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RESEARCH ARTICLE

Voluntary and electrically-induced muscle fatigue differently affect postural control mechanisms in unipedal stance

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Abstract

The repetition of muscle contractions is likely to generate fatigue which can provoke alterations of postural control. Regulatory mechanisms can be triggered to counteract these alterations. However, these mechanisms would occur only when fatigue is induced through voluntary (VOL) contractions and not with electrically stimulated (ES) contractions. Hence the aim was to compare the effects of VOL and ES fatiguing contractions inducing a similar level of strength loss on unipedal postural control (assessed by means of force platform and EMG measurements), maximal voluntary contraction (MVC) and central activation ratio (CAR) to characterize the alterations induced by both modalities of fatigue and the associated regulatory mechanisms. Results showed that the VOL exercise induced a significant decrease of the CAR whereas the ES exercise did not, thus illustrating that central fatigue was present only after voluntary contractions. The VOL exercise also induced greater postural disturbances and larger regulatory mechanisms than the ES exercise, which also induced postural regulatory mechanisms. The present study reveals that postural control mechanisms are modulated according to the nature of the fatiguing contractions, likely due integration of specific fatigue signals according to the modality of the contraction. Because of a larger neurophysiological impact of VOL than ES fatiguing contractions due to greater central disturbances, VOL exercise-induced larger regulatory mechanisms. Nevertheless, the presence of regulatory mechanisms with ES contractions clearly underlines the ability of the central nervous system to display an accurate motor control following acute externally induced neuromuscular perturbations.

Keywords Muscle fatigue · Electrically stimulated contractions · Voluntary contractions · Posture · Balance · Motor control

Introduction

Muscle fatigue can be defined as a disturbance of motor output related to peripheral factors that impair muscle contractile properties and central factors arising within the central nervous system (CNS), with an alteration of the number of motor units recruited for the action as well as the rates at which they discharge action potentials (Bigland-Ritchie and Woods 1984; Contessa et al. 2016). Hence, disturbances can be characterized by a central fatigue i.e. alterations of activation of primary motor cortex, propagation of the descending command, excitability of spinal motoneurons and/or by a peripheral fatigue i.e. alterations of transmission across the neuromuscular junction, excitation–contraction coupling, availability of energetic substrates, hydrogen ion concentration, or formation of cross-bridges (Bigland-Ritchie and Woods 1984). Muscle fatigue can be identified on the basis of a decrease in muscle force, muscle-velocity capacities, a variation in electromyographic (EMG) activity and a degradation of voluntary activation level (Gandevia 2001; García-Ramos et al. 2018). From a functional viewpoint, muscle fatigue leads to a drop in maximal voluntary contraction (MVC) force but also to an increase in motor variability and changes in motor coordination and movement parameters (Huffenus and Forestier 2006; Singh and Latash 2011). This explains why fatigue alters motor performance not only in maximal tasks but also in sub-maximal tasks as well as in finer motor tasks such as postural control (Paillard et al. 2010c; Paillard 2012).

Adaptive neuromuscular strategies can be implemented to counteract or limit the disturbance of postural control

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due to central and/or peripheral fatigue (Paillard 2012; Monjo and Forestier 2015). A reorganization of multijoint coordination usually occurs, characterized by a redistribution of the contribution of active muscles, with an increased demand on the non-fatigued muscles which compensates for the neuromuscular deficit of the fatigued muscles (Bonnard et al. 1994; Gribble and Hertel 2004; Ritzmann et al. 2016). However, these regulatory mechanisms would occur only when fatigue is induced through voluntary (VOL) contractions (Monjo and Forestier 2015). When fatigue is generated through neuromuscular electrical stimulation (ES), the CNS would gate or not interpret the fatigue signals, which consequently prevents any possibility of accurate feedforward postural control, thus resulting in the absence of any motor reorganization (Monjo and Forestier 2015). Nevertheless, when comparing the effects of VOL and ES fatiguing muscular contractions of the quadriceps femoris on postural control, Paillard et al. (2010a) observed that postural control was disturbed more after VOL than after ES muscular contractions. Even though the experimental models were different between the studies of Paillard et al. (2010a) and Monjo and Forestier (2015) (quiet stance paradigm with postural sway measurements versus self-paced arm-raising movements with anticipatory postural adjustments evaluation), taken together, these results suggest that postural control would be more affected after VOL than after ES fatiguing muscular contractions (Paillard et al. 2010a) in spite of more efficient fatigue-related adaptive mechanisms when using VOL than when using ES contractions (Monjo and Forestier 2015). At first glance, these results are not consistent in terms of postural adaptations, and thus deserve to be clarified.

One possible mechanistic explanation could be that fatigue induced by VOL and ES contractions differently affects central drive (Chaubet et al. 2013). More specifically, ES contractions are likely to induce delayed central fatigue compared to VOL contractions, which produce earlier central fatigue (Chaubet et al. 2013). Moreover, it is known that ES and VOL muscular contractions do not produce similar strength loss even though fatiguing exercises are performed with equal duration and intensity (Paillard et al. 2010a, b; Chaubet and Paillard 2012). The effects of fatigue on postural control also depend on the cross-sectional area of the fatigued muscles, the larger the size, the more perturbed the postural control (Bizid et al. 2009). Hence, the unequal strength loss between VOL and ES fatigue in the study of Paillard et al. (2010a) and the large volume-differences between the muscles fatigued in the studies of Paillard et al. (2010a) and Monjo and Forestier (2015) (Quadriceps Femoris vs. Deltoid) can act as confounding factors rendering difficult any reliable and accurate comprehension of the specificity of the postural regulation mechanisms induced by fatigue with ES and VOL contractions.

