Altered Position Sense after Submaximal Eccentric Exercise–inducing Central Fatigue

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ABSTRACT

DA SILVA, F., F. MONJO, F. ZGHAL, F. CHORIN, O. GUÉRIN, and S. S. COLSON. Altered Position Sense after Submaximal Eccentric Exercise–inducing Central Fatigue. *Med. Sci. Sports Exerc.*, Vol. 53, No. 1, pp. 218–227, 2021. **Purpose:** The purpose of this study was to concomitantly investigate the acute and delayed effects of a submaximal eccentric-induced muscle fatigue on the position sense and the neuromuscular function of the right knee extensor muscles. **Methods:** Thirteen young and physically active participants performed a unilateral isokinetic eccentric exercise of their right lower limb until a decrease in maximal voluntary isometric contraction (MVIC) of 20% was reached. Neuromuscular (i.e., MVIC, voluntary activation (VA) level, and evoked contractile properties [DB100 and DB10]) and psychophysical evaluations (i.e., bilateral position-matching task, perceived muscle soreness, and perceived fatigue) were performed at four time points: before (PRE), immediately after (POST), 24 (POST24), and 48 (POST48) the exercise. **Results:** The acute 20% MVIC reduction ($P < 0.001$) was associated with both central (i.e., −13% VA decrease, $P < 0.01$) and peripheral (i.e., −18% and −42% reduction of DB100 and DB10, respectively, $P < 0.001$) fatigue. In the following days (POST24 and POST48), VA levels had recovered despite the presence of a persisting peripheral fatigue and delayed-onset muscle soreness. Knee position sense, as revealed by position errors, was significantly altered only at POST ($P < 0.05$) with participants overestimating the length of their knee extensor. Position errors and VA deficits were significantly correlated at POST ($r = -0.60$, $P = 0.03$). Position errors returned to nonsignificant control values in the following days. **Conclusion:** The acute central fatigue induced by the eccentric exercise contributes to the position sense disturbances. Central fatigue might lead to alterations in the sensory structures responsible for the integration and the processing of position-related sensory inputs. **Key Words:** VOLUNTARY ACTIVATION, PERIPHERAL FATIGUE, ELECTROMYOGRAPHY, DOMS, PROPRIOCEPTION

Everybody experiences fatigue at some point in daily life or during sports activities. It can be caused by the repetition and/or maintenance of muscle contractions. Fatigue leads to an objective decline in neuromuscular performance (e.g., decreased maximal muscle force) and to alterations in the subjective sensations associated with exercise (e.g., perceived fatigue, perceived muscle soreness) (1). The task-performance decline is commonly attributed to adjustments in central (i.e., within the central nervous system at spinal and/or supraspinal levels) and peripheral levels (i.e., contractile capacity of the muscle distant from the neuromuscular junction) (2). The origin of fatigue is therefore multiple and is generally specific to the exercise performed, especially to the contraction mode (3). In this context, previous studies have reported that the repetition of submaximal voluntary eccentric contractions, usually carried out during physical activity, led to an acute decrease in maximal voluntary isometric contraction (MVIC) of knee extensors (KE) after downhill walking (7% to 15%) (4,5), after intense downhill trail running (17% to 19%) (6), and after isokinetic contractions (ranging from 12% up to ~30%) (7–9). Although partially recovered, MVIC decreases were still observed 2 d after the exercise (6,8,9).

Both central and peripheral factors can account for the acute and delayed muscle force decreases observed after submaximal fatiguing eccentric exercises, but central fatigue and peripheral fatigue recover differentially. Through measurements of voluntary activation (VA) levels (5–8), central activation ratio (8), or tetanus/MVIC ratio (9), all the above-mentioned studies reported the presence of acute central fatigue. Two days after the exercise, central fatigue had fully recovered (6,8,9). Peripheral fatigue, assessed by doublet twitches (4–7) or trains of electrical stimuli at 100 Hz (8,9), occurred immediately and remained present 2 d after the exercise. These results evidence that submaximal eccentric exercise induces acute and delayed alterations in the contractile properties of KE muscles. The delayed alterations in muscle contractile properties are often associated with increased perceived muscle soreness (6,8,9) indicating the presence of damage caused to the extrafusal fibers

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(10). In short, although peripheral fatigue lasts several days after a submaximal eccentric exercise, central fatigue recovers fast and is only present immediately after the exercise.

In addition to the decreased neuromuscular function observed after submaximal eccentric exercise, muscle fatigue has also been shown to impair proprioception in the exercised muscles (11). Proprioception covers numerous sensations, including the sense of position, which mainly arises from muscle spindles (i.e., intramuscular sensory structures connected to force-generating extrafusal fibers that inform the central nervous system of muscle length through group Ia and group II afferents) (11,12). Some studies have shown that the central signals related to motor command (i.e., the efference copy) may also contribute to the sense of position (13,14). However, the contribution of these two streams of positional signals has been shown to be dependent on the task used to evaluate the position sense (i.e., during bilateral-matching tasks, positional information mostly arises from muscle spindles) (15). Given that submaximal eccentric exercise induces extrafusal muscle fiber damage (10) and because skeletal muscles contain the sensory receptors primarily responsible for the position sense (i.e., the muscle spindles), it was assumed that eccentric contractions could damage the intrafusal fibers as well and consequently alter the position sense. However, no alteration in muscle spindle afferent firing after bouts of eccentric contractions was reported in cat muscles (16). Although such observations have never been replicated in humans, it is very unlikely that damage would occur in human muscle spindles after eccentric contractions because intrafusal fibers exhibit compliant connections with extrafusal fibers, protecting them from any mechanical muscle damage (17).

Despite the apparent absence of modifications in muscles spindles firing, experiments in humans systematically showed significant disturbances in the position sense after eccentric fatiguing contractions, whether maximal or not (18–24). The first experiments focused on the elbow joint (18–20) and showed, using a bilateral position-matching task, that participants systematically perceived their fatigued elbow as more extended than it actually was. Based on this result, it was suggested that participants used effort cues to match positions between upper limbs. It was assumed that participants adopted a more flexed angle in their fatigued upper limb to match the perceived effort required to maintain their two forearms against gravity (19,20). Nonetheless, Givoni et al. (21), using a bilateral position-matching task at the knee, highlighted that individuals extended their fatigued lower limb more than their unfatigued one. In this situation, individuals thus produced a greater effort against gravity with their fatigued lower limb, suggesting that the effort hypothesis was misleading. Assuming that spindle integrity does not seem to be affected by eccentric contractions, this tendency to overestimate muscle length regardless of the joint led some authors to suggest that position sense alteration after eccentric contractions was due to the central alterations related to fatigue (21–23). However, to the best of our knowledge, no studies have directly investigated the link between central fatigue and position sense alterations.

