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Submaximal fatiguing eccentric contractions of knee flexors alter leg extrapersonal representation

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ABSTRACT

This study assessed the immediate and prolonged effects of eccentric-induced fatigue on position sense, utilizing position-pointing tasks, which had not been previously implemented for this purpose. Fifteen healthy adults underwent a fatiguing eccentric protocol that entailed sets of unilateral submaximal contractions of knee flexor muscles until reaching a 20% decrease in maximal isometric torque production. Evaluations of knee flexor neuromuscular function as well as position-pointing tasks at 40° and 70° of knee flexion were conducted prior to the fatiguing eccentric protocol, immediately after (POST), and 24 h after (POST24) exercise termination. To assess neuromuscular fatigue etiology, electrical myostimulations were administered during and after maximal voluntary isometric contractions. At POST, the voluntary activation level and evoked potentiated doublet amplitude at 100 Hz were significantly reduced. In addition, position-pointing errors exhibited a significant increase at POST regardless of the tested angle, with participants positioning the pointer in a more extended position compared to their hidden exercised limb. At POST24, neuromuscular function and position sense parameters had reverted to their baseline levels. The findings of this experiment demonstrate that position-pointing accuracy was impaired immediately after the fatiguing eccentric protocol, manifesting in the presence of both central and peripheral fatigue. As position-pointing accuracy relies heavily on extrapersonal representation of the body at the brain level, acute changes in exercised limb's extrapersonal representation might have resulted from central fatigue-related mechanisms altering the cognitive processes responsible for converting kinesthetic signals into extrapersonal coordinates.

1. Introduction

Kinesthesia, which encompasses the senses of body positions and movements [1], plays a fundamental role in sensorimotor control [2]. Most studies conducted to investigate kinesthesia focused on position sense using bilateral joint position-matching tasks (*e.g.*,

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[3–6]). During these tasks, it has been shown that muscle spindles, length-sensitive mechanoreceptors composed of intrafusal fibers and innervated by type Ia and II afferents, are essential for providing positional information [1]. This has primarily been highlighted by the observation of significant increases in position-matching errors when altering muscle spindle signals through vibration [7] or manipulation of their thixotropic properties [8].

In addition to using bilateral position-matching tasks, position sense can also be assessed using position-pointing tasks [9–12]. During these tasks, the tested limb, hidden from participants' sight, is passively positioned at a controlled angle by the experimenter. Participants then have to indicate the position of their tested limb in the extrapersonal space with a pointer [12]. Previous experiments have demonstrated that position-pointing accuracy is insensitive to vibration- and thixotropic-related modulations of muscle spindle signals [9,10], showing that position-pointing and bilateral position-matching tasks involve different neural processes [11,12]. In comparison to bilateral position-matching tasks, pointing to a position requires more complex neural computations because the brain must transform the kinesthetic signals into extrapersonal coordinates [13]. This transformation process is closer to the kinesthetic abilities required in sports performance (*e.g.*, in artistic disciplines or during motor imagery exercises) compared to the sensory signal reproduction involved in bilateral position-matching tasks. Position-pointing tasks therefore represent an attractive tool that may increase our understanding of kinesthesia-related processes by focusing on high-level kinesthetic abilities [13].

During physical exercise, a transient alteration in neuromuscular performance (*e.g.*, strength or power) is commonly observed with the repetition or maintenance of voluntary contractions. This performance decline refers to neuromuscular fatigue, which can involve changes in the central nervous system (*i.e.*, reduction in muscle activation resulting from spinal and/or supraspinal adjustments) and at the peripheral level (*i.e.*, alteration in contractile function properties distant to the neuromuscular junction) [14]. In particular, exercise-induced neuromuscular fatigue can lead to significant central alterations, especially through the increased neural flow of group III-IV afferents at the cortical level [15]. The integration of these afferent inputs result in the reduction of the voluntary activation level (VA, central fatigue indicator) [16,17] and/or changes in brain activity, especially in the sensorimotor cortices [18,19]. Given the importance of neural computations at the brain level in position-pointing accuracy, exercise-induced central fatigue might impair the extrapersonal representation of the body. However, to the best of our knowledge, such hypotheses have never been tested in the context of neuromuscular fatigue.

Many studies have explored the effects of exercise-induced neuromuscular fatigue on position sense using bilateral position-matching tasks (*e.g.*, [20–23]). To better delineate the mechanisms accounting for fatigue-induced position sense alterations, these studies predominantly focused on examining the impact of fatigue induced by eccentric contractions on position-matching performance. The hypothesis was that the repetition of eccentric contractions, leading to damage in extrafusal muscle fibers, could potentially propagate to intrafusal fibers and, consequently, alter the position sense [24]. However, contrary to this peripheral hypothesis, position sense alterations were similarly observed after repeated damaging eccentric and non-damaging concentric contractions [21,25]. These observations led the authors to suggest that the increase in position-matching errors following fatiguing eccentric protocols was due to exercise-induced alterations in the central nervous system [22,26]. Specifically, in a recent experiment, our group concurrently examined the effects of a submaximal fatiguing eccentric protocol of knee flexors (KF) on neuromuscular function and position sense at the knee using bilateral position-matching tasks [27]. During such tasks performed in seated position, errors increased in the presence of central fatigue immediately following the fatiguing eccentric protocol, but reverted to baseline levels 24 h post-exercise [27]. Acute eccentric-induced position sense alterations were attributed to disturbances in the integration and/or processing of positional signals at the somatosensory cortex level due to the actions from group III-IV afferents. Nonetheless, because kinesthesia is multifaceted and that position sense evaluations (*i.e.*, bilateral position-matching *vs.* unilateral position-pointing tasks) should not be viewed as interchangeable but rather as complementary [13], investigating the impact of repeated eccentric contractions on position-pointing accuracy would hold significant importance. Specifically, this would broaden our understanding of the consequences of eccentric-induced fatigue on position sense, whether coded in relation to the body or to the extrapersonal space.