Therefore, the aim of this study was to compare the effects of VOL and ES fatiguing contractions on postural control, while standardizing the location (i.e. knee extensors) and the magnitude of the muscle fatigue (i.e. equated level of strength loss). A protocol combining assessments of MVC, central activation ration (CAR) and postural control with force platform and EMG measurements was performed to accurately characterise the alterations induced by both modalities of fatigue (impact on central drive and motor output) and the associated postural regulatory mechanisms. Because central command is a sine qua non condition for VOL but not for ES fatiguing contractions, we hypothesized that central fatigue would be greater after VOL than after ES fatiguing contractions, thus inducing a greater disturbance on the postural control system which would display a motor reorganization only with VOL contractions.

Methods

Ethical approval

All subjects gave their written informed consent to participate in the experiment, which was approved by the University's Institutional Review Board in accordance with the Declaration of Helsinki.

Participants

Seventeen healthy males participated in the study (age 20.4 ± 1.8 years; height 179.7 ± 8.2 cm; body weight 75.9 ± 9.2 kg). Exclusion criteria included a documented postural control disorder or a medical condition that might affect postural control, a neurological or a musculoskeletal impairment in the past 2 years, or current injury making the subjects unable to participate. Participants had to continue their habitual physical activity between the test sessions without taking part to a new physical activity. They were asked to avoid strenuous activity and did not eat and drink excitatory substances 24 h prior to the data collection sessions.

Protocol

The experiment began with a warm-up exercise which consisted of 12 min of pedaling on a cycle ergometer (Monark® Ergomedic E874, Vansbro, Sweden), with a first 5 min phase at a 45–55% maximal heart rate (MHR) target, a second 5 min phase at a 65–75% MHR target and a last 2 min at a 75–85% MHR target. The heart rate was monitored by a heart rate transmitter (Polar© M400, Kempele, Finland).

Then, postural control, isometric MVC and CAR were assessed on the supporting limb (PRE condition). These assessments were repeated immediately after a fatigue protocol (POST condition) and after 5 min, 10 min and 20 min of recovery (respectively POST5, POST10 and POST20 conditions). The fatiguing protocol consisted in two different exercises: voluntary muscular contractions (VOL) and by electrically-induced or stimulated muscular contractions (ES). A randomized cross-over study design was adopted, in which each participant completed each fatiguing exercise (VOL and ES) separated by a period of 6–31 days.

Postural control assessment

Participants were asked to stand barefoot as still as possible on their supporting leg with their arms crossed on their chest in a unipedal stance for 25 s on a force platform (Techno-Concept, Feet-test©6, FRANCE) which recorded the centre of foot pressure (COP) at 40 Hz. When the participants had a dominant right leg for kicking a ball, then the left leg was the supporting leg (inversely when the subjects had a dominant left leg). Surface EMG activity of the following muscles was recorded during the postural task at 1000 Hz (CMMR > 100 dB; input impedance 1 MΩ) with the PowerLab 16/35 data acquisition system (ADInstruments, Castle Hill, Australia) with a resolution of 16 bits using a g.BSamp biosignal amplifier (g.tec, Schiedlberg, Austria): Soleus (SOL), Gastrocnemius Medialis (GM), Tibialis Anterior (TA), Vastus Medialis (VM) and Biceps Femoris (BF). After appropriate skin preparation, pre-gelled self-adhesive disc bipolar Ag/AgCl surface (10 mm recording diameter) electrodes (Kendall Meditrace 100, Covidien, Mansfield, USA) were positioned on the supporting leg of the subjects with 2 cm centre-to-centre spacing according to SENIAM's recommendations (http://www.seniam.org). The foot was placed according to precise landmarks with respect to the medio-lateral (X) and antero-posterior (Y) axes of the platform. Participants were asked to raise the unsupported leg with a 90° knee flexion angle. The two hips were placed in a neutral position (0° of flexion). Participants first performed two familiarization trials in the postural test to avoid any learning effect and to achieve a stable postural score on unipedal stance which was obtained in the third trial within a single test session (Cug and Wikstrom 2014).

From COP signals, the COP surface area (mm^2) and the mean COP velocity (the total COP displacement divided by the total time, in mm.s^{-1}) on the medio-lateral and antero-posterior axes (COPx and COPy velocity respectively) were calculated. It is commonly admitted that the smaller these parameters, the better subjects' ability to minimize and control postural sway (Paillard and Noé 2015).

The raw EMG signals were digitally processed with Matlab R2015b (The Mathworks Inc., Natick, USA) by applying a band-pass filter (fourth-order Butterworth filter, 20–400 Hz). The EMG activity of each muscle was then assessed by computing its root mean-square (RMS) value over the whole trial.

Maximal voluntary contraction assessment

The MVC of the quadriceps of the supporting leg was measured on an ergometer (Leg extensor, Panatta Sport™, Apiro, Italy) in each condition (PRE, POST, POST5, POST10, POST20). This device was equipped with a force sensor (Model SSM Series, PM Instrumentation™, Courbevoie, France) attached to the participants' ankle. Force signals were recorded with a Biopac MP100 data acquisition system (Biopac Systems, Inc, Santa Barbara, USA) at a 200 Hz sampling frequency. Participants sat with a 90° knee flexion and a 90° hip flexion, measured with a goniometer (Comed®, Strasbourg, France). The depth of the seat was fitted to the length of the subjects' thighs. Subjects were strongly attached with straps positioned across the pelvis and chest. Participants were asked to perform two MVC each of 6 s, separated by 30 s while receiving verbal encouragement. The best performance was recorded. Two familiarization trials preceded the test.

