Knee position sense and knee flexor neuromuscular function are similarly altered after two submaximal eccentric bouts

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Abstract

Purpose This study examined eccentric-induced fatigue effects on knee flexor (KF) neuromuscular function and on knee position sense. This design was repeated across two experimental sessions performed 1 week apart to investigate potential repeated bout effects.

Methods Sixteen participants performed two submaximal bouts of KF unilateral eccentric contractions until reaching a 20% decrease in maximal voluntary isometric contraction force. Knee position sense was evaluated with position-matching tasks in seated and prone positions at 40° and 70° of knee flexion so that KF were either antagonistic or agonistic during the positioning movement. The twitch interpolation technique was used to assess KF neuromuscular fatigue. Perceived muscle soreness was also assessed. Measurements were performed before, immediately (POST) and 24 hours after (POST24) each eccentric bout.

Results No repeated bout effect on neuromuscular function and proprioceptive parameters was observed. At POST, central and peripheral factors contributed to the force decrement as shown by significant decreases in voluntary activation level (-3.8 ± 4.8%, $p < .01$) and potentiated doublet torque at 100 Hz (-10 ± 15.8%, $p < .01$). At this time point, position-matching errors significantly increased by 1.7 ± 1.9° in seated position at 40° ($p < .01$). At POST24, in presence of muscle soreness ($p < .05$), although KF neuromuscular function had recovered, position-matching errors increased by 0.6 ± 2.6° in prone position at 40° ($p < .01$).

Conclusion These results provide evidence that eccentric-induced position sense alterations may arise from central and/or peripheral mechanisms depending on the testing position.

Keywords: Proprioception; Kinesthesia; Hamstrings; DOMS; Central fatigue; Peripheral fatigue

Statements and Declarations

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Conflicts of interest

The authors have no conflicts of interest to declare that are relevant to the content of this article.

Ethics approval

Approval was obtained from national Ethics Committee (Protection Committee of People for Biomedical Research Southeast III, France; Authorization Number 2020-A02811-38). This study was conducted in accordance with the latest version of the Declaration of Helsinki.

Consent to participate

Informed consent was obtained from all individual participants included in the study.

Consent for publication

Patients signed informed consent regarding publication of their data.

Data availability

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Code availability (software application or custom code)

Not applicable.

Author contribution

All authors contributed to the study conception and design. F.D.S., B.C., and J.G. conducted the experiments. F.D.S., F.M. and S.S.C analyzed data. F.D.S., F.M. and S.S.C. wrote the first draft of the manuscript. All authors contributed to the writing and approved the final version of the manuscript.

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Abbreviations

ANOVA	Analysis of variance
BF	Biceps femoris
CAR	Central activation ratio
Dt_{sup}	Superimposed doublet torque at 100 Hz
Dt_{10Hz}	Potentiated doublet amplitude at 10 Hz
Dt_{100Hz}	Potentiated doublet torque at 100 Hz

ECC1	First bout of submaximal eccentric contractions
ECC2	Second bout of submaximal eccentric contractions
JPM	Joint position-matching
$JPMS_{40}$	Joint position-matching in seated position at 40° of knee flexion
$JPMS_{70}$	Joint position-matching in seated position at 70° of knee flexion
$JPMP_{40}$	Joint position-matching in prone position at 40° of knee flexion
$JPMP_{70}$	Joint position-matching in prone position at 70° of knee flexion
KF	Knee flexors
MVIC	Maximal voluntary isometric contraction
M-wave	Maximal compound muscle action potentials
RMS	Root mean square
Tw_{pot}	Potentiated single twitch
VA	Voluntary activation level
η^2p	Partial eta-squared
1RM ECC	Eccentric unilateral 1 repetition maximum

Introduction

During motor activities, kinesthetic senses (i.e., senses of body positions and movements) are crucial to execute and adjust motor actions (Taylor 2016; Proske and Gandevia 2018). Human studies investigating kinesthesia-related mechanisms mainly focused on position sense using unilateral joint reproduction tasks and bilateral joint position-matching (JPM) tasks (Hillier et al. 2015). To better delineate the underlying neural correlates, position sense was manipulated through muscle vibration (Proske and Gandevia 2018) and alterations of intrafusal fiber thixotropy (Proske et al. 2014). The observations made highlighted that position sense primarily depends on signals from muscle spindles which are length-sensitive mechanoreceptors innervated by groups Ia and II afferent fibers (Proske and Gandevia 2012).

Given that the repetition of fatiguing muscle contractions is inherent to daily life and physical activity, numerous studies have sought to investigate whether neuromuscular fatigue alters position sense (Proske 2019). Neuromuscular fatigue is defined as the objective decline in neuromuscular performance attributed to transient changes occurring at central (i.e., within the central nervous system at spinal and/or supraspinal levels) and peripheral (i.e., contractile capacity of the muscle distant from the neuromuscular junction) levels (Gandevia 2001; Place and Millet 2020). A special focus was made on the effects of eccentric contractions on position sense with the idea that the damage observed on extrafusal fibers could extend to muscle spindles (Sonkodi et al. 2020). Although position sense alterations have been observed following maximal and submaximal eccentric contractions of knee extensors (Givoni et al. 2007; Torres et al. 2010; Da Silva et al. 2021), current hypotheses regarding the underlying mechanisms head toward the implications of central disturbances rather than to structural damage to muscle spindles (Allen et al. 2010; Tsay et al. 2012; Da Silva et al. 2021). In this line, a recent study showed a correlation between exercise-induced reduction in voluntary activation (VA) and position sense alterations after submaximal eccentric contractions, i.e., the higher VA deficits the greater the position errors (Da Silva et al. 2021). To improve our understanding of the central mechanisms accounting for position sense alterations, the repeated bout effect commonly observed after a first unaccustomed eccentric exercise (Hyldahl et al. 2017) is an interesting approach. After two bouts of eccentric contractions, the second bout is associated with lower voluntary activation failure at similar force loss (Goodall et al. 2017; Prasartwuth et al. 2019). Therefore, observing smaller position errors with a reduced activation failure following the second bout would reinforce the central-based hypothesis of position sense alterations.