In order to extend findings from our previous bilateral-matching experiment on KF [27], the current investigation was conducted to examine the immediate and prolonged effects of eccentric-induced fatigue on position sense employing position-pointing tasks. We expected that position-pointing errors would significantly increase in presence of neuromuscular fatigue induced by a submaximal KF eccentric protocol. More precisely, because position-pointing accuracy seems highly dependent on central processing of kinesthetic inputs at a brain level, it was postulated that alterations in position sense would solely manifest following the exercise in the presence of central fatigue (*i.e.*, reduced KF voluntary activation). We also hypothesized that position-pointing errors and KF VA deficits would return to control values 24 h post-exercise.

2. Materials and methods

2.1. Participants

The study participants were selected from the *FIJAP* project conducted in Nice, France. The primary objective of this project was to investigate the immediate and prolonged impacts of various submaximal fatiguing protocols specifically targeting the hamstring muscles (*e.g.*, eccentric and concentric exercises, simulated soccer game) on neuromuscular function and kinesthetic acuity. The experimental procedures employed in this project, including the present study, received official authorization from a national Ethics Committee (2020-A02811-38).

The required minimum sample size for the current study was determined using G*Power (version 3.1.9.4; Kiel University, Kiel, Germany), taking into consideration the findings of a prior study that revealed position-matching errors following a submaximal KF eccentric exercise in the presence of KF VA deficits [27]. It was found that a minimum of eight participants was necessary to conduct statistical analyses for a within-subject design employing repeated measures with a desired power level of 0.95. However, the study's sample size was determined using a stopping rule based on resource constraints [28]. Therefore, fifteen healthy young men [mean ± standard deviation (SD); age: 23.9 ± 4.9 years; mass: 79.2 ± 9.9 kg; height: 1.81 ± 0.04 m] participated in this study. The inclusion criteria for the participants stipulated that they had to be free from lower limb injuries for a minimum of six months, had no history of knee surgery, and engaged in sports activities (*e.g.*, soccer, rugby or cycling) for less than 6 h per week. Furthermore, a sensitivity power analysis was conducted, employing an α level of 0.05 and a power of .95, which revealed a medium effect ($f = 0.43$) for the study's sample size. Prior to any testing, experimental procedures were fully explained to participants. Subsequently, informed consent was obtained from each participant, confirming their voluntary agreement to participate in the study.

2.2. Experimental design

Throughout the experimental duration, participants came to the laboratory in three occasions. The first session was designed to collect participants' physical characteristics and to familiarize them with position-pointing tasks performed using a custom-made pointing box (see Position sense evaluations using position-pointing tasks for more details). Furthermore, participants were accustomed with the assessment of KF neuromuscular function, along with the eccentric unilateral 1 repetition maximum (1RM ECC) test (for further details, refer to the section Neuromuscular tests). Both evaluations were conducted on a specific ergometer (Hamtech, Human Kinematic, France) [28]. One week subsequent to the familiarization session, assessments were conducted at three distinct measurement intervals: before, directly after, and 24 h after the fatiguing eccentric protocol (*i.e.*, respectively PRE, POST, and POST24; Fig. 1).

2.3. Fatiguing eccentric protocol

The fatiguing eccentric protocol was comprised of sets of unilateral submaximal eccentric contractions executed at an intensity equivalent to 80% of the 1RM ECC measured, which was determined prior to the exercise (*i.e.*, at PRE; see KF torque measurements for more details). Eccentric contractions were realized on participants' right lower limb under conditions close to the Nordic hamstring exercise on a dedicated ergometer. Precise adjustments were made at the onset of each repetition to maintain the hip and knee angles at 65° and 90° (with 0° denoting full extension), while hip and knee joints reached 40° and 30° of flexion in the ending position. Participants performed sets of 5 repetitions at an angular velocity of 10°.s-1 until reaching a 20% reduction in maximal voluntary isometric contraction (MVIC) force. This targeted force loss was selected because it is consistent with the force decrement observed after ecological fatiguing exercise (*i.e.*, simulated soccer game) [29]. The participants were actively engaged in managing the angular velocity, utilizing signals derived from a potentiometer (P4500, Novotechnik U.S., Inc., Southborough, MA, USA) which were presented on a screen in front of them. Each repetition lasted 5 s and were separated by a rest period of 10 s. Sets were interspersed by a 25-s rest period during which the neuromuscular tests were conducted. The total number of repetitions required to reach task failure