Central activation ratio assessment

Four rectangular self-adhesive conducting electrodes (Compex®, 50 mm x 50 mm, USA; Sport-Elec®, 89 × 50 mm, France) were placed over the motor point of the vastus medialis, vastus lateralis and rectus femoris muscles, and one electrode was placed on the proximal part of the quadriceps across the vastus lateralis and rectus femoris. To quantify central activation failure during each MVC, an electrical stimulation (STIM) was triggered manually after force plateau (i.e. after 3 s), for a duration of 3 s. Muscles were stimulated using biphasic symmetrical rectangular waves (pulse duration 450 µs; 100 mA, frequency 80 Hz) while using a high-voltage constant-current stimulator (model DS7, Digitimer, Hertfordshire, UK). CAR was calculated according to the following equation (Kent-Braun and Le Blanc 1996):

CAR = MVC/(MVC + STIM), where MVC + STIM = voluntary + stimulated forces.

In the case where there was no increase in force during the electrical stimulation, CAR = 1.0 and voluntary activation was considered as complete.

Fatiguing exercise

Two minutes after the MVC and CAR tests (in the PRE condition), participants began the fatigue exercise which was only completed with the supporting leg. The fatiguing exercise consisted in repeating 5 s isometric knee extension followed by 2 s of recovery. There were two modes of exercise: VOL and ES. Electrostimulation was completed with a portable stimulator (Cefar™ Rehab 4 Pro®, Lund, Sweden), which delivered a biphasic symmetrical rectangular wave current with a 350 µs pulse duration and a 50 Hz frequency. The electrodes that were used to assess the central activation ratio were used in the ES fatiguing exercise. The intensity of the contraction was set at a target force value of 20% of MVC force (determined from PRE MVC test) and controlled on-line on a computer screen using the AcqKnowledge® software (Biopac Systems, Inc, Santa Barbara, USA). The knee extension continued until the force output dropped below the 20% MVC target force value for three consecutive repetitions, despite strong verbal encouragement by the investigators in the VOL condition or an increase of the intensity of electrostimulation to maintain the 20% of force level in the ES condition. The exercise duration was recorded as the time to task failure. The rating of perceived exertion (RPE) was assessed according to the Borg scale (from 6 to 20) -on the basis of identical verbal instructions for both exercises- immediately after the completion of the fatiguing exercise (Borg 1990). The experimental set-up was organised to limit subjects' displacement and to perform the MVC, CAR and postural assessments as quickly as possible after the fatiguing exercise.

Statistical analysis

Normality was tested using the Shapiro–Wilk test. As most of the variables did not meet the assumption of normal distribution, non-parametric tests were applied and data were expressed as median (interquartile range—IQR). For each fatiguing exercise (VOL and ES), MVC, CAR, EMG and COP parameters were analysed using a Friedman test to characterise a fatigue effect. The follow-up of the Friedman test was performed by means of Nemenyi's multiple comparisons to evaluate the differences between each condition (PRE, POST, POST5, POST10 and POST20). Wilcoxon signed rank tests for paired samples were used to determine differences between VOL and ES exercises for each parameter in each condition. Wilcoxon signed rank tests were also used to compare the time to task failure and the RPE between VOL and ES exercises. Results were considered significant for $P<0.05$.

Results

VOL exercise

The Friedman test revealed a significant fatigue effect regarding the MVC (X^2 $(4)=42.49$; $P<0.001$), the CAR ($X^2(4)=25.682$; $P<0.001$), the COP surface ($X^2(4)=16.329$; $p<0.003$), the COPx velocity (X^2 $(4)=12.8$; $P<0.02$), the COPy velocity (X^2 $(4)=17.271$; $P<0.002$), the EMG of the TA (X^2 $(4)=14.447$; $P<0.006$), SOL (X^2 $(4)=23.247$; $p<0.001$) and BF (X^2 $(4)=10.118$; $P<0.04$) muscles.

As illustrated on Fig. 1, the MVC was significantly higher at PRE than at POST ($P<0.001$), POST5 ($P<0.001$) and POST10 ($P<0.001$). MVC values at POST20 were higher than at POST ($P<0.002$) and POST5 ($P<0.03$). Results of CAR are presented in Fig. 2. A significant difference of the CAR was observed between PRE and POST5 $P<0.002$) and between PRE and POST10 ($P=0.01$), with higher values in the PRE condition.

As illustrated on Fig. 3, COP surface showed a significant increase between PRE and POST ($P<0.002$) and a significant decrease between POST and POST10 ($P<0.03$). Data from COP velocities revealed significant rises between PRE and POST for both the COPx ($P<0.04$) and COPy velocity ($P<0.003$). Significant reductions between POST and POST10 ($P<0.007$) and between POST and POST20 ($P<0.04$) were also observed for the COPy velocity. Concerning the EMG signals (Fig. 4), results revealed a significant increase of the RMS value of the TA and SOL muscles between PRE and POST (TA: $P<0.007$; SOL: $P<0.001$). For the SOL muscle, there was also a significant difference between PRE and POST5 ($P<0.005$) and between PRE and POST20 ($P<0.02$).