In this study, the acute and delayed effects of KE muscles fatigue induced by a unilateral submaximal fatiguing eccentric exercise on knee position sense were evaluated. For this purpose, a bilateral position-matching task was used before and immediately after the fatiguing exercise as well as 24 and 48 h postexercise. In addition to these measurements, neuromuscular tests intended to assess the involvement of central and peripheral fatigue were performed. The concomitant assessments of position sense and neuromuscular function were innovative and intended to establish a potential link between central fatigue and position sense alterations. We hypothesized that the submaximal eccentric fatiguing protocol would induce an acute central fatigue that would be associated with position sense alterations immediately after the exercise. Based on previous research (6,8,9), we also assumed that central fatigue, contrary to peripheral fatigue, would not persist in the days after the eccentric exercise and that position-matching errors would therefore turn to control values.

METHODS

Participants

Sample size was estimated *a priori* with G*Power (version 3.1.9.7) based on previous studies where similar VA decrease (7) and position errors from bilateral-matching tasks (21) were obtained after eccentric exercise of the KE muscles. From these studies, the highest minimum sample size obtained was six participants for a repeated-measures within-subject analysis with a power set at 0.95. For the sample size of the participants included in our study, a sensitivity power analysis with an α of 0.05 and a power of 0.95 led to a large effect of f = 0.55. Thirteen young and physically active participants (nine males, four females; mean ± SD: 25.3 ± 3.6 yr old, 1.77 ± 0.08 m, 71.6 ± 12.5 kg) volunteered to participate in this study. Considering that the magnitude of eccentric exercised-induced muscle damage does not seem to be influenced by gender (25), both men and women were recruited. The participants recruited had never undergone any kind of knee surgery and had been free from knee neuromuscular injuries for at least 6 months. They were informed of the testing procedures and gave informed written consent before the beginning of the first experimental session. They came to the laboratory for three experimental sessions separated by 24 h. The procedures had been approved by the local research ethics committee and were conformed to the latest version of the Declaration of Helsinki (2013).

Experimental Procedures

Three consecutive days of testing were required to assess the acute and delayed effects of a submaximal unilateral fatiguing eccentric exercise on the neuromuscular function of the KE muscles and the knee position sense. Neuromuscular and psychophysical evaluations were performed at four time points; before (PRE), immediately after (POST), 24 h after

(POST24), and 48 h after (POST48) the eccentric exercise (Fig. 1).

PRE. Upon arrival at the laboratory, participants were equipped with EMG electrodes (for details, see EMG Recordings section) and placed on an isokinetic dynamometer (Biodex™, System 4; BIODEX Corporation, Shirley NY). Participants received instructions about the entire experimental procedures and were familiarized with the measurements. Once the familiarization completed, participants performed the bilateral position-matching trials to assess the knee position sense at two angles (i.e., at 30° and 70°, during the JPM_{30} and JPM_{70} tasks; for details, see Position-Matching Task section). After having identified the optimal stimulation site and determined the intensity of the percutaneous electrical stimulations, peak-to-peak M-wave amplitudes (M_{MAX}) of the KE muscles at rest were obtained (for details, see Femoral Nerve Stimulation section). Participants then performed a progressive standardized warm-up protocol consisting of 24 unilateral submaximal concentric-to-eccentric contractions of increasing intensity at angular velocities ranging from $90°\cdot s^{-1}$ to $30°\cdot s^{-1}$ (12 contractions at $90°\cdot s^{-1}$, 8 contractions at $60°\cdot s^{-1}$, and 4 contractions at $30°\cdot s^{-1}$). Neuromuscular function was subsequently assessed at baseline (PRE) with two MVIC, which were associated with electrical stimulations, two ECC (maximal voluntary eccentric contraction), and two CON (maximal voluntary concentric contraction) (for details, see Neuromuscular Evaluations section). To conclude PRE evaluations, both perceived muscle soreness of the KE muscles (for details, see Perceived Muscle Soreness section) and the perceived fatigue state (for details, see Perceived Fatigue section) were assessed.

POST. Immediately after the end of the submaximal unilateral fatiguing eccentric exercise (for details, see Fatiguing Eccentric Exercise section), perceived fatigue was assessed. After that, participants successively carried out one MVIC with electrical nerve stimulations, one ECC, and one CON. M_{MAX} values of the KE muscles during the posteccentric exercise condition (POST) were then assessed. Afterward, participants were asked to perform two sets of bilateral position-matching trials (i.e., one set at each tested angle). The two matching sets were separated by additional submaximal eccentric contractions to maintain the fatigue level induced by the submaximal unilateral fatiguing eccentric exercise. At the end of the second matching set, participants performed one MVIC with electrical nerve stimulations (POST') and perceived muscle soreness of the KE muscles was measured.

POST24 and POST48. During the testing sessions of the two following days, participants performed the same sequence of psychophysical and neuromuscular tests as described in the PRE section above, without the familiarization period.

