor output is well maintained during brief contractions. Where evidenced, force deficits evoked by prior, remote exercise have primarily been observed in anticipation of (Li, Power, Marchetti, & Behm, 2019) or toward the end of the protracted or repeated activity (Halperin, Aboodarda, & Behm, 2014). Based on the outcomes of *experiment one*, it is possible that such declines may simply reflect changes in motivational and decision-making processes determining the allocation of effort (e.g., Meyniel, Sergent, Rigoux, Daunizeau, & Pessiglione, 2013) rather than direct physiological inhibitory feedback mechanisms.

The corticospinal excitability of the KE was also unchanged by the prior HG task. To the best of our knowledge, the present study represents the first quantification of MEPs in the lower limbs following prior exercise in the upper limbs. Conflicting responses have been reported in the elbow flexors following lower limb activity (Aboodarda et al., 2017; Šambaher et al., 2016; Sidhu et al., 2014). Aboodarda et al. (2017) reported that effects to the supra-spinal excitability of the elbow flexors were force dependent, with an increase in the ratio of corticospinal to spinal motoneuronal responses evident at 100% MVC, no change evident at 50% MVC and a decrease observed at 5% MVC. The discrepancy between these results and those of the present study may be attributed to various methodological differences (e.g., stimulator intensity; McNeil, Giesebrecht, Gandevia, & Taylor, 2011). Of particular interest may be differences between upper and lower limb neurophysiology. Stronger connectivity between pre-motor and primary motor cortex has previously been reported during the activity of the upper limbs compared to the lower limbs (Volz, Eickhoff, Pool, Fink, & Grefkes, 2015). Increased connectivity between premotor areas and M1 in order to facilitate or maintain motor output during demanding activity (Jiang, Wang, Kisiel-Sajewicz, Yan, &

Yue, 2012) may, therefore, be more effective in non-exercised upper limb muscles, leading to greater MEP facilitation at maximal force intensities in the upper limbs. We did not measure the excitability of the spinal motoneuron pool so could not evaluate the excitability of supra-spinal circuitries specifically, which appear the most likely site of effects within non-activated muscles (Aboodarda et al., 2017; Šambaher et al., 2016). Increased motoneuron excitability of the KE has been reported following sustained maximal contractions of the elbow flexors (Aboodarda et al., 2015). As the total excitability of the corticospinal tract is the product of both supra-spinal and spinal influences, we cannot discount that supra-spinal excitability of the KE motoneurons may have in fact seen a relative reduction. Future research is thus required to further quantify the supra-spinal excitability of the lower limbs following prior upper body motor activity.

Some methodological limitations of the present study should also be considered: First, we treated our perceptual and affective ratings as continuous, rather than ordinal variables (e.g., Bishop & Herron, 2015), adopting parametric factorial analyses. It is suggested that, due to the length of the scales used, such an approach may be justified (Harpe, 2015). However, as debate concerning the most appropriate statistical analysis of this form of data continues (Carifio & Perla, 2008; Knapp, 1990), we urge interested parties to reanalyze our data as they see fit (https://osf.io/kbzvn/). Next, it is important to acknowledge that RoF was assessed at rest, while effort and affect were measured during the KE task. Unlike effort perception, fatigue ratings are not inherently dependent upon motor signals (Micklewright et al., 2017), however, the disassociation of response intensity and behavioral correlates between fatigue and effort/affect may have been influenced by the absence of central motor commands when assessing fatigue. In *experiment two*, the main effects of condition for voluntary and evoked contractions were evident, with lower responses recorded in the prior HG condition. This reduction could account for the altered perceptual and affective responses of *experiment one*. Importantly, deficits were evident between conditions prior to the respective interventions. As conditions were performed in a constant order, this most likely represents an effect of order or time. Moreover, the reductions were small (~4%–6%) and within the typical error associated with these measures at rest and therefore we believe do not represent an acute effect of prior remote activity (Dekerle et al., 2019). Replication studies of the presented effects are required. Finally, at least six stimulations have been recommended for the reliable assessment of corticospinal excitability (Lewis, Signal, & Taylor, 2014).

5 | CONCLUSION

In conclusion, we provide evidence that prior, remote exercise may be used as an effective paradigm in isolating and studying the interactions between perceptual and affective factors and associated consequences to physical endurance performance. When preceded by demanding exercise in the upper limbs, lower body endurance performance is limited through complex cognitive–emotional interactions, independent of acute challenges to the integrity of the neuromuscular system. While effort and affective responses were shown to be associated with the termination of endurance performance specifically, perceptions of fatigue were implicated in performance regulation indirectly, through an overarching control of these perceptual and affective constructs.

CONFLICT OF INTERESTS
No competing interests declared.

AUTHOR CONTRIBUTIONS
All authors were involved in the design of the study. AGT and MR performed the data collection. AGT drafted the first version of the manuscript, with all authors involved in subsequent revisions and approval of the final document.

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