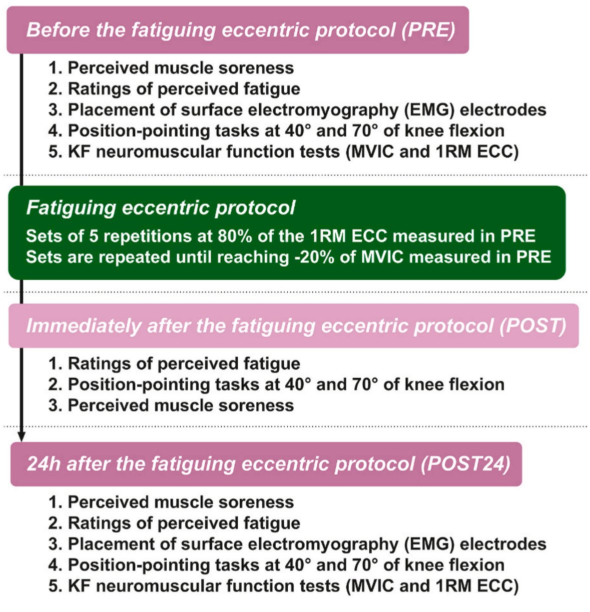

Fig. 1. Outline of the study design encompassing measurements conducted prior to the fatiguing eccentric protocol, immediately after, and 24 h after exercise termination. The measurements involved the evaluations of knee flexor (KF) neuromuscular function during maximal voluntary isometric contractions (MVICs), as well as during eccentric unilateral 1 repetition maximum tests (1RM ECCs). For more details, please refer to the text.

criterion (*i.e.*, −20% MVIC force) as well as the average peak torques of the eccentric contractions were recorded and used for further statistical analysis.

2.4. Data collection and analysis

2.4.1. Neuromuscular tests

2.4.1.1. KF torque measurements. The measurement of right lower limb KF force was conducted using the aforementioned ergometer, which has shown good reliability for this purpose [28]. To measure unilateral isometric and eccentric force production, an S-beam force transducer (LS02-s, Tech Co. Ltd, Shenzhen, China; capacity: 1 kN) was placed 5 cm above the participants' right malleolus on their Achilles tendon. Force data were recorded with the version 4.1 of the Acknowledge software (Biopac Systems, Inc., Goleta, CA., USA; sampling rate: 1 kHz). Torque values were subsequently calculated based on the lever arm of each participant, *i.e.*, the distance between the force transducer and the lateral tibial condyle. To ensure minimal pelvic movement, participants were securely fastened to the ergometer using two elastic bands, meticulously positioned above and below the sacroiliac joint and the gluteal fold, respectively.

MVICs, executed in a position combining 40° of knee hip flexion and 30° of knee flexion, were consistently performed with electrical myostimulations (see Contractile properties and voluntary activation level for more details). Participants were asked to perform one MVIC at exercise termination, while the highest peak torque of the two MVICs carried out at the other measurement times (*i.e.*, at PRE and POST24) was retained for analysis. In addition to the isometric torque production measurements, peak 1RM ECC torques were determined before as well as 24 h subsequent to the fatiguing protocol. This determination was accomplished by incrementally increasing the load until participants could no longer control the required angular velocity ($10^{\circ}.s^{-1}$). 1RM ECC was performed under the conditions previously mentioned (*i.e.*, hip and knee angles as well as angular velocity of eccentric contractions; see Fatiguing eccentric protocol).

2.4.1.2. Contractile properties and voluntary activation level. The current study assessed both central and peripheral aspects of KF neuromuscular fatigue by employing electrical myostimulations during and after MVICs [30]. For this purpose, rectangular electrical pulses with a maximum voltage of 400V and a duration of 1 ms were delivered using an electrical stimulator (Digitimer Stimulator DS7, Digitimer Ltd., Hertfordshire, UK). To deliver electrical pulses, self-adhesive rectangular electrodes (5 cm × 9 cm - Stimex, Wetzlar, Germany) were employed. The cathode electrode was carefully positioned beneath the gluteal fold, precisely at the site that elicited the maximum single twitch and amplitude of the compound muscle action potential for the biceps femoris (BF M-wave) at rest. The anode electrode was positioned at the level of the popliteal fossa, and precise electrode locations were demarcated on the skin using permanent ink to ensure consistent stimulation electrode placement across experimental sessions. In order to optimize spatial recruitment of motor units during the neuromuscular tests, the stimulation intensity was set at 120% of the intensity that elicited the maximum single twitch and BF M-wave amplitude (141.3 ± 26.7 mA).

To investigate peripheral factors of KF neuromuscular fatigue, potentiated torques evoked by paired electrical myostimulations at a frequency of 100 Hz (Dt_{100Hz}) and 10 Hz (Dt_{10Hz}) as well as by a single electrical myostimulation (Tw_{pot}) were delivered 2 s, 4 s, and 6 s after each MVIC. The Dt_{10Hz}-to-Dt_{100Hz} ratio (Dt_{10Hz}/Dt_{100Hz}) was calculated and utilized as a low-frequency peripheral fatigue indicator [17]. To determine KF VA, superimposed 100-Hz stimuli (Dt_{sup}) were automatically delivered during MVICs 2.5 s after the onset of the contraction. Because Dt_{sup} was generated automatically (*i.e.*, and thus possibly not always delivered at peak torque), VA was calculated using Strojnik and Komi's formula [31]:

$$VA\,(\%) = \left(1 - \left[\frac{Dt_{sup} \times \text{Voluntary torque before } Dt_{sup}}{\frac{MVIC}{Dt_{100Hz}}}\right]\right) \times 100$$

2.4.2. Recordings of biceps femoris (BF) electromyographic activity

Pairs of Ag/AgCl surface electrodes (diameter = 10 mm; inter-electrode distance = 20 mm; Contrôle-Graphique, Brie-Comte-Robert, France) were used to record the electrical activity of the right lower limb BF. Prior to electrode placement, participants' skin was shaved, lightly abraded and cleaned with alcohol to reduce skin impedance below 3kΩ. The placement of electrodes on the muscle belly was conducted in accordance with the SENIAM recommendations [32]. Additionally, a reference electrode was positioned on the lateral tibial condyle, and the location of the electrodes which optimized the BF M-wave was marked with indelible ink to ensure consistent repositioning across experimental sessions. The Biopac MP150 system (Biopac Systems, Inc., Goleta, CA, USA) was used to amplify and filter the electromyographic signals, employing a bandwidth frequency of 10–500Hz, a common mode rejection ratio of 110 dB, a Z Input of 1000MΩ, and a gain of 1000. The aforementioned Acknowledge software was used to record signals at a sampling frequency of 2 kHz. At each measurement time, maximal peak-to-peak amplitude of the potentiated BF M-wave was measured during Tw_{pot} and used for statistical analysis.