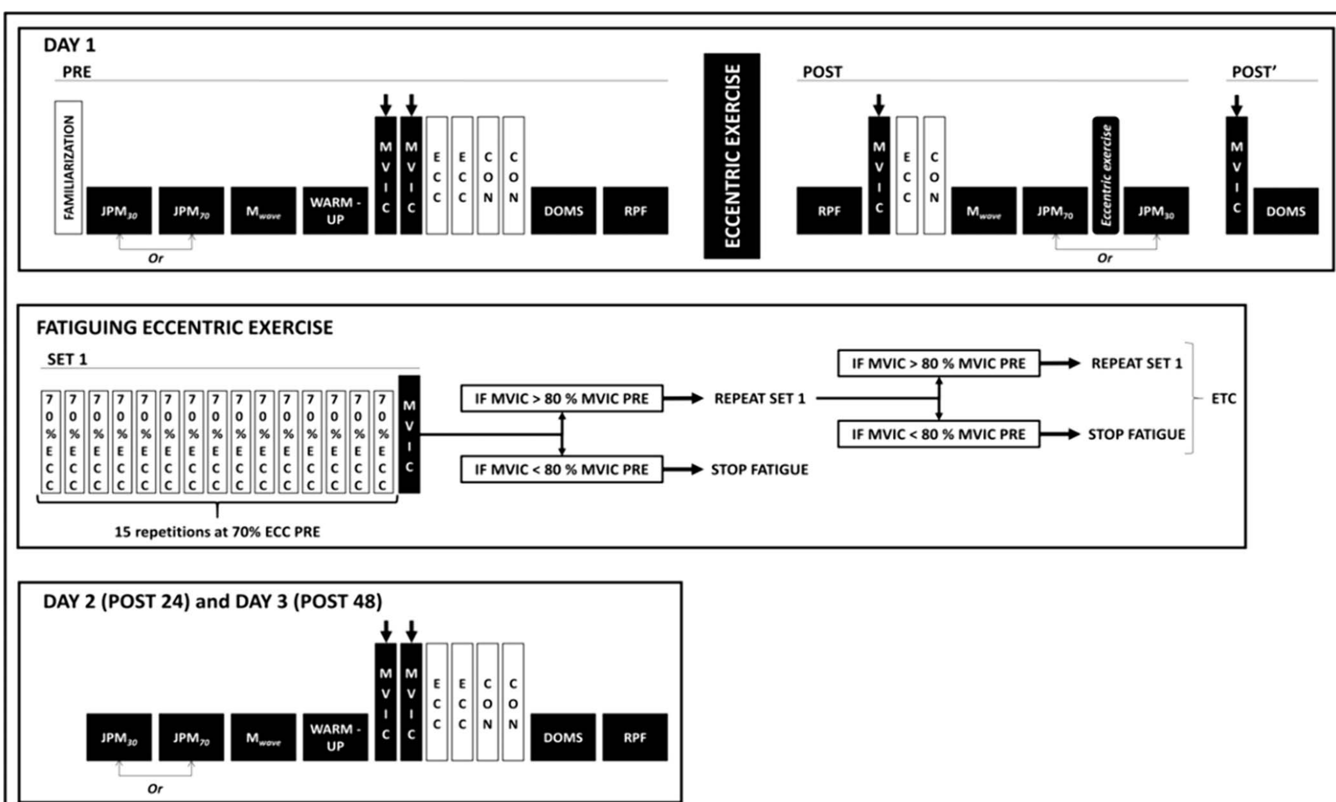

FIGURE 1—Schematic representation of the experimental design. Neuromuscular and psychophysical evaluations were performed before (PRE), immediately after (POST), 24 h after (POST24), and 48 h (POST48) after the fatiguing unilateral eccentric exercise. Please refer to the text for detailed explanations of the fatiguing exercise. JPM_{30}, bilateral position-matching task at 30°; JPM_{70}, bilateral position-matching task at 70°; ECC, maximal voluntary eccentric contraction; CON, maximal voluntary concentric contraction; RPF, rating of perceived fatigue.

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Fatiguing Eccentric Exercise

The eccentric exercise consisted of the submaximal unilateral eccentric contractions of the right limb with a contraction intensity set at 70% of the ECC measured in PRE. Participants had visual feedback of the target torque to reach thanks to an automatically horizontal scaled on the screen. They performed several sets of 15 submaximal eccentric contractions at angular velocity of $30°\cdot s^{-1}$. After each eccentric contraction, the limb was passively returned by the motor of the dynamometer to a full extended position at an angular velocity of $90°\cdot s^{-1}$. At the end of each set of 15 contractions, participants performed an MVIC without electrical nerve stimulations intended to evaluate the loss of force. If the MVIC torque decrement was less than 20% of the PRE value, participants continued with a new set of 15 repetitions. The sets were repeated until participants reached a force loss representing a 20% MVIC decrease. Note that in POST, participants performed an additional set of seven eccentric contractions with similar parameters (i.e., 70% of ECC PRE at $30°\cdot s^{-1}$) between the two angles of the bilateral position-matching trials.

Neuromuscular Evaluations

Torque measurements. Voluntary and electrically evoked contractions were assessed using the isokinetic dynamometer. Participants were seated and strapped with belts over the chest and hips to avoid any movements during the protocol. Participants adopted a standardized position on the dynamometer with a trunk-thigh angle of 95° and an alignment of the axes of rotation of the knee and of the dynamometer lever arm. This allowed measurements over an angular range of motion of 100°, from 5° to 105° (0° = full knee extension). The dynamometer lever arm was fixed to the motor and strapped to the leg of the participants, 2 cm above the external malleolus of the tested limb. Torque measurements of the dynamometer were also recorded by a commercially available software (Acknowledge 4.1; Biopac®Systems, Inc., Holliston, MA) and sampled at 500 Hz. During MVIC, ECC, and CON, verbal encouragement was provided for each contraction. MVIC was performed at a knee angle set at 60°. ECC and CON were performed over the full angular range of motion, at an angular velocity of $30°\cdot s^{-1}$. A 2-min rest was assigned between each maximal voluntary contraction. MVIC torques were calculated as the mean value of the torque signal over a 500-ms window around the highest torque value. For ECC and CON, the highest peak torque value recorded was used. In PRE tests, the best MVIC, ECC, and CON trials were analyzed.

EMG recordings. Electrical muscle activity was recorded by six pairs of Ag/AgCl surface electrodes (diameter = 10 mm, interelectrode distance = 20 mm; Contrôle-Graphique, Brie-Comte-Robert, France) placed on the rectus femoris (RF) and the biceps femoris (BF) of both limbs as well as on the vastus lateralis (VL) and the vastus medialis (VM) of the exercised limb. Electrodes were placed according to the SENIAM recommendations (26). A reference electrode was placed on the lateral tibial condyle of the participants' exercised limb. Each electrode placement was marked on the skin to ensure a similar repositioning at POST24 and POST48. To reduce impedance below 3 kΩ, the subject's skin was prepared (i.e., shaving, abrading, and cleaning with alcohol). EMG signals were amplified (MP 150, Biopac® Systems Inc.; CMRR = 110 db, Z Input = 1000 MΩ, gain = 1000), filtered (bandwidth frequency, 10–500 Hz), and recorded (sampling frequency, 2 kHz) using the above-mentioned Acknowledge software. The root mean square (RMS) values of KE EMG during MVIC, ECC, and CON computed over a 500-ms period were normalized to the M_{MAX} (i.e., average of the three responses) recorded at each time point measurement and were considered as central fatigue indicators. The RMS of the BF muscle was computed over the same period, and the coactivation level was expressed by the ratio between the BF RMS value and the sum of the RMS/M_{MAX} values of VM, VL, and RF muscles.