Although it is clearly admitted that signals from both agonist and antagonist muscles contribute to joint position sense (Gilhodes et al. 1986), studies essentially investigated eccentric-induced fatigue of knee extensors on position sense while overlooking eccentric-induced fatigue of knee flexors (KF). Despite their functional importance during sporting activities (e.g., during sprinting or decelerating actions), only one study, to our knowledge, reported knee position sense alterations following fatiguing KF eccentric contractions (Paschalis et al. 2008). In this experiment, besides using repeated maximal contractions which are not representative of exercise-induced fatigue in ecological conditions, position sense was evaluated using unilateral joint reproduction tasks that exhibit a major limitation associated with memory bias (Bewick and Banks 2021). It thus remains unknown whether knee position sense alterations using bilateral JPM tasks may occur after submaximal KF eccentric contractions and whether they may be attenuated with the repeated bout effect.

In this context, the purpose of this study was to compare changes in KF neuromuscular function parameters and knee position sense following a first (ECC1) and a second (ECC2) bout of unilateral submaximal KF eccentric contractions. In most studies investigating neuromuscular fatigue effects on position sense during JPM task, the positioning movement performed to match the perceived contralateral limb position is achieved by the fatigued muscle group (i.e., agonist muscles). In this experiment, participants performed JPM tasks in seated and prone positions so that KF were either antagonistic or agonistic during the positioning movement. Based on recent papers showing associations between impaired VA and kinesthetic alterations (Da Silva et al. 2021, 2022), it was hypothesized that knee position sense alterations would only be observed in presence of VA decreases. It was also hypothesized that knee position sense alterations would be attenuated after ECC2.

Methods

Participants

Sample size was estimated *a priori* using G*Power (version 3.1.9.4; Kiel University, Kiel, Germany) based on previous studies that reported attenuated VA decreases with the repeated bout effect (Goodall et al. 2017) and position-matching errors (Da Silva et al. 2021) after submaximal eccentric exercise of knee extensors. The minimum sample size required was seven participants for a repeated measures within-subject analysis with the power set at .95. Sixteen healthy young men [means ± standard deviation (SD) values; age: 23.1 ± 3.7 years; body mass: 79.1 ± 10.6 kg; height: 180.8 ± 3.8 cm] from the sports science department of Université Côte d'Azur volunteered to participate in this study. For the sample size of the participants included in our study, a sensitivity power analysis with an α of .05 and a power of .95 led to a large effect of $f = .53$. An inclusion criterion was that participants had to exercise on a weekly basis (soccer, rugby, cycling, etc.) but less than 6 hours per week. They were also free from lower limb injuries for at least six months and had never undergone any kind of knee surgery. Before any testing, participants were informed of the experimental protocol and gave their written informed consent. All experimental procedures were conducted in accordance with the latest version of the Declaration of Helsinki and were approved by a national Ethics Committee (Protection Committee of People for Biomedical Research Southeast III, France; Authorization Number 2020-A02811-38).

Experimental design and warm-up protocol

The experiment was conducted over three weeks with participants visiting the laboratory on five occasions. During the first session, anthropometric data were collected (i.e., age, body mass and height) directly upon their arrival to the laboratory. Participants were then familiarized with knee position sense evaluations (for more details, see Knee position sense section) and KF neuromuscular function measurements, including eccentric unilateral 1 repetition maximum (1RM ECC) (see KF neuromuscular function for more details). These tests were performed on a specific ergometer which allows measuring KF force production in isometric and dynamic conditions. One week later, evaluations were performed before (PRE ECC1), immediately after (POST ECC1) and 24 hours after (POST24 ECC1) the first bout of eccentric contractions (ECC1, see Unilateral KF eccentric bouts for more details). These experimental procedures were repeated 1 week after with measurements performed before (PRE ECC2), immediately after (POST ECC2) and 24 hours (POST24 ECC2) after the second bout of unilateral eccentric contractions (ECC2).

Before the evaluations of KF neuromuscular function, participants performed a standardized warm-up protocol. For this purpose, 2 sets of 6 repetitions of the "Extender" and the "Diver" exercises (Askling et al. 2013), and a single-leg bridges exercise were performed with both limbs. Then, participants achieved 10 submaximal isometric contractions of their right exercised limb in a standardized position (for more details, see Unilateral torque measurements section). The intensity of these contractions was progressively increased during the warm-up protocol from ~30% to ~90% of the perceived maximal force production (i.e., 4 contractions at ~30%, 3 contractions at ~50%, 2 contractions at ~70% and 1 contraction at ~90%).

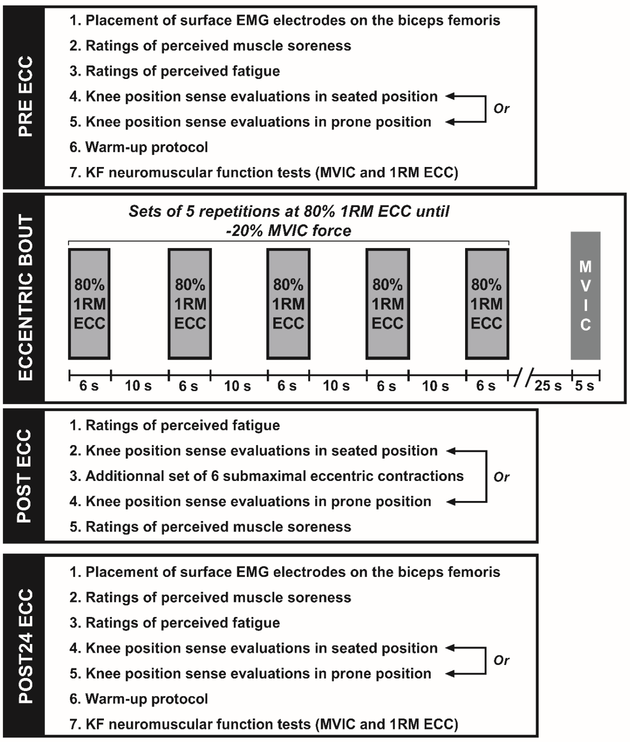

Figure 1: Schematic representation of the measurements performed before (PRE ECC), immediately after (POST ECC) and 24 hours after (POST24 ECC) the eccentric bouts. This design was repeated across two experimental sessions performed 1 week apart to investigate potential repeated bout effects on neuromuscular function and position sense parameters. Please refer to the text for more details. EMG electromyography, KF knee flexors, MVIC Maximal voluntary isometric contraction, 1RM ECC eccentric unilateral 1 repetition maximum.