2.5. Psychophysical evaluations

2.5.1. Position sense evaluations using position-pointing tasks

Immediate and prolonged effects of neuromuscular fatigue resulting from repeated eccentric contractions on knee position sense of the exercised limb were studied using position-pointing tasks (Fig. 1). They were performed in seated position on the extremity of a massage table with a custom-made pointing box at 40° and 70° of knee flexion (Fig. 2). At each measurement time, six pointing trials were performed, *i.e.*, 3 at 40° and 3 at 70° of knee flexion. These six trials were randomized across participants and measurement times. Special attention was paid to ensure identical positioning of participants during position-pointing tasks throughout the experiment. For this purpose, the height of the pointer (placed on the right side of the pointing box, Fig. 2) as well as the distance between the pointing box and the massage table were measured during the familiarization session to ensure that the rotation axis of the pointer corresponded to the knee joint axis of each participant. This configuration was then strictly reproduced during the other experimental sessions.

Before each trial, the exercised lower limb hidden from participants' sight with the pointing box and the pointer were repositioned to 90° so that participants were not influenced by the previous position. The participants' limb was then passively moved by the experimenter to 40 or 70° of knee flexion with the help of a digital inclinometer. Participants were instructed to maintain the position of their knee joint while moving the pointer until they perceived it to be aligned with their hidden lower limb (*i.e.*, participants were told that the pointer represented the line between the axis of knee rotation and the lateral malleolus). When participants achieved satisfactory pointing, the experimenter recorded the angles of the knee and the pointer using a digital inclinometer. Position-pointing errors were calculated using the following formula:

$$\text{Position} - \text{pointing errors } (^\circ) = \text{Knee joint angle of the right lower limb} - \text{Pointer angle}$$

Positive position-pointing errors denote that the pointer was placed in a more extended position than the hidden exercised lower limb, indicating that participants perceived their fatigued KF muscles to be more stretched than their actual length.

2.5.1.1. Muscle soreness. Perceived muscle soreness scores were recorded at each measurement time using a numerical rating scale from 0 to 10 (0, no pain; 10, worst pain; Fig. 1). During these measurements, participants were in supine position on the massage table, completely relaxed. They were asked to indicate the perceived muscle pain induced by a constant pressure of 25 N applied by the experimenter just above and below BF electromyographic electrodes with a cylindrical object of 0.5 cm diameter [33]. Muscle soreness was assessed before the realization of position-pointing tasks at PRE and POST24. In contrast, at POST, scores of perceived muscle soreness were acquired at the very end after the last pointing trial (Fig. 1). The scores obtained above and below the electrodes were averaged for each measurement time to facilitate statistical analysis.

2.5.1.2. Perceived fatigue. As illustrated in Fig. 1, the evaluation of perceived fatigue, described as "a feeling of diminishing capacity to cope with physical stressors" [34], was conducted at each measurement time. For this purpose, a validated French numerical rating scale ranging from 0 (not fatigue at all) to 10 (total fatigue and exhaustion) [35] was utilized.

2.6. Statistical analyses

The data presented in the results section are expressed as means ± SD values. The normality of each dependent variable and the

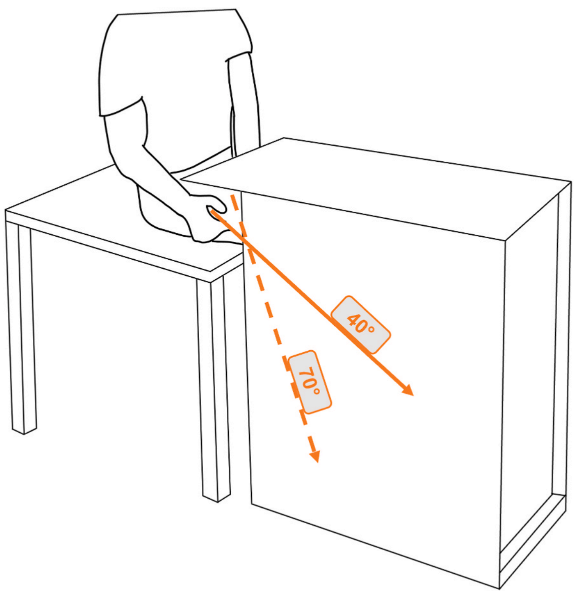

Fig. 2. Illustration of the custom-made pointing box used to assess knee position sense of the right exercised lower limb at 40° and 70° of knee flexion. For more details, please refer to the text.

homogeneity of variance in the distributions were verified using the Kolmogorov-Smirnov test and the Bartlett test, respectively.