Femoral nerve stimulation. Supramaximal electrical stimulations of the femoral nerve were used to obtain, among others, the maximal electrophysiological response (M_{MAX}), which reflects the level of sarcolemma excitability. For this purpose, the optimal stimulation site and the intensity of the percutaneous electrical stimulation were determined using a stimulation pen. Electrical nerve stimulations were then delivered to the femoral nerve by a self-adhesive surface electrode (diameter: 10 mm, Ag/AgCl, Contrôle-Graphique) whose positioning was marked on the skin. The anode electrode (self-adhesive rectangular electrode, 5 × 9 cm; Stimex®, Wetzlar, Germany) was positioned at the level of the great trochanter. Rectangular pulses (400-V maximum voltage and 1-ms duration) were delivered by an electrical stimulator (DS7 Digitimer®, Hertfordshire, UK). The stimulation intensity was fixed 20% above the intensity, allowing maximal mechanical twitches and M-waves to ensure adequate assessment of the central and peripheral fatigue of the KE muscles. Overall, the intensity of the pulses varied from 90 to 190 mA. In addition to M_{MAX} measurements, electrical nerve stimulations were used during some MVIC to assess the central and peripheral fatigue induced by the exercise (Fig. 1). In that case, MVIC was associated with three electrical nerve stimulations delivered during and after the contraction (i.e., a superimposed doublet at 100 Hz [DBsup] and two potentiated doublets at 100 Hz [DB100] and 10 Hz [DB10], respectively). Both central and peripheral components of the neuromuscular fatigue were assessed. DB100, DB10, and DB10:100 ratio measurements were used as peripheral fatigue indicators. The VA level of the KE muscles was used as a central fatigue indicator and was computed using the following formula (27):

$$\mathrm{VA}\ (\%) = \left(1 - \left[\frac{\mathrm{DBsup} \times \text{voluntary torque before DBsup}}{\frac{\mathrm{MVIC}}{\mathrm{DB100}}}\right]\right) \times 100.$$

Psychophysical Evaluations

Position-matching task. The bilateral position-matching trials were performed on the dynamometer and consisted of

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matching knee angles across limbs with blindfolded participants. In the seated position described above, joint angles were measured using a digital inclinometer and the potentiometer signals from the dynamometer which were calibrated and synchronized before each experimental session. The nonexercised left limb was used as the reference limb, and the right exercised limb was used as the indicator. One matching trial was performed as follows: (i) the two limbs were positioned in a nearly fully extended position (5° of knee flexion), the reference limb supported by an experimenter and the indicator limb automatically supported by the arm of the dynamometer; (ii) an experimenter positioned the nonfatigued reference limb at one of the two tested angles (i.e., 30°, JPM_{30} and 70°, JPM_{70}) using the digital inclinometer; (iii) once in position, the arm of the dynamometer was released, and the participant was required to actively reproduce the reference limb's position with his indicator limb; and (iv) when the participant was satisfied with his/her match, he/she pressed a button placed in his/her left hand and the matching value was recorded for further analyses. Before each set of trials, both limbs were conditioned at 90° of knee flexion with a 5-s low-intensity voluntary isometric contraction (~30% MVIC). This was done to put muscle spindles in a similar thixotropic state across limbs (28). In each testing time point, three matching trials were performed per tested angle. JPM_{30} and JPM_{70} were performed in a random fashion across participants and testing time points. At each testing time point, position-matching errors during JPM_{30} and JPM_{70} were calculated as the mean angular difference between the knee angle joint of the indicator limb and the reference limb from the three tests performed. Positive errors indicate errors toward extension relative to the reference limb. During the joint position sense measures, the RMS/M_{MAX} EMG values of the VL, VM, and RF of the indicator limb were calculated over a 2-s window just before the matching angle was reached. This was done to evaluate the participants' neural outputs generated toward their KE to maintain the joint position.

Perceived muscle soreness. The level of perceived muscle soreness (i.e., delayed-onset muscle soreness [DOMS]) was taken as an indicator of the amount of possible muscle damage. Participants were asked to evaluate the perceived level of pain of their indicator limb using a 0–10 numerical rating scale (0, no pain; 10, worst pain). To evaluate the perceived pain, an experimenter applied a steady 25-N pressure with a cylindrical object (0.5 cm diameter) next to the proximal EMG electrode of the corresponding KE muscle (i.e., at the level of the RF, VL, and VM). For purpose of analysis, RF, VL, and VM scores were averaged and used as indicators of global perceived KE muscle soreness at each time point.

Perceived fatigue. Participants were asked to estimate the perceived level of fatigue using a modified Borg CR 10 scale called rating of perceived fatigue (29). The perceived fatigue, which was explained to participants as being "a feeling of diminishing capacity to cope with physical stressors" (30), was rated from 0 (not fatigued at all) to 10 (total fatigue and exhaustion). Unlike DOMS, which was specific to each KE muscle, the assessment of perceived fatigue was intended to reflect the general fatigue of the participants at each time point.

Statistical analysis. Statistical analyses were performed using Statistica software (version 8.0, Statsoft, Tulsa, OK). Data were checked for normality and variance using the Kolmogorov–Smirnov test. To study the effects of fatigue, repeated-measures ANOVA (PRE vs POST vs POST24 vs POST48) was performed. Effect sizes were determined from partial eta square values (η_p^2) with interpretation thresholds fixed at 0.01, 0.08, 0.26, and 0.50 for small, moderate, large, and very large effect sizes, respectively. When ANOVA displayed significant main effects, *post hoc* analyses were realized using the Newman–Keuls test. A Pearson correlation coefficient was used to assess the relation between (i) VA and position errors of the JPM_{70} task, (ii) perceived fatigue and VA, and (iii) VA or MVIC and position errors over the four time points. Significance level was set at $P < 0.05$ for all statistical analyses. The values presented in the manuscript, tables, and figures are mean (SD).

RESULTS

To reach the targeted MVIC decrease of 20%, the average number of submaximal eccentric contractions performed by the participants during the fatiguing exercise was 74 (34). The average peak torque value reached by the participants during the submaximal eccentric contractions was 259.1 N·m (82.5 N·m).