KF neuromuscular function

Unilateral torque measurements

Participants were placed on a specific ergometer based on an exoskeleton-like light frame (Hamtech device, Human Kinematic, Carros, France) (Corcelle et al. 2022). Unilateral KF force production in isometric and eccentric conditions was measured via an S-beam force transducer (Capacity: 1000N, LS02-s, Tech Co. Ltd, Shenzhen, China) positioned 5 cm above the malleolus on the right Achilles tendon. Force measurements were recorded at a sampling frequency of 1 kHz using Acknowledge software version 4.1 (Biopac Systems, Inc., Goleta, CA., USA) and converted into torque *a posteriori* using participants' lever arms (i.e., distance between the force transducer and the right lateral tibial condyle). To limit movements at the pelvis level during contractions, participants were strapped to the ergometer with two elastic bands positioned ~5 cm above participants' sacroiliac joint and below the gluteal fold.

During maximal voluntary isometric contraction (MVIC), participants adopted a standardized position with the hip and the knee flexion angles set at 40° and 30° (0° meaning full extension), respectively. One MVIC was performed immediately after each bout of eccentric contractions (i.e., at POST ECC1 and POST ECC2). Before and 24 hours post-exercise (i.e., PRE ECC1, POST24 ECC1, PRE ECC2 and POST24 ECC2), two MVIC were performed and only the highest peak torque was considered for data analysis.

During eccentric contractions, participants actively controlled knee angular velocity fixed at $10°.s^{-1}$ using real time feedback displayed on a screen. Angular velocity was measured with a potentiometer (P4500, Novotechnik U.S., Inc., Southborough, MA, USA) placed on the exoskeleton-like light frame at the level of the participants' knee rotation axis. Maximal (1RM ECC) and submaximal eccentric contractions were performed from a starting position combining 65° of hip flexion and 90° of knee flexion to a final position combining 40° of hip flexion and 30° of knee flexion. Each contraction lasted about 6 s. Highest peak 1RM ECC torque values were recorded at PRE ECC1, POST24 ECC1, PRE ECC2 and POST24 ECC2 (Fig. 1). During 1RM ECC determination, familiarization data were used to quickly identify the maximum load added on the exoskeleton-like light frame and to limit fatigue induction.

KF neuromuscular fatigue parameters

Immediate and long-lasting effects of ECC1 and ECC2 on central and peripheral components of KF neuromuscular fatigue were investigated using the electrical myostimulation technique during and after MVIC (Place and Millet 2020). Self-adhesive rectangular electrodes (5 cm × 9 cm - Stimex, Wetzlar, Germany) were placed on the proximal part of the hamstrings below the gluteal fold (cathode) and at the popliteal fossa level (anode). Electrode positions were marked on the skin to ensure identical placement across experimental sessions. Electrical myostimulations (400 V maximum voltage and 1ms duration) were delivered (Digitimer Stimulator DS7, Digitimer Ltd., Hertfordshire, UK) to induce maximal twitch (Tw) force output and maximal amplitude of the compound muscle action potential of the biceps femoris (BF) (i.e., maximal BF M-wave) at rest. The stimulation intensity which elicited maximal Tw and BF M-wave was increased by 20% (154.1 ± 38.2 mA) to ensure adequate assessment of central and peripheral components of neuromuscular fatigue.

Superimposed paired electrical stimulations at a frequency of 100 Hz (Dt_{sup}) were delivered over MVIC plateau. Potentiated twitch torque was evoked 2, 4 and 6 s after each MVIC in the following order: (i) a paired electrical stimulation at a frequency of 100 Hz (Dt_{100Hz}), (ii) a paired electrical stimulation at a frequency of 10 Hz (Dt_{10Hz}) and (iii) a single electrical stimulation (Tw_{pot}). Peak Dt_{100Hz}, Dt_{10Hz} and Tw_{pot} torques as well as potentiated BF M-wave were used as peripheral fatigue parameters. The ratio Dt_{100Hz}-to-Dt_{10Hz} (Dt_{10Hz}/Dt_{100Hz}) was also computed and used as an indicator of low-frequency peripheral fatigue (Martin et al. 2004). In addition, voluntary activation level (VA) and central activation ratio (CAR) were calculated at each time point and used as central fatigue parameters. VA was computed according to Strojnik and Komi's formula (1998) and CAR was calculated based on Kent-Braun's proposal (1996):

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

$$\text{CAR (\%)} = \left(\frac{\text{Voluntary torque before Dt}_{\text{sup}}}{\text{Voluntary torque before Dt}_{\text{sup}} + \text{Dt}_{\text{sup}}}\right) \times 100$$

Biceps femoris (BF) electromyographic activity

Right BF electromyographic activity was recorded using pairs of surface electromyography electrodes (Ag/AgCl, diameter = 10 mm; inter-electrode distance = 20 mm; Contrôle-Graphique, Brie-Comte-Robert, France). Electrodes were placed on muscle belly in accordance with the SENIAM (Surface ElectroMyoGraphy for the Non-Invasive Assessment of Muscles) recommendations (Hermens et al. 2000). A reference electrode was also placed on the right lateral tibial condyle. Electrode positions were marked with indelible ink to ensure similar repositioning throughout the different sessions. Before electrode placement, the skin was shaved, lightly abraded with emery paper and cleaned with alcohol to reduce skin-electrode impedance below 3 kΩ. Electromyographic signals were amplified using the Biopac MP150 system (Biopac Systems, Inc., Goleta, CA, USA), filtered (bandwidth frequency = 10 – 500 Hz, common mode rejection ratio = 110 dB, Z Input = 1000 MΩ, gain = 1000) and recorded at a sampling frequency of 2 kHz with the Acknowledge software. The root mean square values of BF electromyographic signals (BF RMS) were computed on a 500-ms window around MVIC and 1RM ECC peak torques. BF RMS were then normalized to the potentiated M-wave recorded at each time point (BF RMS/M-wave) and considered as central fatigue parameters (Place and Millet 2020).

Unilateral KF eccentric bouts

During ECC1 and ECC2, participants performed consecutive sets of 5 unilateral eccentric contractions at 80% of the 1RM ECC measured in PRE of each session, until a 20% MVIC force decrement was reached. Repetitions and sets were interspaced by recovery periods of 10-s and 25-s, respectively. MVICs were performed at the end of each set. Exercise was stopped when 20% MVIC force decrement was reached to correspond to fatigue levels achieved in studies on knee extensors (Da Silva et al. 2021, 2022). An additional set of 6 eccentric contractions was performed between the seated and prone JPM tasks described below to maintain the target force loss during the POST condition (Fig. 1**)**. Mean peak torques of eccentric contractions and torque-time integral values were measured during the two eccentric bouts.