ES exercise

The Friedman test revealed a significant fatigue effect for the MVC ($X^2(4)=57.074$; $P<0.001$), the COPx velocity (X^2 $(4)=18.494$; $P<0.001$), the COPy velocity (X^2 $(4)=15.671$; $P<0.004$), the EMG of the SOL (X^2 $(4)=14.588$; $P<0.006$), VM (X^2 $(4)=14.4$; $P<0.007$) and BF (X^2 $(4)=10.118$; $P<0.04$) muscles. There were no significant effects of fatigue for the CAR (Fig. 2) and for the COP surface (Fig. 3).

The MVC decreased significantly after the fatiguing exercises (POST condition) compared to the PRE condition ($P<0.001$) and remained lower in POST5 ($P<0.001$) and POST10 ($P<0.006$) conditions than in PRE. A first sign of recovery was observed at POST10 since the MVC values were significantly higher than in POST ($P<0.002$). At POST20, the MVC values remained significantly different from those observed at POST ($p<0.001$) (Fig. 1).

The COPx velocity significantly increased between PRE and POST ($P<0.02$) whereas it significantly decreased between POST and POST20 ($P<0.002$). Data from COPy velocity revealed a significant decrease between POST and POST20 ($P<0.002$) (Fig. 3). When focusing on the

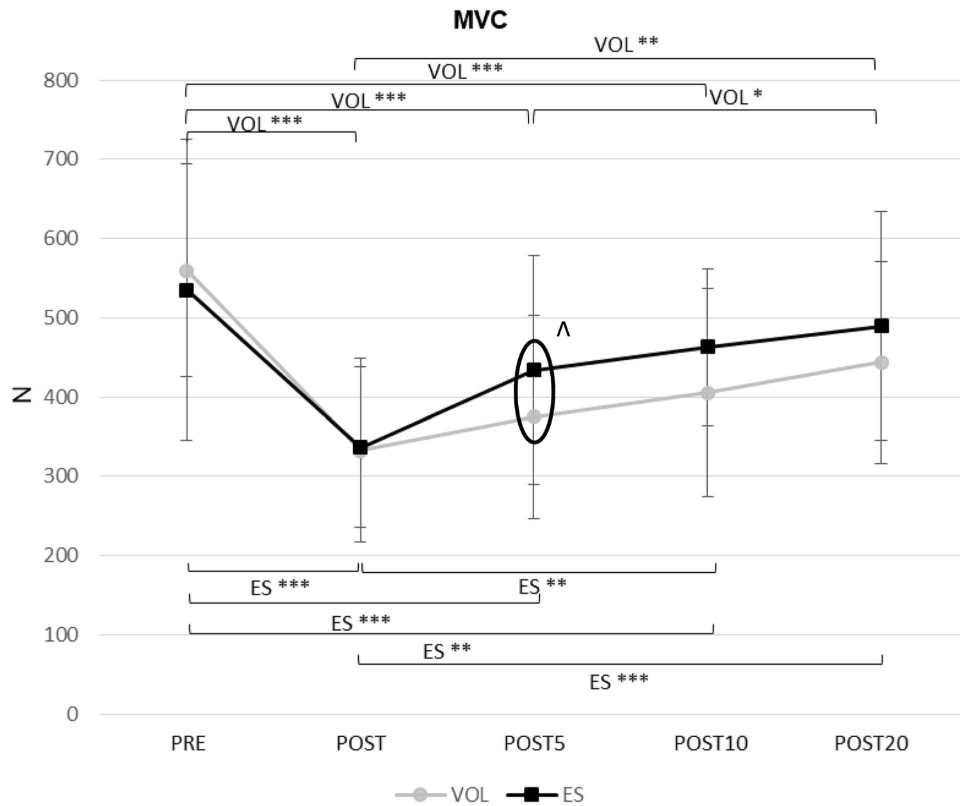


Fig. 1 Effects of two fatiguing exercises (VOL and ES) on maximal voluntary contraction (MVC). Filled circles and squares represent the median value (error bars: interquartile range) for the VOL and ES exercises, respectively, in five conditions (PRE, POST, POST5, POST10, POST20). * indicates significant pairwise differences between the conditions in each exercise modality (***$P<0.001$; **$P<0.01$; *$P<0.05$). $^{\Delta}$indicates significant differences between the VOL and ES exercises in a specific condition - visualized by an ellipse ($^{\Delta\Delta\Delta}P<0.001$; $^{\Delta\Delta}P<0.01$; $^{\Delta}P<0.05$)