Neuromuscular Evaluations

Torque measurements and EMG recordings. A significant effect was found for MVIC ($F_{4, 48} = 17.8$, $P < 0.001$, $\eta_p^2 = 0.60$), ECC ($F_{3, 33} = 12.9$, $P < 0.001$, $\eta_p^2 = 0.51$), and CON ($F_{3, 33} = 24.3$, $P < 0.001$, $\eta_p^2 = 0.67$). MVIC, ECC, and CON decreased significantly at POST compared with PRE, by 19.7% (6.0%), 19.2% (8.9%), and 17.8% (11.5%), respectively ($P < 0.001$; Fig. 2A). At POST24 and POST48, MVIC and CON values remained significantly lower as compared with the values measured at PRE ($0.001 < P < 0.05$). ECC values were significantly lower at POST24 in comparison with PRE values ($P < 0.001$). Whatever the contraction mode (i.e., MVIC, ECC, and CON), no significant effect was observed for the EMG RMS/M_{MAX} values of the KE muscles between PRE and POST ($P > 0.05$; Table 1). Likewise, no significant differences were observed for the coactivation level ($P > 0.05$; Table 1).

Central and peripheral fatigue indicators. A significant effect was found for VA ($F_{4, 48} = 6.6$, $P < 0.001$, $\eta_p^2 = 0.35$) leading to a decrease of 12.9% (13.5%) at POST compared with PRE ($P < 0.01$, Fig. 2B). A significant effect was also found for DB100 ($F_{4, 48} = 20.1$, $P < 0.001$, $\eta_p^2 = 0.63$), DB10 ($F_{4, 48} = 69.0$, $P < 0.001$, $\eta_p^2 = 0.85$), and DB10:100 ratio ($F_{4, 48} = 18.4$, $P < 0.001$, $\eta_p^2 = 0.61$). At POST, DB100, DB10, and DB10:100 ratio decreased significantly by 17.6% (9.9%), 41.7% (13.1%), and 29.5% (11.7%), respectively ($P < 0.001$). DB100 and DB10 were still significantly

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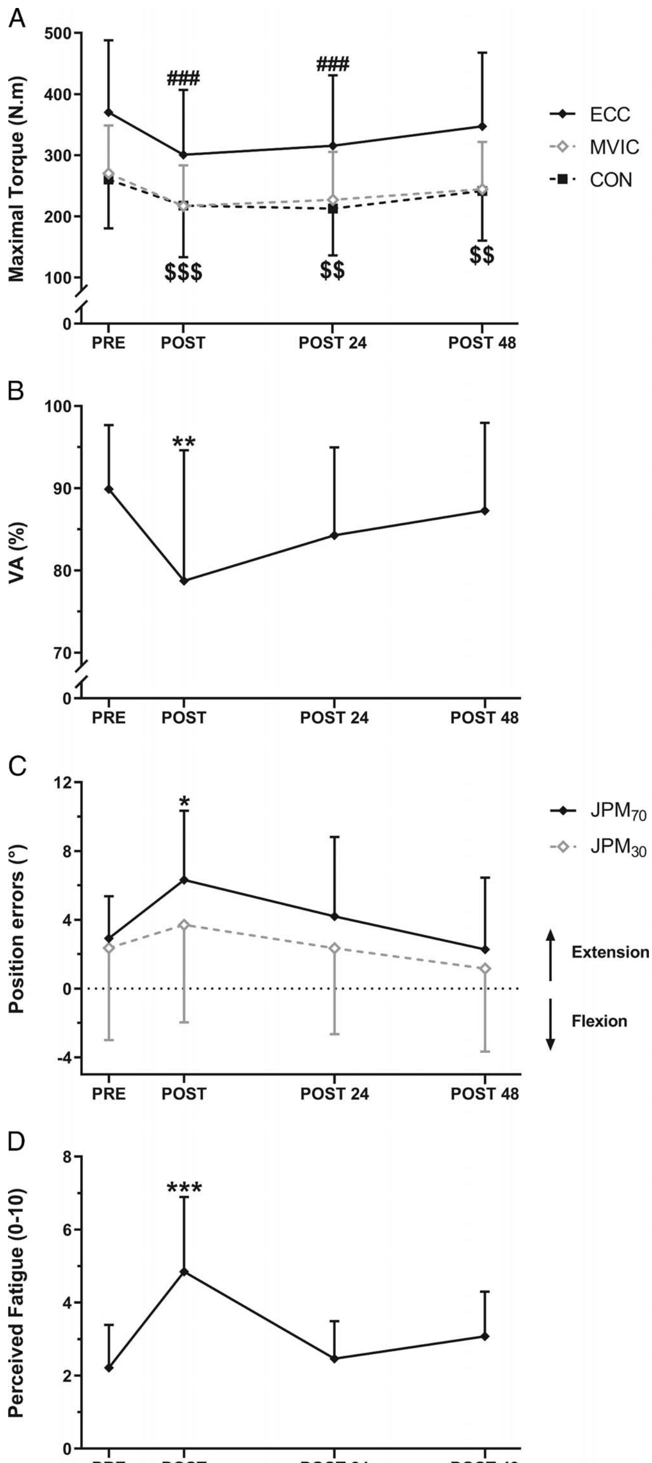

FIGURE 2—Maximal voluntary torque (A), VA (B), position-matching errors values (C), and perceived fatigue scores (D) measured before (PRE), immediately after (POST), 24 h after (POST24), and 48 h after (POST48) the fatiguing unilateral eccentric exercise. ECC, maximal voluntary eccentric contraction; CON, maximal voluntary concentric contraction; JPM_{30}, bilateral position-matching task at 30°; JPM_{70}, bilateral position-matching task at 70°. ###P < 0.001, significant differences from PRE values for ECC. $$$P$ < 0.01, $$$$P$ < 0.001, significant differences from PRE values for MVIC and CON. *P < 0.05, **P < 0.01, ***P < 0.001, significant differences from PRE values for the parameter considered.

reduced at POST24 ($P < 0.01$, Figs. 3A and 3B) in comparison with PRE. No significant effect was observed for the M_{MAX} values of the different muscles of the exercised limb (i.e., RF, VL, and VM; $P > 0.05$; Table 1).