Psychophysical evaluations

Knee position sense

To evaluate the effects of eccentric bouts on knee position sense, JPM tasks were performed in seated and prone positions on a massage table with blindfolded participants (Fig. 2). JPM tasks in seated position were randomly performed at 40° (long KF muscle length, JPMS40; Fig. 2a) and 70° (short KF muscle length, JPMS70; Fig. 2b) of knee flexion. JPM tasks in prone position were also randomly performed at 40° (JPMP40, Fig. 2c) and at 70° (JPMP70, Fig. 2d) of knee flexion. The seated and prone JPM tasks were randomly performed across participants and time points (Fig. 1). The left non-exercised lower limb was used as the reference limb whereas the right exercised lower limb was used as the indicator limb. To put muscle spindles in a similar thixotropic state across limbs before each JPM task (Proske et al. 2014), both reference and indicator limbs were conditioned at 90° of knee flexion with 5-s isometric contractions of knee extensors and flexors at ~30% MVIC (i.e., flexion and extension conditionings). Participants were then asked to relax while the experimenter moved the reference limb into one of the two tested angles (i.e., to 40° or 70° of knee flexion) using a digital inclinometer. Once the position was reached, participants were asked to hold their reference limb and to actively match this position with their indicator limb. When satisfied with their match, participants pressed simultaneously two buttons placed in each hand (Bluetooth camera shutter remote control, Camkix, Dayton, Wyoming, USA) generating hands-free photos with two iPhones 6 (240 Hz high-speed camera, Apple Inc., Cupertino, CA, USA) located at exactly same distance on both sides (i.e., 1.5m from each limb). A custom-made MatLaB (MatLaB 9.4, MathWorks, Natick, MA, USA) algorithm was used to automatically compute knee angles of both reference and indicator limbs from anatomical markers placed on the external malleoli and lateral tibial condyles of each limb. Knee angles were calculated as angles formed by the condyle-malleolar line and by the horizontal line added on each side of the massage table (Fig. 2). To ensure correct knee angle calculations and similar positioning across subjects, participants' popliteal fossa were positioned 5 cm from the extremity of the massage table during the JPMS tasks and the participants' patella were positioned 5 cm from the extremity of the massage table during the JPMP tasks. At each time point, participants performed three trials by angle conditions in the seated and prone positions. For each trial, position-matching errors were calculated as the reference limb angle minus the indicator limb angle. The three error values calculated for each angle were then averaged for further analyses. Positive position-matching errors indicate errors toward extension relative to the reference limb whereas negative position-matching errors indicate errors toward flexion

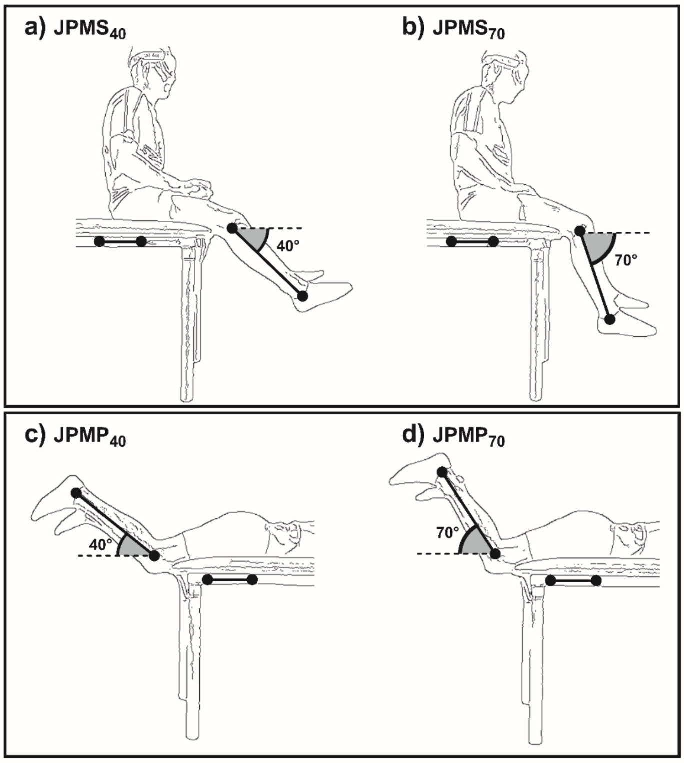

Figure 2: Bilateral joint position-matching (JPM) tasks used in the present study to evaluate knee position sense at 40° and 70° of knee flexion in both seated [upper panel, (a) $JPMS_{40}$ and (b) $JPMS_{70}$] and prone [lower panel, (c) $JPMP_{40}$, and (d) $JPMP_{70}$] positions. Knee position sense was evaluated at short and long KF lengths during JPM tasks at 70° and at 40°, respectively. KF muscles were antagonistic during the seated JPM tasks, while they were agonistic during the prone JPM tasks. Note that 0° corresponds to full knee extension.

Ratings of perceived fatigue and muscle soreness

Perceived fatigue was presented to participants as "a feeling of diminishing capacity to cope with physical stressors" (Micklewright et al. 2017). Ratings of perceived fatigue were obtained to reflect participants' general fatigue using a 0-10 French translated and validated version of the Rating-of-Fatigue Scale (0, not fatigued at all; 10, total fatigue and exhaustion) (Brownstein et al. 2021). Perceived fatigue was evaluated at the beginning of each time point (Fig. 1).

Perceived muscle soreness scores were recorded using a 0-10 numerical rating scale (0, no pain; 10, worst pain) and were used as indirect markers of muscle damage. For this purpose, a steady 25-N pressure was applied by the experimenter with a 0.5-cm diameter cylindrical object just above and below BF electromyographic electrodes (Proske et al. 2004) while participants were passively lying on the massage table. At PRE and POST24, perceived muscle soreness was obtained before knee position sense evaluations (Fig. 1). At POST, participants rated their muscle soreness after the last JPM task. The two scores obtained at each time point were averaged for statistical analysis.