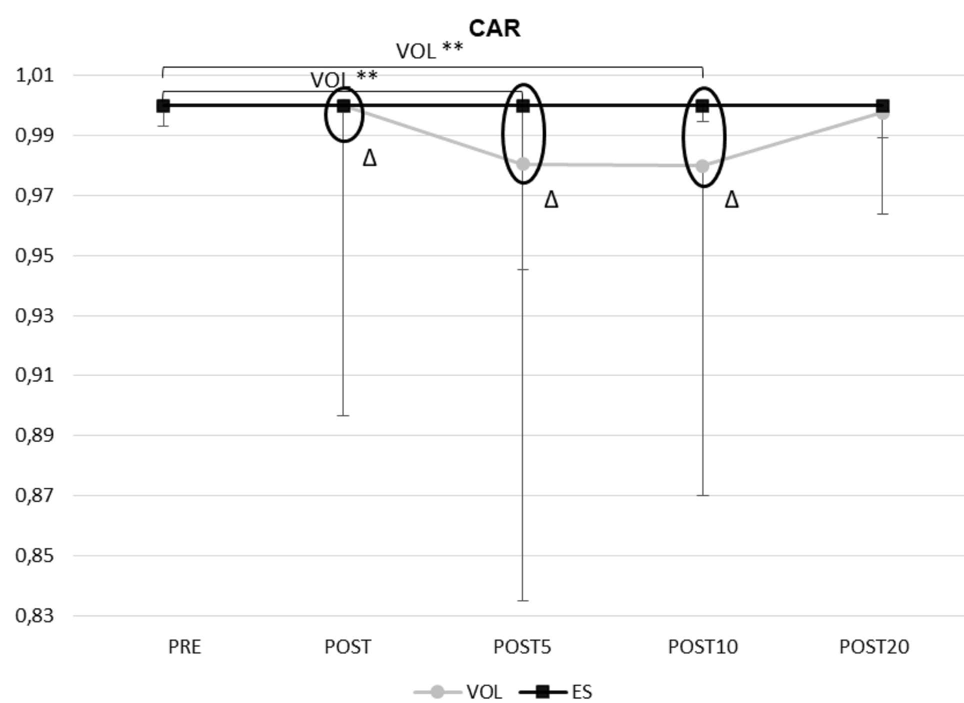
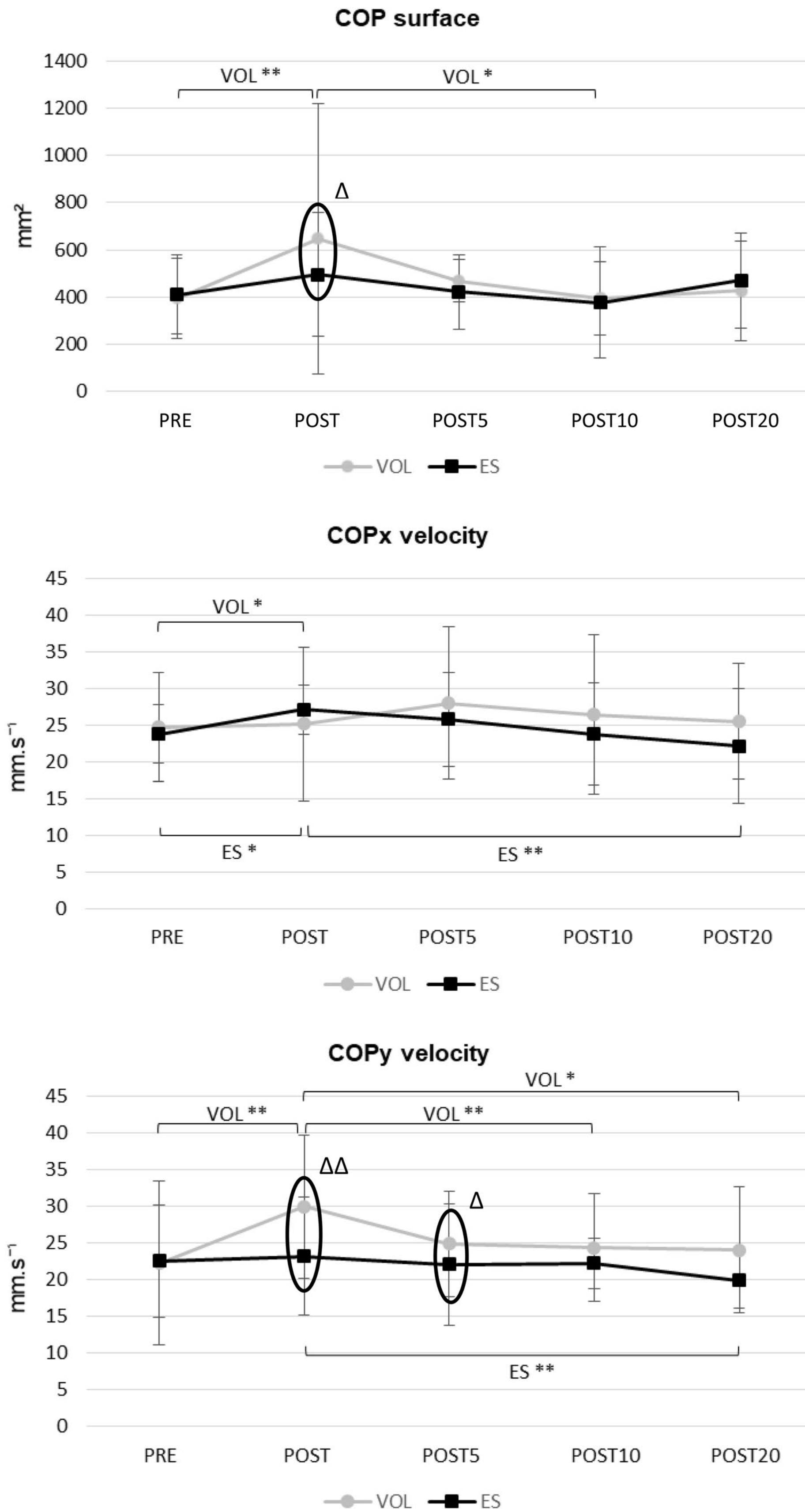


Fig. 2 Effects of two fatiguing exercises (VOL and ES) on the central activation ratio (CAR). Filled circles and squares represent the median value (error bars: interquartile range) for the VOL and ES exercises, respectively, in five conditions (PRE, POST, POST5, POST10, POST20). * indicates significant pairwise differences between the conditions in each exercise modality (***$P<0.001$; **$P<0.01$; *$P<0.05$). $^{\Delta}$ indicates significant differences between the VOL and ES exercises in a specific condition—visualized by an ellipse ($^{\Delta\Delta\Delta}P<0.001$; $^{\Delta\Delta}P<0.01$; $^{\Delta}P<0.05$)

EMG activity of the thigh and leg muscles during the postural task, the RMS value of the EMG signal of the SOL muscles was significantly higher at POST ($P<0.04$) and POST5 ($P<0.004$) than at PRE. The RMS value of the VM muscle EMG signal was reduced at POST20 compared to POST5 ($P<0.007$) (Fig. 4).