Psychophysical Evaluations

Position-matching task. A significant increase in position-matching errors was found for the JPM_{70} task ($F_{3,\ 36} = 3.86$, $P = 0.017$, $\eta_p^2 = 0.24$), whereas no significant effect was observed for the JPM_{30} task ($P = 0.43$). At POST, participants adopted a more extended position with the fatigued indicator limb compared with PRE ($P = 0.03$; Fig. 2C). A significant correlation was observed between position errors and VA deficits ($r = -0.60$, $P = 0.03$; Fig. 4). Over the four time points, a tendency to a significant correlation fitting a linear function was found between the errors of the JPM_{70} task and VA values ($r = -0.94$, $P = 0.06$; Fig. 5A), whereas the correlation was not significant between the errors of the JPM_{70} task and MVIC decreases ($r = -0.84$, $P = 0.16$; Fig. 5B).

A significant effect was found for RMS values of EMG activity during JPM_{70} ($F_{3,\ 36} = 4.18$, $P = 0.01$, $\eta_p^2 = 0.26$) and JPM_{30} ($F_{3,\ 36} = 13.79$, $P < 0.001$, $\eta_p^2 = 0.53$). The sum of the normalized EMG RMS values of the KE muscles was significantly higher at POST in comparison with PRE for both angles ($P < 0.001$; Table 1). Overall, this shows that subjects generated higher neural outputs in their fatigue indicator limb to match the position of their nonfatigued reference limb during the postcondition.

DOMS and perceived fatigue. DOMS of the KE muscles increased significantly ($F_{3,\ 36} = 7.8$, $P < 0.001$, $\eta_p^2 = 0.39$)

TABLE 1. Mean (SD) of M_{MAX}, EMG RMS normalized to M_{MAX} (RMS/M_{MAX}), and coactivation before (PRE), immediately after (POST), and 24 h after (POST24), and 48 h after (POST48) eccentric exercise.

	PRE	POST	POST24	POST48
M_{MAX} (mV)				
RF	5.6 (1.5)	5.4 (1.5)	5.7 (1.8)	5.4 (1.8)
VL	5.5 (4.1)	5.4 (3.9)	5.8 (4.0)	5.7 (3.7)
VM	5.1 (2.0)	4.9 (2.3)	4.5 (1.6)	4.6 (1.4)
EMG RMS values during MVIC (a.u.)				
RF	0.06 (0.02)	0.06 (0.02)	0.06 (0.03)	0.06 (0.02)
VL	0.07 (0.03)	0.06 (0.02)	0.07 (0.03)	0.07 (0.03)
VM	0.08 (0.05)	0.07 (0.03)	0.07 (0.04)	0.07 (0.03)
Coactivation	0.20 (0.16)	0.21 (0.15)	0.20 (0.19)	0.18 (0.12)
EMG RMS values during ECC (a.u.)				
RF	0.07 (0.02)	0.06 (0.02)	0.07 (0.02)	0.07 (0.02)
VL	0.08 (0.03)	0.06 (0.02)	0.07 (0.03)	0.08 (0.03)
VM	0.08 (0.04)	0.08 (0.03)	0.07 (0.03)	0.08 (0.03)
Coactivation	0.17 (0.04)	0.31 (0.46)	0.17 (0.07)	0.21 (0.18)
EMG RMS values during CON (a.u.)				
RF	0.06 (0.01)	0.06 (0.01)	0.06 (0.02)	0.07 (0.01)
VL	0.08 (0.02)	0.07 (0.03)	0.07 (0.03)	0.07 (0.02)
VM	0.07 (0.03)	0.07 (0.03)	0.07 (0.03)	0.08 (0.02)
Coactivation	0.19 (0.08)	0.17 (0.07)	0.18 (0.07)	0.18 (0.11)
Sum of the EMG RMS values of the KE muscles during the JPM_{70} task (a.u.)	0.006 (0.001)	0.008 (0.004)***	0.006 (0.002)	0.006 (0.003)
Sum of the EMG RMS values of the KE muscles during the JPM_{30} task (a.u.)	0.01 (0.001)	0.04 (0.03)***	0.02 (0.006)	0.01 (0.004)

***P < 0.001, significant difference from PRE values.
ECC, maximal voluntary eccentric contraction; CON, maximal voluntary concentric contraction; M_{MAX}, maximal M-wave amplitude; JPM_{70}, bilateral position-matching task at 70°; JPM_{30}, bilateral position-matching task at 30°.