Statistical analyses

Statistical analyses were performed using IBM SPSS Statistics software for Windows version 27 (IBM Corp., Armonk, NY, USA). The normality of distribution and the homogeneity of variances of each dependent variable were confirmed using the Kolmogorov–Smirnov test and the Bartlett test, respectively. The effects of eccentric bouts on KF neuromuscular function parameters, muscle soreness scores and perceived fatigue ratings were studied using two-way repeated measures analyses of variance (ANOVA) with a 2 sessions (ECC1 *vs*. ECC2) × 3 time (PRE *vs*. POST *vs*. POST24) design. 1RM ECC values were submitted to a 2 sessions (ECC1 *vs*. ECC2) × 2 time (PRE *vs*. POST24) repeated measures ANOVA. A 2 sessions (ECC1 *vs*. ECC2) × 2 testing positions (seated *vs*. prone positions) × 2 angles (40° *vs*. 70°, $JPMS_{40}$, $JPMS_{70}$, $JPMP_{40}$, $JPMP_{70}$) × 3 time (PRE *vs*. POST *vs*. POST24) repeated measures ANOVA was performed on position-matching errors during JPM tasks. Tukey's HSD *post-hoc* test was performed when a significant main effect or interaction effect was found. Effect sizes were determined from partial eta square (η^2p) values with interpretation thresholds fixed at .01, .13 and .26 for small, medium and large effect sizes, respectively (Cohen 1988).

Paired *t*-tests were performed to: i) compare number of contractions performed during both eccentric bouts and ii) compare mean eccentric peak torques and torque-time integral values across eccentric bouts. Cohen's d_z were calculated and used as effects sizes for paired *t*-tests (Rosenthal 1991). Cohen's d_z were considered as small when $d_z \leq .20$, medium when $.20 \leq d_z \leq .80$, and large when $d_z \geq .80$ (Cohen 1988). Data of 16 participants are presented in this paper as means ± SD values, unless otherwise stated. The statistical significance was set at $p < .05$.

Results

Baseline measurements and eccentric bouts

Baseline 1RM ECC torque was significantly higher during PRE ECC2 compared to PRE ECC1 ($p < .01$; Table 1). No significant differences were found at baseline for any other variable of KF neuromuscular function or psychophysical parameters ($p > .17$).

The number of submaximal eccentric contractions necessary to reach the 20% MVIC torque decrement was not statistically different between ECC1 (37 ± 12) and ECC2 (33 ± 14); [t(15)= .98, $p = .34$, $d_z = .25$]. Torque-time integral values were not significantly different during both eccentric bouts [ECC1: 55165 ± 20241 N.m.s and ECC2: 54677 ± 24547 N.m.s; t(15) = .07, *p*

= .95, d_z = .02]. In accordance with the greater 1RM ECC torque during PRE ECC2, mean peak torque during ECC2 (152 ± 34 N.m) was also significantly higher compared to ECC1 values (129 ± 33 N.m); [t(15) = 3.07, $p < .01$, d_z = .77].

		PRE	POST	POST24
BF potentiated M-wave (mV)	*ECC1*	3.7 ± 2.8	3.5 ± 2.9	4.0 ± 2.9*
	ECC2	3.1 ± 2.0	2.9 ± 1.7	3.5 ± 2.0*
BF RMS/M-wave during MVIC (a.u.)	*ECC1*	0.18 ± 0.14	0.19 ± 0.17	0.19 ± 0.14
	ECC2	0.17 ± 0.15	0.15 ± 0.08	0.19 ± 0.16
1RM ECC (N.m)	*ECC1*	177 ± 40	-	182 ± 51
	ECC2	197 ± 47#	-	200 ± 55#
BF RMS/M-wave during 1RM ECC (a.u.)	*ECC1*	0.13 ± 0.10	-	0.14 ± .09
	ECC2	0.16 ± 0.12	-	0.15 ± .10
Perceived fatigue (0-10)	*ECC1*	1.1 ± 1.4	6.6 ± 1.7***	2.0 ± 1.6
	ECC2	1.4 ± 2.0	6.6 ± 1.6***	2.0 ± 1.3
Muscle soreness (0-10)	*ECC1*	0.3 ± 0.5	1.0 ± 1.4*	1.0 ± 1.3*
	ECC2	0.3 ± 0.5	0.9 ± 1.4*	0.9 ± 1.4*

*$p < .05$, **$p < .01$ and ***$p < .001$ for time effects. #$p < .01$ for session effect.

Table 1. *Mean values ± SD of BF potentiated M-wave, BF RMS/M-wave, 1RM ECC torques, perceived fatigue and muscle soreness before (PRE), immediately after (POST) and 24 hours after (POST24) the first (ECC1) and the second (ECC2) eccentric bouts. BF biceps femoris, M-wave maximal compound muscle action potentials, RMS/M-wave root mean square values of the electromyographic recordings normalized to potentiated M-wave, MVIC maximal voluntary isometric contraction, 1RM ECC eccentric unilateral 1 repetition maximum.*

Maximal torque production

No session × time interaction effect nor main effect of the session was found for MVIC torque ($p > .10$), while there was a significant main effect of time ($F_{2, 30}$ = 74.2, $p < .001$, η^2p = .83; Fig. 3a). MVIC torque significantly decreased at POST by 27.9 ± 6.5% during ECC1 and by 25.8 ± 6.2% during ECC2 ($p < .001$). MVIC torque measured at POST24 were no longer different from PRE values for both sessions (p = .14).

ANOVA did not reveal significant session × time interaction or time effects for 1RM ECC torque ($p > .54$), while there was a significant main effect of the session ($F_{1, 15}$ = 11.0, $p < .01$, η^2p = .42; Table 1). In accordance with the baseline differences reported between eccentric bouts, 1RM ECC torque was greater during ECC2 compared to ECC1 ($p < .01$). Nonetheless, no delayed effects of eccentric bouts (i.e., ECC1 or ECC2) were observed on 1RM ECC torque at POST24.

Central and peripheral fatigue parameters

A significant time effect was found for VA ($F_{2,30}$ = 9.85, $p < .001$, η^2p = .40; Fig. 3b) and CAR ($F_{2,30}$ = 11.7, $p < .001$, η^2p = .44; Fig. 3c). VA values were significantly reduced at POST by 3.6 ± 4.6% during ECC1 and by 3.9 ± 5.1% during ECC2 ($p < .01$). Similarly, CAR values were significantly lower at POST compared to PRE values with significant reductions during ECC1 and ECC2 by 1.6 ± 1.9% and 1.8 ± 2.4%, respectively ($p < .001$). At POST24, VA and CAR values were no longer different from PRE values ($p > .96$). There was no session × time interaction nor session effect for both VA and CAR ($p > .53$). During MVIC and 1RM ECC, no significant main or interaction effect was observed for BF RMS/M-wave ($p > .24$; Table 1).