Given that position-pointing tasks are rarely used in the literature to assess position sense, we decided to determine intra- and inter-session reliability of the errors measured during non-fatigue measurement times (*i.e.*, during familiarization and at PRE) at 40° and 70°

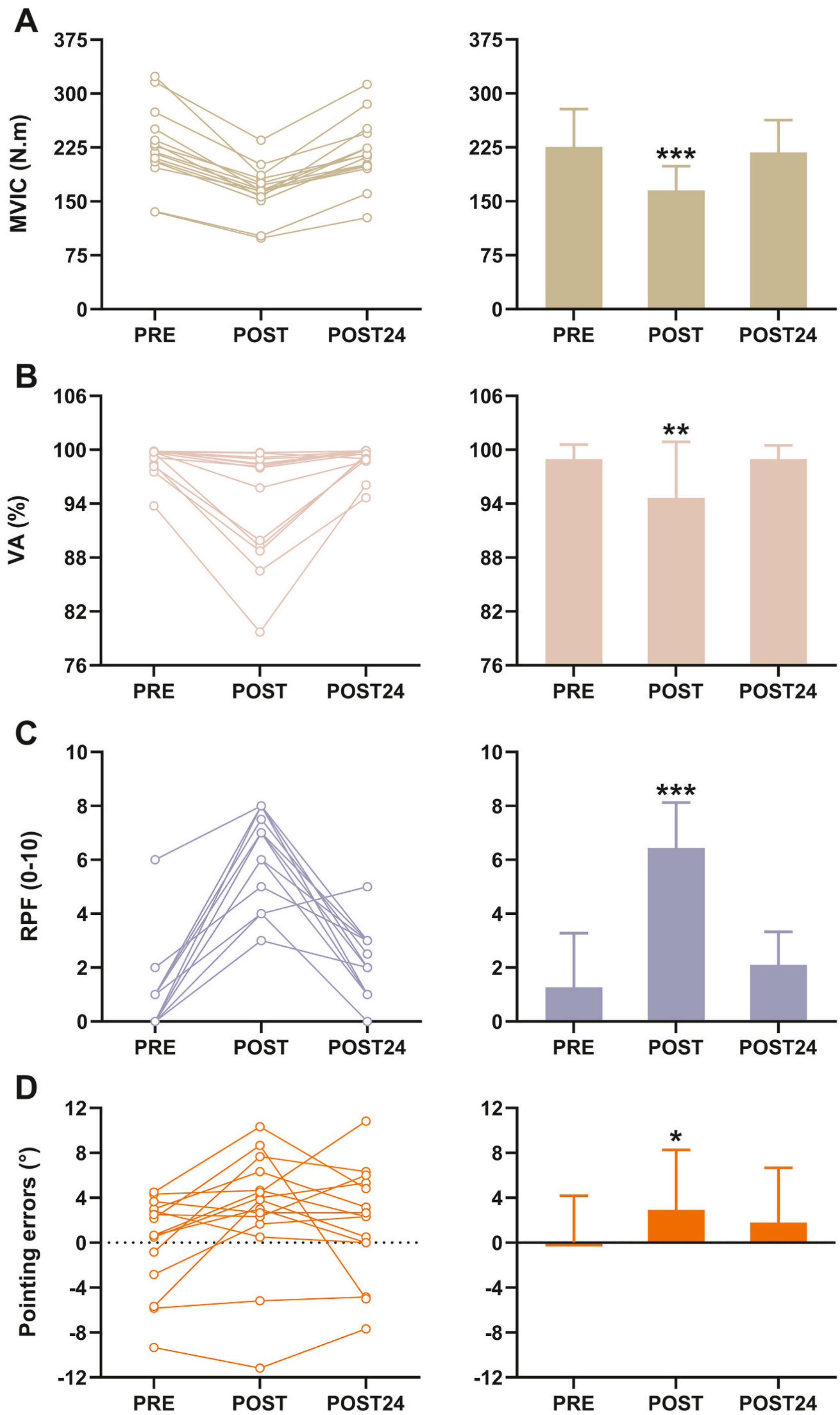

Fig. 3. Individual data (left) and means ± standard deviation (right) of A) torque production during maximal voluntary isometric contraction (MVIC), B) voluntary activation level (VA), C) ratings of perceived fatigue (RPF), and D) pointing errors obtained at three measurement times: prior to the fatiguing eccentric protocol (PRE), immediately after (POST), and 24 h after exercise termination (POST24). Statistical analyses indicated that POST values exhibited significant differences in comparison to PRE measurements, with significance levels denoted as *, **, *** for $p < .05$, $p < .01$ and $p < .001$, respectively.

of knee flexion. Intra-session reliability was determined by intraclass correlation coefficients (ICCs: 2,1 [36]) calculated with 95% confidence intervals on the three trials performed per angle during familiarization and before the fatiguing eccentric protocol (*i.e.*, at PRE). At both measurement times, one-way analyses of variance (ANOVAs) for repeated measures (trial 1, trial 2, trial 3) were also