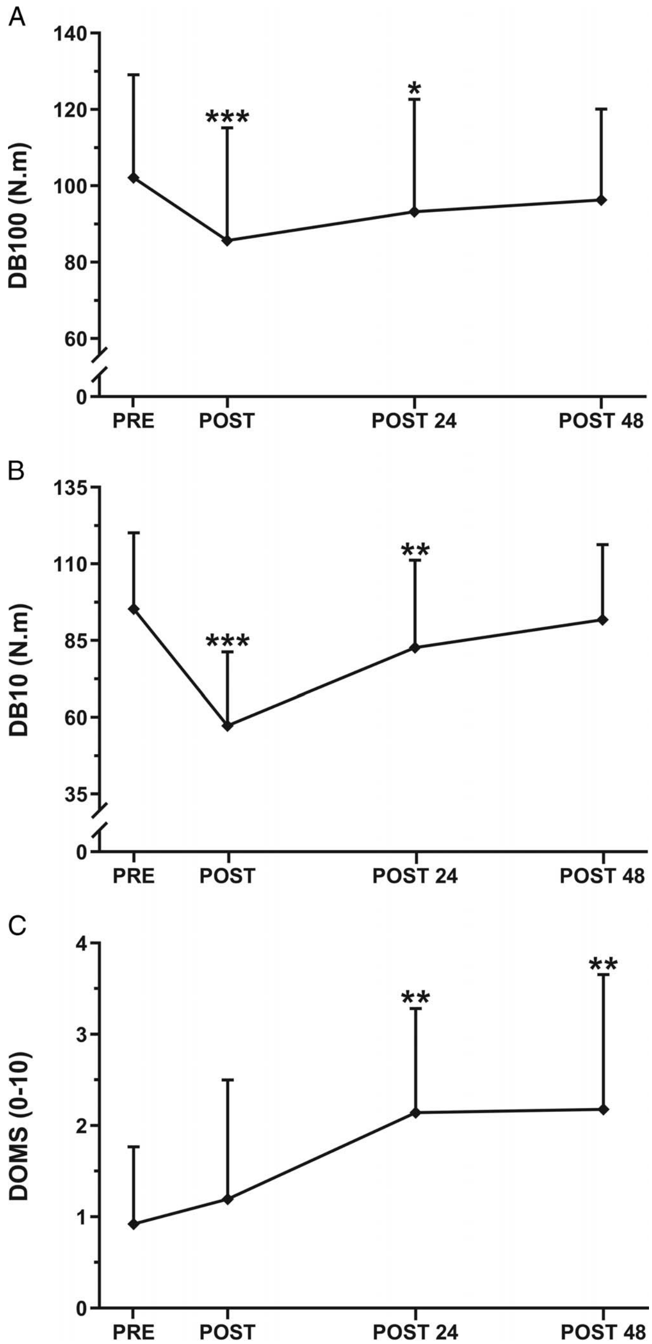

FIGURE 3—Electrically evoked torques (DB100 [A] and DB10 [B]) and DOMS (C) measured before (PRE), immediately after (POST), 24 h after (POST24), and 48 h after (POST48) the fatiguing unilateral eccentric exercise. *$P < 0.05$, **$P < 0.01$, and ***$P < 0.001$, significant differences from PRE values for the parameter considered.

at POST24 and at POST48 ($P < 0.01$; Fig. 3C) compared with PRE.

Perceived fatigue scores were significantly increased at POST compared with PRE ($F_{3,\ 36} = 11.1$, $P < 0.001$, $\eta_p^2 = 0.48$; Fig. 2D). A tendency to a significant correlation fitting a linear function was found between the score of perceived fatigue and VA decreases at POST ($r = -0.54$, $P = 0.06$).

DISCUSSION

The main purpose of this study was to investigate the potential link between eccentric-induced central fatigue and position sense alterations. For this purpose, bilateral position-matching tasks at the knee and neuromuscular tests of KE muscles intended to characterize fatigue origins were performed. These measurements were carried out before, immediately after, and 24 and 48 h after a submaximal eccentric fatiguing exercise. In line with our assumptions, the submaximal eccentric exercise induced an acute (i.e., POST) decrease in VA (i.e., central fatigue) that was significantly correlated with position sense alterations (Fig. 4), only for the JPM_{70} task. Despite the presence of peripheral fatigue and DOMS (Fig. 3) in the following days (i.e., POST24 and POST48), position-matching errors returned to PRE values (Fig. 2C).

The 20% MVIC reduction induced by our submaximal fatiguing eccentric exercise at POST was associated with both central and peripheral fatigue, as observed in previous studies generating similar decreases in MVIC (4–9). In addition to these MVIC decreases, ECC and CON were reduced to a similar extent (i.e., 19% and 18%, respectively) and agreed with other studies (4,8,9). Except for ECC, MVIC and CON were still significantly depressed at POST48 (6,8,9). Acute and delayed (i.e., POST and POST24, respectively) peripheral fatigue, as highlighted by significant decreases in DB10 and DB100, was observed after the exercise and recovered to PRE values at POST48. Consistent with previous research (4–6), we observed a 30% lower DB10:100, which is an indicator of low-frequency fatigue. All these observations account for excitation–contraction coupling failure, possibly including reduced calcium release from the sarcoplasmic reticulum, decreased calcium sensitivity and/or force production of the cross-bridges (31), as well as structural damage to muscle fibers (32). Persisting peripheral fatigue at POST24, reduced MVIC until POST48 and significant DOMS noted at POST24 and POST48 (Fig. 3C) suggest the presence of persisting delayed muscle damage (10).

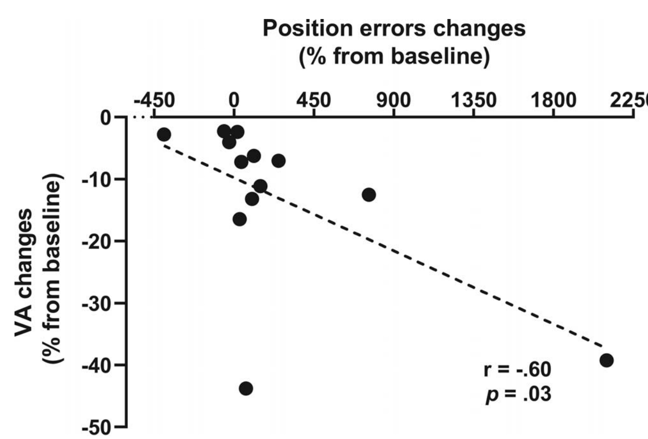

FIGURE 4—Correlation between VA changes and bilateral position-matching errors changes of the JPM_{70} task measured immediately after the fatiguing eccentric exercise (POST).

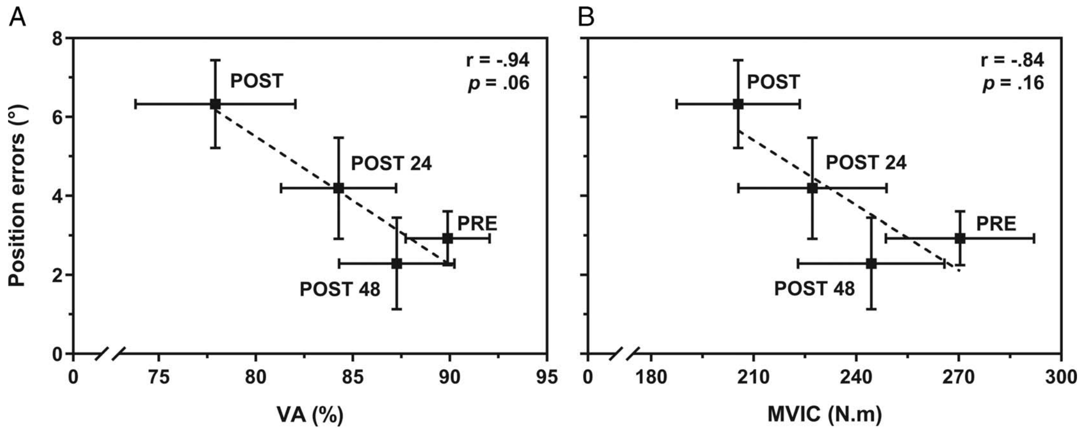

FIGURE 5—Correlations between VA (A) and MVIC (B) and bilateral position-matching errors of the JPM_{70} task measured before (PRE), immediately after (POST), 24 h after (POST24), and 48 h after (POST48) the fatiguing unilateral eccentric exercise. Note that for these correlations, the two values obtained at POST and POST′ for MVIC and VA were averaged.