ANOVA did not show session × time interaction nor session effect for all peripheral fatigue parameters ($p > .10$). There was a significant time effect for Dt_{100Hz} ($F_{2,30} = 6.90$, $p < .01$, $\eta^2p = .32$), Dt_{10Hz} ($F_{2,30} = 4.06$, $p < .05$, $\eta^2p = .23$) and Tw_{pot} ($F_{2,30} = 5.32$, $p < .01$, $\eta^2p = .26$) but not for Dt_{10Hz}/Dt_{100Hz} ($F_{2,30} = .22$, $p = .80$). Dt_{100Hz} values were significantly reduced at POST during both ECC1 and ECC2 by 10.0 ± 15.5% and 9.9 ± 16.7%, respectively ($p < .01$; Fig. 3d). Dt_{10Hz} was significantly reduced at POST during ECC1 (-6.4 ± 23.4%) and ECC2 (-11.7 ± 16.9%) ($p < .05$; Fig. 3e). Tw_{pot} also significantly decreased at POST during ECC1 (-21.2 ± 36.8%) and ECC2 (-9.8 ± 29.2%) ($p < .01$; Fig. 3f). Dt_{100Hz}, Dt_{10Hz} and Tw_{pot} were no longer different from PRE at POST24 during both ECC1 and ECC2 ($p > .37$). There was no session × time interaction nor session effect for BF M-wave ($p > .24$), while a significant time effect was found ($F_{2,30} = 5.41$, $p < .01$, $\eta^2p = .27$). However, no differences were observed between PRE and POST values but POST24 values were higher compared to POST ($p < .01$; Table 1).

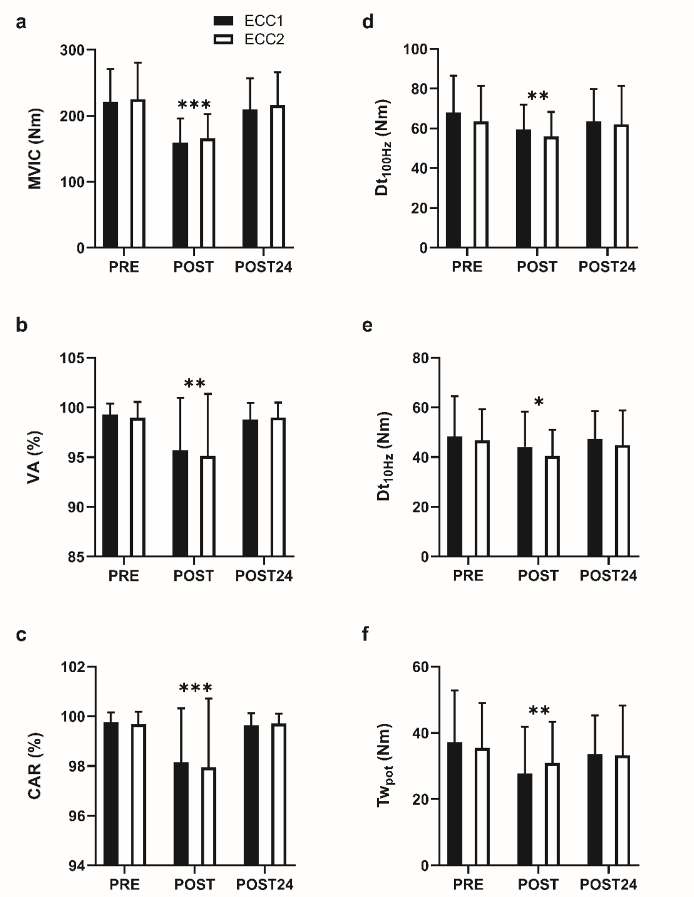

*Figure 3: Effect of the first (ECC1) and the second (ECC2) bout of eccentric contractions on knee flexor neuromuscular function. (a) MVIC torque, central [i.e., (b) VA and (c) CAR] and peripheral [(d) Dt_{100Hz}, (e) Dt_{10Hz} and (f) Tw_{pot}] fatigue parameters before (PRE), immediately after (POST) and 24 hours after (POST24) ECC1 (dark bars) and ECC2 (white bars). Means ± SD values of 16 participants are shown. Only significant main effects of the time point are displayed in the figure with POST values significantly different from PRE (*p < .05, **p < .01 and ***p < .001). MVIC maximal voluntary isometric contraction, VA voluntary activation level, CAR central activation ratio, Dt_{100Hz} potentiated doublet amplitude at 100 Hz, Dt_{10Hz} potentiated doublet amplitude at 10 Hz and Tw_{pot} potentiated single twitch.*

Position-matching errors after the two eccentric bouts

No session effect was found for position-matching errors ($p > .10$). However, a significant testing position × angle × time point interaction effect for position-matching errors during JPM tasks was found ($F_{2,30} = 6.35$, $p < .01$, $\eta^2p = .30$; Fig. 4). In other words, the eccentric bouts had distinct effects depending on the testing position (i.e., seated *vs.* prone position) and the tested angle (i.e., 40° *vs.* 70° of knee flexion). While position-matching errors measured at 70° of knee flexion (i.e., during $JPMS_{70}$ and $JPMP_{70}$ tasks) remained unchanged throughout the experiment ($p > .22$), the eccentric bouts resulted in significant position-matching errors at 40° of knee flexion, i.e., at long KF muscle length (Fig. 4). However, the onset and durations of these alterations were task-dependent. At POST, position-matching errors increased only in seated position during $JPMS_{40}$ tasks ($p < .01$) with participants adopting a more flexed position with their exercised indicator limb compared to their non-exercised reference limb. At POST24, while knee position sense was no longer altered in seated position ($p > .92$), significant delayed position-matching errors were detected in prone position during $JPMP_{40}$ tasks ($p < .01$). The direction of errors was similar to that observed during $JPMS_{40}$ tasks at POST, i.e., participants adopted a more flexed position with their indicator limb compared to their non-exercised reference limb at long KF muscle length.