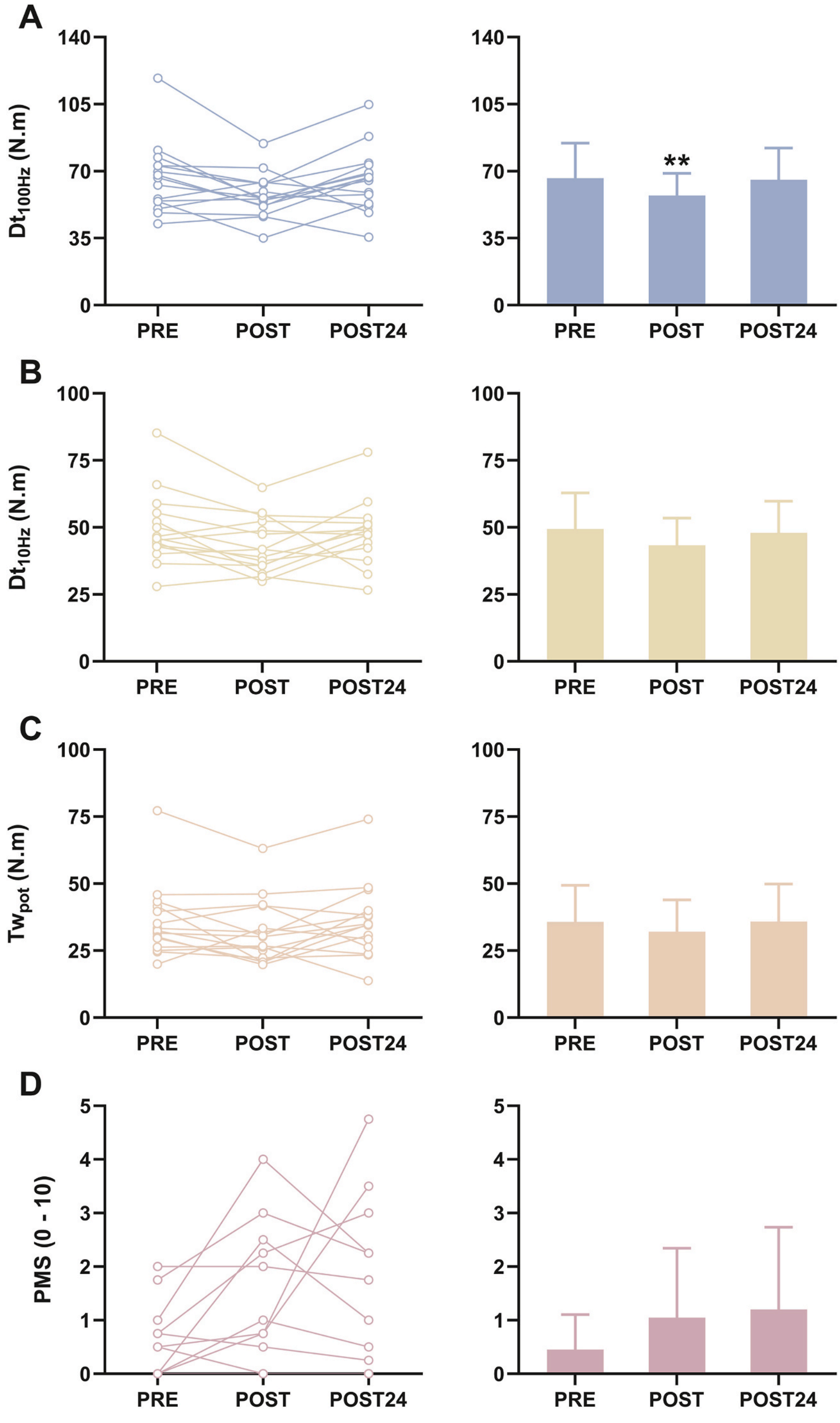

Fig. 4. The individual data (left) and means ± standard deviation (right) of electrically evoked torques [A) potentiated doublet amplitude at 100 Hz (Dt_{100Hz}), B) potentiated doublet amplitude at 10 Hz (Dt_{10Hz}), and C) potentiated single twitch (Tw_{pot})] as well as D) perceived muscle soreness (PMS) scores are presented. These measurements were performed at three time points: before, immediately after, and 24 h following the fatiguing eccentric protocol (*i.e.*, at PRE, POST, and POST24, respectively). Significant differences were detected between PRE and POST values (with *, **, *** corresponding to $p < .05$, $p < .01$ and $p < .001$, respectively).

performed for each tested angle to ensure no significant differences across trials. Inter-session (or test-retest) reliability of position-pointing errors measured at 40° and 70° of knee flexion was determined by ICC type (3,1) [36]. Additionally, for each tested angle, a repeated measures ANOVA with a 2-measurement time (familiarization *vs*. PRE) × 3 trials (trial 1 *vs*. trial 2 *vs*. trial 3) design was performed to ensure no significant differences on position-pointing errors between measurement times or trials. ICC values were categorized as follows: poor if less than 0.50, moderate if between 0.50 and 0.75, good if between 0.75 and 0.90, and excellent if greater than 0.90 [36].

To investigate immediate and prolonged eccentric-induced fatigue effects, one-way ANOVA with repeated measures (PRE, POST, POST24) were performed on KF neuromuscular function parameters. Peak 1RM ECC torques were submitted to a one-way repeated measures ANOVA (PRE, POST24). Immediate and prolonged effects of the fatiguing eccentric protocol on position-pointing accuracy were analyzed using a 2-angle (40°, 70°) × 3 measurement times (PRE, POST, POST24) repeated measures ANOVA. When a significant main or interaction effect was found, a Bonferroni *post-hoc* test was performed. Partial eta square (η^2p) values allowed to determine effect sizes and were considered small, medium and large when η^2p values were closed to 0.01, 0.13 and 0.26, respectively [37]. For pairwise comparisons, effects sizes were computed with Cohen's d [37] with small, medium, and large effect sizes indicated by $d \leq 0.2$, $0.2 < d \leq 0.8$, and $d > 0.8$, respectively). Scores of perceived muscle soreness and perceived fatigue levels were analyzed using the nonparametric Friedman test. Upon detecting a significant effect, an adjusted pairwise comparison was conducted with a Bonferroni correction. Effects sizes of Friedman tests were calculated using Kendall's coefficient values (*i.e.*, using Kendall's W values). The statistical analyses were carried out using the version 27 of the IBM SPSS Statistics software for Windows (IBM Corp., Armonk, NY, USA), with a predefined level of statistical significance set at $p < .05$.