Fig. 3 Effects of two fatiguing exercises (VOL and ES) on postural parameters. Filled circles and squares represent the median value (error bars: interquartile range) for the VOL and ES exercises, respectively, in five conditions (PRE, POST, POST5, POST10, POST20). * indicates significant pairwise differences between the conditions in each exercise modality (***$P < 0.001$; **$P < 0.01$; *$P < 0.05$). $^{\Delta}$ indicates significant differences between the VOL and ES exercises in a specific condition—visualized by an ellipse ($^{\Delta\Delta\Delta}P < 0.001$; $^{\Delta\Delta}P < 0.01$; $^{\Delta}P < 0.05$)



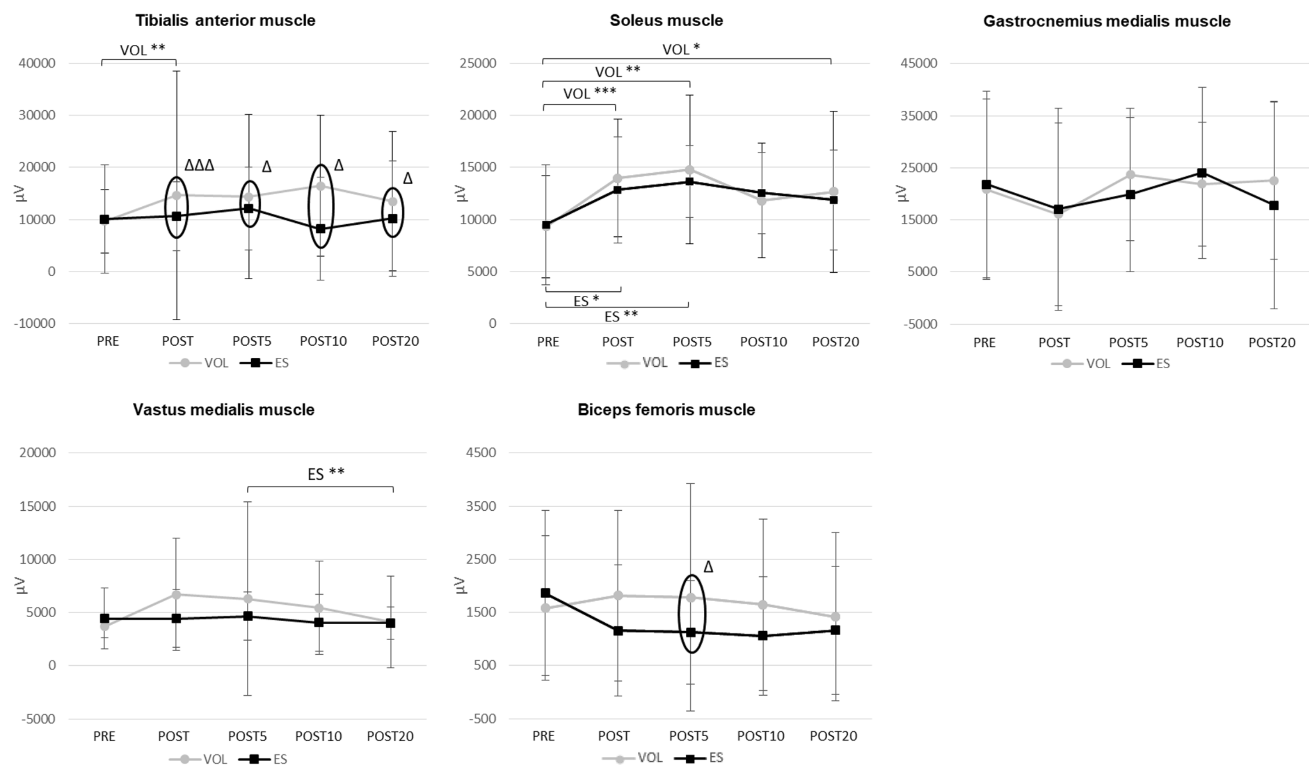


Fig. 4 Effects of two fatiguing exercises (VOL and ES) on EMG RMS. Filled circles and squares represent the median value (error bars: interquartile range) for the VOL and ES exercises, respectively, in five conditions (PRE, POST, POST5, POST10, POST20). *indicates significant pairwise differences between the conditions in each exercise modality (***$P<0.001$; **$P<0.01$; *$P<0.05$). $^{\Delta}$indicates significant differences between the VOL and ES exercises in a specific condition—visualized by an ellipse ($^{\Delta\Delta\Delta}P<0.001$; $^{\Delta\Delta}P<0.01$; $^{\Delta}P<0.05$)

VOL vs ES

The different fatigue modalities did not result in a similar duration of exercise. With median durations of 41.53 min (IQR = 37.71) and 6.95 min (IQR = 5.17) respectively, the exercise was significantly longer with VOL than with ES muscular contractions (V = 153; $P<0.001$). Values of RPE were not significantly different between VOL (17, IQR = 3) and ES (17, IQR = 3) exercises.