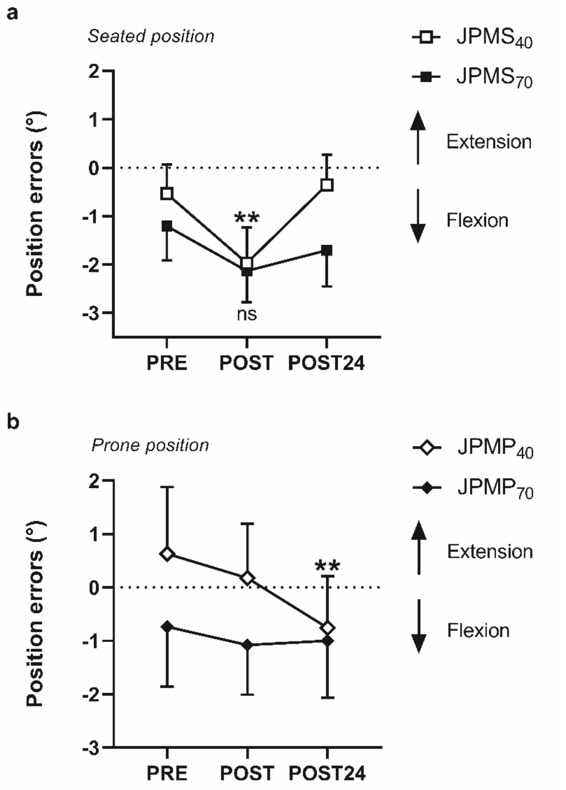

*Figure 4: Immediate and long-lasting effects of knee flexor eccentric contractions on knee position sense. Position-matching errors measured before (PRE), immediately after (POST) and 24 hours after (POST24) two bouts of eccentric contractions during bilateral joint position-matching (JPM) tasks in both seated (JPMS, upper panel a) and prone (JPMP, upper panel b) positions at two tested angles (40° of knee flexion, $JPMS_{40}$ and $JPMP_{40}$; 70° of knee flexion, $JPMS_{70}$ and $JPMP_{70}$). Pooled data (means ± standard error of the mean) of the first and second eccentric bouts are shown for 16 participants. Only significant main effects of the time point are displayed. **significantly different from PRE at p < .01.*

Perceived fatigue and muscle soreness

Neither session × time interaction effect nor session effect was found for perceived fatigue values ($p > .69$), while a significant time effect was found ($F_{2,30} = 91.1$, $p < .001$, $\eta^2p = .96$; Table 1). Following both eccentric bouts, the level of perceived fatigue significantly increased at POST compared to PRE ($p < .001$) but returned to baseline at POST24 ($p > .16$).

Neither session × time interaction nor session effect was found for perceived muscle soreness scores ($p > .92$). There was however a significant time effect ($F_{2,30} = 4.57$, $p < .05$, $\eta^2p = .23$; Table 1), with perceived muscle soreness measured at POST and POST24 significantly higher compared to PRE ($p < .05$) during ECC1 and ECC2.

Discussion

The present study investigated changes in KF neuromuscular function and knee position sense after ECC1 and ECC2 aiming to induce controlled force decrements (i.e., -20% MVIC force).

KF neuromuscular function and position sense parameters did not differ between the two consecutive eccentric bouts, showing the absence of a repeated bout effect. At POST, the eccentric exercise generated (i) KF neuromuscular fatigue involving central and peripheral components and (ii) position-matching errors in seated position at 40° of knee flexion (i.e., $JPMS_{40}$). At POST24, despite the probable presence of muscle damage (as revealed by significant increases in perceived muscle soreness), KF neuromuscular function had recovered whereas position-matching errors were observed in prone position at 40° of knee flexion (i.e., $JPMP_{40}$). Independently of the JPM task and the delay following exercise (i.e., from a few minutes to 24 hours), fatigue led participants to adopt a more flexed knee position at long muscle lengths.

Effect of eccentric bouts on KF neuromuscular function

Considering that no interaction effect was found for any neuromuscular function parameters, it is unlikely that a repeated bout effect occurred. Our findings thus contrast with previous results on knee extensors (Goodall et al. 2017) and elbow flexors (Prasartwuth et al. 2019) showing lower VA failure after the second eccentric bout. Here, the same levels of central and peripheral fatigue were observed immediately post-exercise (i.e., at POST ECC1 and POST ECC2) after each eccentric bout (Fig. 3) and returned to baseline levels within 24 hours.

At POST, acute central fatigue was evidenced by significant decreases in VA (approximately -3.7%, Fig. 3b) and CAR (approximately -1.8%, Fig. 3c). Although the interpolated twitch technique does not allow to dissociate spinal from supraspinal changes, our observations indicate central activation failure occurring upstream of the neuromuscular junction (Gandevia 2001). The central alterations found in the present study might result from an increase in the inhibitory actions from group III-IV afferents with the repetition of eccentric contractions (Martin et al. 2009). Interestingly, in comparison with previous investigations (Marshall et al. 2014; Baumert et al. 2021), our study is the first to report significant reduction in KF VA after fatiguing exercise. Nevertheless, it is worth mentioning that Behrens et al. (2012) and Da Silva et al. (2021, 2022) observed more pronounced activation failures (i.e., 13-16% VA decreases) after damaging fatiguing protocols of knee extensors that led to similar MVIC torque decrement.

In addition to acute central fatigue, the presence of acute peripheral fatigue was demonstrated by significant decreases in Dt_{100Hz}, Dt_{10Hz} and Tw_{pot} at POST by approximately 10%, 9% and 16%, respectively (Fig. 3d-f). Given that the Dt_{10Hz}/Dt_{100Hz} ratio and M-wave amplitude remained unchanged, the reductions of electrically evoked torques were probably not due to alterations of excitation-contraction coupling or reduced sarcolemma excitability (Allen et al. 2008). Therefore, several factors at POST such as the accumulation of intramuscular metabolites and ATP depletion may have led to the acute peripheral fatigue by decreasing the force produced at cross-bridge levels (Allen et al. 2008). Similar to central alterations, the magnitude of peripheral fatigue appears relatively low in comparison with the aforementioned studies (e.g., 18-36% reductions in potentiated doublet torque at 100 Hz) (Behrens et al. 2012; Da Silva et al. 2021).

Indices of KF peripheral fatigue had recovered 24 hours after the end of the eccentric bouts (Fig. 3), despite the likely presence of muscle damage indicated by increases in perceived muscle soreness (Table 1). Our observations conflict with previous studies showing prolonged peripheral alterations after eccentric exercises of knee extensors targeting similar amount of MVIC torque decrement (Behrens et al. 2012; Da Silva et al. 2021). Despite the lack of data on KF neuromuscular fatigue in the literature, our findings suggest that KF may exhibit some specificities in terms of etiology (e.g., relatively low activation failure) and recovery (e.g., only acute peripheral alterations) of neuromuscular fatigue, but this requires further investigations.