3. Results

Exercise was interrupted (*i.e.*, −20% MVIC) after participants completed 33 ± 15 submaximal eccentric contractions. These contractions were performed with an average peak torque of 149 ± 39 N m.

3.1. MVIC and 1RM ECC torques

A significant effect of the time was found for MVIC torque ($F_{2, 28} = 59.1$, $p < .001$, η^2p = .81; Fig. 3A). MVIC torque significantly decreased at POST by 26.0 ± 6.3% ($p < .001$, $d = 1.36$), but returned to baseline values 24 h post-exercise (*i.e.*, at POST24; $p = .66$, $d = 0.15$). Regarding 1RM ECC torque values, no significant change was observed between PRE (201 ± 47 N m) and POST24 (205 ± 54 N m) ($p = .63$, $d = 0.07$).

3.2. Indicators of central and peripheral fatigue

ANOVA showed a significant effect of the time for VA ($F_{2,28} = 10.5$, $p < .001$, η^2p = .43; Fig. 3B). with significant reductions at POST of about 4.4% ($p < .01$, $d = 0.95$).

Regarding peripheral fatigue indicators, there was a significant effect of the time for Dt_{100Hz} ($F_{2,28} = 4.32$, $p < .05$, η^2p = .24; Fig. 4A), with Dt_{100Hz} values significantly reduced at POST by 10.8 ± 17.3% ($p < .05$, $d = 0.58$). Dt_{10Hz}, Tw_{pot} and Dt_{10Hz}/Dt_{100Hz} were not statistically different throughout the experiment (*i.e.*, $p = .06$, $d = 0.51$, Fig. 4B; $p = .17$, $d = 0.28$, Fig. 4C; $p = .74$, $d = 0.06$, respectively). In addition, potentiated BF M-wave values (3.0 ± 1.9 mV) were not affected by the fatiguing eccentric protocol (*i.e.*, $p = .07$, $d = 0.19$).

3.3. Position sense alterations using position-pointing tasks

3.3.1. Intra- and inter-session reliability

Whether during familiarization or at PRE, position-pointing errors showed good to excellent intra-session reliability with ICC values ranging from 0.88 (0.72–0.96) to 0.95 (0.89–0.98). At both measurement times, repeated measures ANOVAs revealed no significant differences across trials on position-pointing errors measured at the two tested angles ($p > .13$). ICC values of position-pointing errors showed good to excellent inter-session (or test-retest) reliability between familiarization and PRE, ranging from 0.89 (0.78–0.96) to 0.95 (0.90–0.98). Additionally, there was no significant main (*i.e.*, measurement times or trials) or interaction effect on position-pointing errors measured during familiarization and at PRE ($p > .26$).

3.3.2. Eccentric fatigue and position-pointing errors

The two-way repeated measures ANOVA conducted on position-pointing errors showed no significant main effect of angle (p = .07) or angle × time interaction effect (p = .24). However, a significant effect of the time was found (F2,28 = 3.51, p < .05, η^2p = .20; Fig. 3D). Position-pointing errors exhibited a significant increase at POST regardless of the tested angle (p < .05, $d = 0.49$), but reverted to baseline values at POST24 (p = .36, $d = 0.31$). Significant positive position-pointing errors at POST indicated that participants moved the pointer to a more extended position (+2.9°) than their hidden exercised lower limb, *i.e.*, they perceived their fatigued KF muscles to be more stretched than their actual length.

3.3.3. Perceived fatigue and muscle soreness

There was a significant time effect on perceived fatigue levels [$\chi^2(2) = 23.7$, $p < .001$; Kendall's W: 0.79]. Perceived fatigue levels were higher at POST in comparison to the PRE values ($p < .001$, $d = 2.77$; Fig. 3C). In contrast, the ratings of perceived muscle soreness were not statistically different between measurement times ($p = .28$, $d < 0.49$; Fig. 4D).

4. Discussion

The current study aimed to investigate the immediate and prolonged consequences of eccentric-induced neuromuscular fatigue on position sense with a position-pointing task. Upon completion of the fatiguing eccentric protocol (POST), both central and peripheral factors were found to contribute to the observed force decrement. As hypothesized, position-pointing errors exhibited a significant increase irrespective of the tested angle in the presence of central fatigue at exercise termination (Fig. 3C). However, it is noteworthy that, 24-h after the exercise (POST24), both neuromuscular function and position sense parameters had reverted to their baseline levels.

The 20%-MVIC force drop at POST led to acute alterations in KF neuromuscular function and was associated with both central and peripheral fatigue, as evidenced by significant decreases in VA (Fig. 3B) and Dt_{100Hz} (Fig. 4A). Because Dt_{10Hz} and Dt_{10Hz}/Dt_{100Hz} values were not statistically different across the experiment, it seems unlikely that low frequency force depression contributed to KF neuromuscular function alterations. One could assume that acute high frequency fatigue was involved given the significant reductions of Dt_{100Hz} at POST (Fig. 4A). However, high frequency fatigue is usually explained by alterations in sarcolemmal excitability [38] that we did not observe as potentiated BF M-wave amplitude remained unchanged. The acute decreases in Dt_{100Hz} values could thus be attributed to fatigue-induced changes in intramuscular metabolites and/or ATP depletion [39]. Although spinal and supraspinal factors of central fatigue cannot be dissociated with the interpolated twitch technique [14], participants showed a reduced ability to recruit their KF muscle fibers at POST. Significant KF VA reduction at POST was potentially caused by increased inhibitory actions from group III-IV afferents at spinal and/or cortical levels with the accumulation of intramuscular metabolites [16,40].