Contrary to the persisting peripheral fatigue, central fatigue was only present at POST as shown by the 13% VA decrease. This acute VA failure indicates the presence of alterations in the neural pathways upstream the neuromuscular junction that can be related to several neural adjustments at both spinal and supraspinal levels leading *in fine* to modulations of α-motoneuron excitability (2). Although the recording of VA does not allow distinguishing spinal from supraspinal adaptations, increased discharge rate of group III and group IV afferents (33,34) could modulate descending central drive via presynaptic inhibition of group Ia afferents and inhibition of α-motoneuron. These afferents have also been proposed to induce neural adjustments in supraspinal structures (35) partially evidenced in recent studies after submaximal fatiguing eccentric exercise (5,7). In addition, perceived fatigue was significantly increased at POST, and this subjective sensation tended to be significantly correlated with the decreased VA. Consequently, and whatever the exact mechanism involved, our submaximal fatiguing eccentric exercise led to an acute central failure that reduced the participants' capacity to recruit their KE muscles fibers.

A key point of this study is that the position errors during the JPM_{70} were only significant in the presence of central fatigue with significant correlations between the VA deficits and the degree of position errors at POST (Fig. 4). Furthermore, the correlation presented in Figure 5 underscores a linear evolution between VA levels and position errors over the four time points. Finally, in contrast to the observations of Givoni et al. (21), in our study, position errors were better correlated with VA levels than with MVIC (Fig. 5). These different outcomes emphasize the role of central fatigue in position sense disturbance. As proposed earlier with thorough explanations (i.e., internal model disturbances and body map distortion), the central disturbances caused by fatigue could be responsible for the position sense alterations observed after our eccentric exercise (21,23). Group III and group IV afferents, similar to group Ia and group II afferents, are integrated at the level of the somatosensory cortex (36). With the development of muscle fatigue, the neural flow of III and IV afferents signals reaching the somatosensory cortex increases. This important neural flow could affect the integration and the processing of Ia and II afferents and consequently participate in position sense alterations. Knowing that the integration of the afferents signals gives rise to the unpleasant muscle sensations caused by the exercise (37), one can argue that the increased perceived fatigue observed here could also account for the greater errors of the bilateral position-matching task. Therefore, in addition to central alterations that led to a force production capacity decreased, it is very likely that central fatigue affects both fatigue perception and the sensory functions (1).

Despite a long-lasting MVIC decrease and the presence of DOMS up to 48 h postexercise, position errors were not significant at POST24 and POST48. This demonstrates that muscle damage might not be involved in the impairment of joint position perception. This also strengthens the observation that position sense alterations are due to the central perturbations. The current results also clearly demonstrate that effort cues are not used to match the positions across limbs, as proposed earlier (19). Indeed, the greater EMG RMS values in the fatigued indicator limb during the JPM_{70} at POST showed that participants generated higher neural outputs toward their fatigued KE muscles to match the reference position. This necessarily implies that they generated a different effort to activate their muscles (i.e., a greater effort to reach and maintain this position in their fatigued indicator limb as compared with the reference one).

Interestingly, the position sense was unaffected by the fatiguing exercise during the JPM_{30}. Various explanations for this observation can be found. First, the tested angle was very close to the starting position that may have contributed to allowing participants to memorize the displacement of the reference limb more easily than for the displacement until 70° and thus to less important position-matching errors in the direction of extension. Perhaps starting trials at 90° of knee flexion would have led to different results. Second, the tested angle of 30° was not far from the complete extension. The

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results obtained by Givoni et al. (21) could reinforce this idea because they observed that position-matching errors were less important at 50° than at 70°. In any event, although nonsignificant, errors led in the same direction as at 70° and progressively decreased in the days after the submaximal eccentric exercise. The absence of significant errors at 30° may hardly be attributed to methodological issues in that we gave a considerable importance to muscle conditioning before the bilateral-matching trials. Conditioning muscles is intended to control the thixotropy of muscle spindles, a property by which spindle stiffness varies depending on the recent contractile history of muscles and which can critically affect the firing of spindle afferents (17). For example, a differential conditioning between limbs can lead to position errors up to 10° (15). Therefore, during the bilateral position-matching tasks, in which position estimations are performed based on a comparison between spindle signals from the two limbs, it was crucial to avoid any misinterpretations related to thixotropy, to put spindles in a similar thixotropic state across limbs.

Historical overview. Numerous hypotheses have been put forward regarding the mechanisms responsible for position sense alterations during muscle fatigue in the last decades, especially after damaging-eccentric exercise. Pioneer studies attributed the alterations of the joint position sense to eccentric-induced damages in intrafusal fibers and in tendon organs (18,38). More recent studies performed on cats showed that the eccentric exercise does not alter the functions of muscle spindles and tendon organs (16,39), discrediting, to some extent, the peripheral hypothesis. Later, it was proposed that joint positions were perceived through a sense of effort and that fatigue-induced misperceptions were due to an alteration between effort and muscle activation (19,20). Yet, this hypothesis fell short after the study of Givoni et al. (21) on the lower limbs. These authors associated the alterations of the sense of position to a central disturbance involving internal models. Since then, the hypotheses have been narrowed and remain focused on alterations occurring within the brain (21,23), especially in the somatosensory cortex (22). In the present study, and in line with these explanations, we assume that central fatigue affects the integration and the processing of muscle spindle afferents.

CONCLUSION

Based on previous experiments, we designed a study that assessed for the first time the effects of a submaximal eccentric fatiguing exercise on the position sense with concomitant investigation of the neuromuscular function to determine the central and peripheral origins of fatigue. Our results showed that the eccentric exercise of the KE muscles only affected the position sense in presence of central fatigue, (i.e., in the minutes after the eccentric exercise). Because of the lack of position-matching errors at POST24 and POST48, our results also highlight that the damages caused to the extrafusal fibers did not affect intrafusal fibers, reinforcing the idea that muscle spindles are protected from damages during eccentric exercises (40). In addition to the decreased capacity to generate maximal force, this leads us to assume that central fatigue affects the sensory structures responsible for the integration and the processing of position-related sensory inputs. Future experiments should be designed (i) to evaluate the effects of central fatigue induced by other contraction modes on the position sense and (ii) to investigate the impact of central fatigue on the integration and processing of proprioceptive signals at a cortical level.

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