Effect of eccentric bouts on knee position sense

Along with the absence of repeated bout effect on KF neuromuscular function, our results suggest that no repeated bout effect occurred on knee position sense acuity neither. Based on previous studies reporting repeated bout effect on VA (Goodall et al. 2017; Prasartwuth et al. 2019), reduced position sense alterations were expected with lower central activation failure during the second eccentric bout. However, as discussed above, KF exhibited low activation failure that was not significantly different across sessions. Therefore, our experimental approach failed to reinforce the central-based hypothesis of fatigue-induced position sense alterations.

One of the main outcomes of this study is that position-matching errors evolved differently over time depending on the testing position, and, by extension, on the role of KF muscles during the matching task. In seated position, when KF were antagonistic during the positioning movement, position-matching errors significantly increased only at POST during the $JPMS_{40}$ tasks (Fig. 4a). Errors laid in the direction of flexion with participants perceiving their fatigued KF as more extended than they really were. This length overestimation pattern is consistent with the findings of a study recently conducted by our research team in which participants overestimated the length of their eccentrically fatigued knee extensors (Da Silva et al. 2021). Because position-matching errors were only significant in presence of central fatigue, these changes were attributed to fatigue-related central mechanisms. In the present study, a similar time course between central fatigue and position-matching errors in seated position was also found (i.e., only at POST; Fig. 3b and Fig. 4a). Therefore, it seems that matching performances in seated position, when knee extensors are agonistic during the positioning movement, are strongly influenced by exercise-induced central alterations, irrespective of the fatigued muscles. Overall, our findings *in seated position* tend to reinforce the central-based hypothesis of fatigue-induced position sense alterations formulated in previous research (Givoni et al. 2007; Allen et al. 2010; Tsay et al. 2012; Da Silva et al. 2021).

The novelty of this study is that we also assessed position sense in a prone position where KF were agonistic during the positioning movement. In this situation, the outcome is totally different. While no significant errors were detected at POST, position-matching errors became significant at POST24 during the $JPMP_{40}$ tasks (Fig. 4b). The direction of position-matching errors was similar to that observed during $JPMS_{40}$ at POST (length overestimation). However, at that time, all neuromuscular function parameters had recovered. Because perceived muscle soreness scores were significantly higher at POST24 compared to PRE values (Table 1), matching errors during $JPMP_{40}$ could have resulted from peripheral alterations related to possible muscle damage. In this regard, it has recently been proposed that excessive stretching of intrafusal and extrafusal fibers with the repetition of eccentric contractions could lead to increased firing rates of Ia and II afferents due to microinjury of muscle spindle nerve endings (Sonkodi et al. 2020). Increased spindle sensitivity to stretches may thus account for position sense disturbances during $JPMP_{40}$ at POST24. However, this does not explain the task specificity of our results. The absence of significant position-matching errors at POST during prone tasks was also surprising. Simply put, compared to the seated task, the prone task required a KF activation necessarily associated with fusimotor activity and muscle exposure to gravity forces. The implication of the fusimotor system during the prone JPM tasks may modulate exercise-induced effects on position sense and account for this task specificity.

Another important result of this study is that position-matching errors were only significant at 40° (Fig. 4), i.e., at long KF muscle lengths. Although not significant, increased spindle firing rate was reported following repeated eccentric contractions of cat muscles (Gregory et al. 2002), and this was all the more pronounced at long muscle lengths. Despite the absence of data in humans, it can be assumed that position-matching errors increase at long muscle length due to greater differences in spindle frequency discharges between the fatigued and the reference limb. It is however important to note that the magnitude of position-matching errors observed in the present study is low in comparison with previous experiments conducted on knee extensors (Givoni et al. 2007; Da Silva et al. 2021). This suggests that knee position sense may be less sensitive to KF fatigue and, consequently, could be more influenced by knee extensor fatigue. From an applied perspective, if participants perceive their muscles more extended than they really are, lower degrees of stretch will probably be reached at long muscle length. This perception bias could thus represent a protective mechanism limiting muscle-tendon unit from risky strain in fatigue conditions.

Overall, depending on the position and the role of KF muscles in the matching task, the mechanisms underpinning kinesthetic alterations seem different. While the central-based hypothesis could account for the significant increase in position-matching errors during $JPMS_{40}$ at POST, they certainly cannot rule out those observed during $JPMP_{40}$ at POST24. Our findings thus suggest muscle- and task-specificities of eccentric-induced fatigue effects on position sense. In view of our results, it would be important to assess immediate and prolonged effects of eccentric fatigue on firing rates of groups Ia and II afferent fibers with microneurography, as well as to identify how fusimotor control and muscle length could modulate these effects (i.e., active *vs.* passive conditions at short *vs.* long muscle lengths). Moreover, to better appreciate the possible relationship between delayed-onset muscle soreness and position sense alterations, future experiments should seek to investigate the effects of eccentric fatigue on knee position sense using longer follow-up (e.g., up to 72 hours after exercise).

Conclusion

The repeated bout effect commonly observed after a first unaccustomed eccentric bout has been attributed in part to central mechanisms (Hyldahl et al. 2017) with lower VA deficits after a second eccentric bout (Goodall et al. 2017; Prasartwuth et al. 2019). Our study does not corroborate these observations when generating a similar amount of torque decrement across eccentric bouts. Straightly linked to fatigue-related central mechanisms, current hypotheses on the mechanisms of eccentric-induced position sense alterations head toward the implications of central disturbances (Allen et al. 2010; Da Silva et al. 2021, 2022). However, our results partly support this idea as position sense alterations exhibited different time course depending on the testing position: alterations in presence of VA deficits during $JPMS_{40}$ at exercise termination and delayed alterations in absence of VA deficits during $JPMP_{40}$. In addition, our observations suggest that position sense alterations may depend on the action of the fatigued muscle (agonistic or antagonistic to the positioning movement), but this original result remains to be ascertained. Noteworthy, participants adopted a less extended position at the knee during matching tasks in fatigue conditions, this perception bias potentially representing an injury protective mechanism. In conclusion, considering that the central-based hypothesis of fatigue-induced position sense alterations cannot fully explain our findings, more complex mechanisms than central or peripheral disturbances alone might be involved in KF eccentric-induced position sense alterations.

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