Results about MVC revealed a significant difference in POST5 condition only (V = 34; $P<0.05$) with a greater MVC for the ES exercise (Fig. 1). Differences were more marked for the CAR since significantly higher values were observed for the ES than for the VOL exercise in POST (V = 4; $P<0.04$), POST5 (V = 17; $P=0.05$) and POST10 (V = 8; $P<0.02$) conditions (Fig. 2).

Considering the COP parameters, both the COP surface (V = 120; $P<0.04$) and the COPy velocity (V = 130; $P<0.01$) were significantly higher in VOL than in ES in the POST condition (Fig. 3). The COPy velocity was also significantly higher in VOL than ES in the POST5 condition (V = 124; $P<0.03$). No significant differences were observed for the COPx velocity between the VOL and ES exercises. When focusing on the EMG signals, the TA muscle demonstrated a significantly higher level of activation in VOL than in ES in POST (V = 142; $P<0.001$), POST5 (V = 127; $P<0.02$), POST10 (V = 123; $P<0.03$) and POST20 (V = 120; $P<0.04$) conditions. Moreover, the RMS value of the BF muscle was significantly higher in VOL than in ES in POST5 condition (V = 108; $P<0.04$) (Fig. 4).

Discussion

The aim was to compare the effects of standardized VOL and ES fatiguing contractions (while equating the level of strength loss) on postural control, MVC and CAR to accurately characterise the alterations induced by both modalities of fatigue and the associated postural regulatory mechanisms. Since central fatigue would be greater after VOL than after ES fatiguing contractions, the hypothesis was that VOL contractions would have a greater disturbance than ES contractions on the postural control system which would display a motor reorganization only with VOL contractions. This hypothesis was partially confirmed by our results since VOL contractions induced greater postural disturbances than

ES contractions, but the ES fatiguing exercise also induced a motor reorganization.

Following the different fatiguing exercises which induced the same muscle strength loss, results showed that the restoration of MVC strength began earlier with the ES than with the VOL exercise, since first signs of recovery were observed at POST10 for the ES exercise whereas they were observed at POST20 for the VOL exercise (differences between the POST and the POST 10 and POST 20 conditions respectively). Moreover, only the VOL exercise induced a significant decrease of the CAR, which presented lower values in POST5 and POST10 than in the pre-fatigue condition, thus illustrating that central fatigue was present only after voluntary contractions (Kent-Braun 1999; Chaubet et al. 2013), which could explain the longer MVC recovery time observed with the VOL exercise. Central disturbance results from changes related to intrinsic cortical processes and/or descending drive and/or excitability of spinal motoneurons (Taylor et al. 1996, 2006). However, in the case of central fatigue, it is possible that voluntary drive can increase cortical output but it cannot achieve the levels necessary to overcome the reduced responsiveness of the spinal motor apparatus (Rothwell 2009). This could explain why the EMG activity of leg muscles (i.e., TA and SOL) increased more after the VOL exercise than after the ES exercise to limit the altering effects of fatigue on postural control. The fact that VOL contractions totally depend on central command whereas ES contractions are independently and artificially generated without any central drive's involvement can be viewed as the main cause of a central fatigue with VOL contractions (Hortobagyi et al. 1999; Paillard et al. 2010b). Nevertheless, the longer duration of exercise in voluntary mode (41.53 min time to task failure) than in stimulated mode (6.95 min time to task failure) can constitute another potential origin of central fatigue presence with VOL exercises that could have impacted motor control of ankle muscles. It has been reported that the longer the exercise, the more important the central fatigue for a given exercise intensity (Paillard et al. 2014; Froyd et al. 2016). The longer duration of exercise with the VOL exercise could be related to the fact that for a given submaximal muscular contractions intensity, the energy cost of force development is higher for stimulated than for voluntary contractions (Vanderthommen et al. 2003). These authors have shown that stimulated contractions degrade glycogen reserves, acidify the cytoplasm and reduce the intracellular pH more than voluntary contractions. However, our results suggest that despite this higher glycolytic activity induced by stimulated contraction, ES exercise did not generate a greater peripheral fatigue since MVC values remained lower for the VOL exercise than for the ES exercise after 5 min of recovery. This lower value of muscle strength could also result from the longer duration of exercise in voluntary mode, which would induce greater changes in contractile properties (Jones et al. 2006; Fitts 2008; Fauler et al. 2012). Moreover, the similar RPE at the end of each exercise could be also related to the longer duration of the VOL exercise (which involves physiological and psychological efforts over a longer period) in comparison with the ES exercise, in which the high perception of exertion is rather related to the painful sensation of the electrical stimulation.