In the present study, neuromuscular function parameters had returned to baseline values at POST24. This was somewhat surprising as long-lasting peripheral fatigue has been observed following damaging eccentric protocols generating similar force decrement [23, 41]. However, a recent study reported that KF muscle-tendon unit lengthening was primarily due to tendon stretching during a nordic hamstring exercise, with BF fascicles being stretched only at long muscle-tendon unit lengths [42]. Based on this observation, it is likely that the fatiguing eccentric protocol performed in the present study induced a limited eccentric stress on extrafusal muscle fibers. In this regard, given the lack of significant changes in perceived muscle soreness (Fig. 4D), the fatiguing eccentric protocol performed here may have not induced muscle damage. This could also account for the rapid recovery observed on KF neuromuscular function parameters (Figs. 3 and 4).

The main outcome of this study is the observation of significant increase in position-pointing errors immediately post-exercise (Fig. 3D), in the presence of both central and peripheral fatigue (Figs. 3 and 4). This study is the first to demonstrate that exercise-induced neuromuscular fatigue can impair extrapersonal representation of the body, showing that the repetition of submaximal KF eccentric contractions affects complex kinesthetic perceptions. Specifically, at POST, participants positioned the pointer in a more extended position relative to their exercised limb (Fig. 3D). In line with earlier investigations which employed bilateral position-matching tasks to assess the impact of exercise-induced neuromuscular fatigue on position sense [23,27], our study's results demonstrated that participants perceived their fatigued muscles to be more stretched than their actual length.

Given that representing body segments in extrapersonal space require complex neural computations at the brain level [13], it is likely that the increase in position-pointing errors at POST resulted from fatigue-induced central alterations (Fig. 3B). We propose that increased neural flow from group III-IV afferents at the cortical level is primarily involved in the alterations of position-pointing accuracy by disrupting the integration and/or processing of kinesthetic inputs. Knee position sense alterations could also have arisen from exercise-induced changes in brain neurotransmitters [43] and in cortical activity [19]. All these fatigue-related central mechanisms could have distorted the extrapersonal representation of the exercised limb by altering the cognitive processes that transform the kinesthetic signals into extrapersonal coordinates. The proposed mechanism would also be in line with the central-based hypothesis formulated in previous studies in which fatigue-induced position sense alterations were identified during bilateral position-matching tasks [22,23,26]. Using functional magnetic resonance imaging, future research should aim to identify fatigue-induced changes in the integration and/or processing of kinesthetic inputs in the cortical regions involved in position-pointing tasks.

From a practical standpoint, due to the observed perceptual alteration, athletes would reach lower hamstring stretch amplitude in fatigue conditions, thereby limiting the strain exerted on their fatigued muscles. Because hamstring injuries frequently occur at long muscle length (*e.g.*, during the late swing phase of sprinting [44]), this perceptual alteration may represent an adaptive mechanism that could reduce the risk of hamstring injury. However, this perceptual alteration affecting the body schema may have an adverse impact on sensorimotor control and sports performance. Specifically, the fatigue-induced alteration of body representations could negatively affect artistic disciplines like gymnastics by disrupting the maintenance of body postures and the precise execution of body movements.

The present study introduces novel perspectives for future kinesthetic studies, especially regarding the use of position-pointing tasks in fatigue contexts. Position-pointing tasks cannot substitute to bilateral joint position-matching tasks because they involve distinct neurophysiological processes [12]. However, position-pointing tasks offer an attractive methodological approach to evaluate the effects of exercise-induced neuromuscular fatigue on position sense in ecological settings because, contrary to bilateral position-matching tasks, position-pointing tasks do not require the execution of unilateral fatiguing protocols.

In the current experiment, a controlled laboratory setting was employed to target hamstring muscles' fatigue using a unilateral fatiguing protocol. Future investigations should aim to explore the effects of ecologically induced neuromuscular fatigue on position sense using position-pointing tasks, such as following repeated sprints or gymnastics training sessions. This would enhance the applicability of our original findings to real-life sporting scenarios. Furthermore, expanding the use of position-pointing tasks in other fatigue contexts could provide a better understanding of the implications of exercise-induced alterations in position sense on injury risk and motor performance.

Lastly, in the current experiment, it is essential to acknowledge the potential influence of factors such as sports specialization, years of sports practice, and training level on kinesthetic performance during position-pointing tasks. Hence, future studies should be designed to investigate the impact of these factors on extrapersonal representation accuracy, both in resting and fatigued conditions. Such studies would significantly contribute to the enrichment of the existing literature on kinesthesia, providing a more comprehensive and nuanced understanding of the acute and prolonged effects of exercise-induced neuromuscular fatigue on position sense.

Ethics statement

The present study received approval by a French national ethics committee (Ethics Committee for Biomedical Research in Southeast III, France; authorization number: 2020-A02811-38).

Declarations

Author contribution statement

Flavio Da Silva: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Wrote the paper; **Enzo Piponnier**: Conceived and designed the experiments; Contributed reagents, materials, analysis tools or data; Wrote the paper; **Baptiste Corcelle and Jennifer Gioda**: Conceived and designed the experiments; Performed the experiments; Wrote the paper; **Grégory M. Blain and Florian Monjo**: Conceived and designed the experiments; Analyzed and interpreted the data; Wrote the paper; **Serge S. Colson**: Conceived and designed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Data availability statement

Data will be made available on request.

Additional information

No additional information is available for this paper.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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