When focusing on the effects of VOL and ES fatiguing exercises on postural control, results showed that the COP surface, COPx and COPy velocity were significantly increased immediately after the completion of the VOL exercise (difference between the PRE and the POST condition), whereas only the COPx velocity was increased following the ES exercise. These results indicate that the subjects' ability to minimize and control postural sway was more disturbed after completing the VOL than the ES exercise (Paillard and Noé 2015), in spite of similar strength loss induced by both exercises modalities. Concordant findings were reported by Paillard et al. (2010a, b) with VOL and ES exercises of equal duration and intensity that induced different magnitude of strength loss. Taken together, these findings illustrate that VOL and ES fatiguing exercises produce specific impacts on postural control with more deleterious effects with VOL exercises, regardless of the duration of the exercise and the level of loss of strength. Two reasons could explain these results. First, the greater central fatigue after the VOL exercise than after the ES exercise would affect a fine motor task such as postural control more after the VOL exercise than after the ES exercise (Paillard 2012; Paillard et al. 2014). Second, during submaximal voluntary muscle actions, motor units are progressively recruited in an orderly fashion from small to large (Henneman et al. 1965), i.e. from the depth of the muscle to the surface (Lexell et al. 1983). Conversely, neuromuscular electrical stimulation activates the motor units located directly beneath the stimulation electrodes (Vanderthommen et al. 2003). Since the large motor units are mainly located on the surface of the quadriceps femoris (Lexell et al. 1983), they are progressively recruited from the surface of the muscle to the depth i.e. in an orderly fashion from large to small. Posture being specially controlled by type I muscle fibers (Paillard 2017) mainly located in the depth of the muscle, these fibers could be more exhausted after a VOL than after an ES exercise. In the present study, since the intensity of the VOL exercise was 20% of MVC, the small motor units were first activated which could degrade postural control more than the ES exercise. This result tends to validate the suggestion formulated by Paillard et al. (2010a) about a more severe fatigue in the type I muscle fibers induced by VOL exercises, which are mainly active in postural regulation, and a less accentuated effect of ES exercises which instead generate severe fatigue in the type II muscle fibers which are not especially required in postural regulation.

The CNS can develop regulatory mechanisms to attenuate the detrimental effects of muscle fatigue on postural control (Paillard 2012). Among these mechanisms, a reorganization of multi-joint coordination usually occurs, while taking advantage of motor redundancy with an increased participation of the non-fatigued muscles (Bonnard et al. 1994; Gribble and Hertel 2004; Singh and Latash 2011; Ritzmann et al. 2016). In the present study, the EMG results illustrate an increased activity of the the SOL muscle after both the VOL and ES exercises, with a more persistent effect with VOL contractions (a significant difference was observed between PRE and POST20 only with VOL contractions). The EMG activity of the TA muscle also increased immediately after the VOL exercise (significant difference between PRE and POST) with overall higher RMS values with VOL than with ES contractions at POST, POST5, POST10 and POST20 (and to a lesser extent that of the BF muscle at POST 5). Such an increased contribution of the ankle muscles after quadriceps femoris fatigue typically characterizes a postural regulatory mechanism which accentuates the participation of the non-fatigued distal muscles to limit the postural disturbances related to fatigue of the proximal musculature (Paillard 2012; Ritzmann et al. 2016). These results also illustrate a more active postural control with larger regulatory mechanisms following the VOL fatiguing exercise. This higher neuromuscular activity of the subjects after the VOL exercise thus emphasizes a less economic postural control. This is totally in accordance with the higher values of COP parameters observed with this fatiguing condition which induced greater central disturbance. The increased participation of the TA muscle following the VOL exercise also characterizes a classically observed postural response in the presence of fatigue, with an enhanced muscle co-activation in order to increases joint stiffness and moderate postural sway (Kennedy et al. 2012; Paillard 2012; Ritzmann et al. 2016). The fact that postural control was only altered immediately after the fatiguing tasks (POST condition), but not after some minutes of recovery (at POST5, POST10 and POST20) show that these regulatory mechanisms were fairly efficient in counteracting the postural disturbance and that a short recovery period was sufficient to restore postural control.

Even though VOL contractions induced greater muscle regulatory actions than ES contractions, it is important to notice that regulatory mechanisms were present following the ES fatiguing exercise. This result does not corroborate the suggestions of Monjo and Forestier (2015) and Monjo et al. (2015) who postulated that fatigue generated through ES, because of its passive nature, could not be accurately interpreted by the CNS. Hence the CNS could not predict the sensory consequences of movement because restricted internal representation updating, thus resulting in inappropriate predictive motor control and absence of regulatory actions (Monjo et al. 2015; Monjo and Forestier 2015). The changes in the activity in a distal non-fatigued muscle observed after ES fatiguing contractions rather suggest that fatigue signals evoked by externally-generated contractions are not gated by the CNS despite their peripheral nature. This would validate the hypothesis formulated by Paillard (2015) who assumed that fatigue signals evoked by stimulated contractions could not be gated by the CNS since the sensory inputs associated with ES were cortically integrated. Veldman et al. (2014) have shown that stimulated contractions achieved at sub-maximal intensities (even below the motor threshold), can excite Ia and Ib afferents, group II afferents from slow and rapidly adapting skin receptors and group II muscle afferents and affect the excitability of the contralateral S1, supplementary motor area, dorsal premotor cortex, posterior parietal cortex M1, and ipsilateral cerebellum and bilateral S2. The different postural control mechanisms observed after both VOL and ES contractions can be typically explored through the central governor theory, which states that motor performance (including sub-maximal tasks such as fine motor tasks) is regulated centrally in the brain by a complex and dynamic integration of physiological, biochemical, and other sensory feedback from the periphery (Noakes et al. 2005).

The present study reveals that postural control mechanisms are modulated according to the nature of the fatiguing contractions, likely due to the integration of specific fatigue signals according to the modality of the contraction. Because of a larger neurophysiological impact of VOL than ES fatiguing contractions due to greater central disturbances, VOL exercises induced larger postural regulatory mechanisms. Even though it is widely accepted that the chronic use of ES can provide major neuromuscular parameter improvements in rehabilitation and/or training programs, this technique is often believed to have a detrimental impact on motor control since the CNS is not involved in motor activation (Monjo et al. 2015). Nevertheless, the presence of regulatory mechanisms with ES contractions clearly underlines the ability of the CNS to display an accurate motor control following acute externally induced neuromuscular perturbations, which can explain the positive chronic effects of ES on postural control and gait observed with elderly subjects (Paillard 2018).

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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