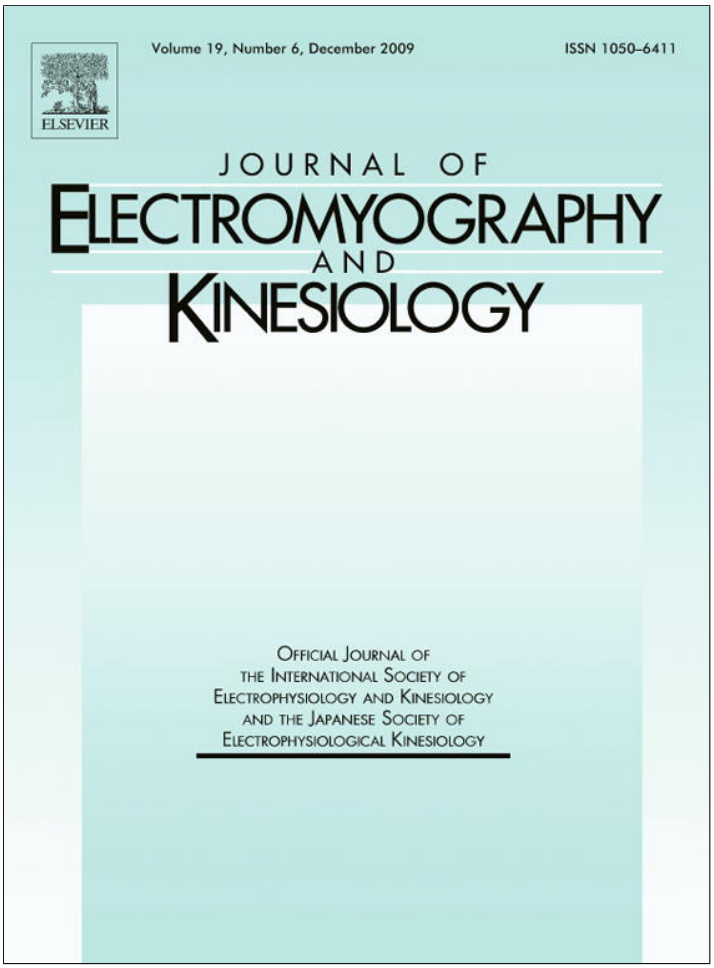

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Unchanged *H*-reflex during a sustained isometric submaximal plantar flexion performed with an EMG biofeedback

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ABSTRACT

The aim of this study was to assess *H*-reflex plasticity and activation pattern of the plantar flexors during a sustained contraction where voluntary EMG activity was controlled via an EMG biofeedback. Twelve healthy males (28.0 ± 4.8 yr) performed a sustained isometric plantar flexion while instructed to maintain summed EMG root mean square (RMS) of gastrocnemius lateralis (GL) and gastrocnemius medialis (GM) muscles fixed at a target corresponding to 80% maximal voluntary contraction torque via an EMG biofeedback. Transcutaneous electrical stimulation of the posterior tibial nerve was evoked during the contraction to obtain the maximal *H*-reflex amplitude to maximal *M*-wave amplitude ratio (H_{sup}/M_{sup} ratio) from GL, GM and soleus (SOL) muscles. Neuromuscular function was also assessed before and immediately after exercise. Results showed a decrease in SOL activation during sustained flexion (from 65.5 ± 6.4% to 42.3 ± 3.8% maximal EMG, $p < 0.001$), whereas summed EMG RMS of GL and GM remained constant (59.7 ± 4.8% of maximal EMG on average). No significant change in the H_{sup}/M_{sup} ratio was found for SOL, GL and GM muscles. Furthermore, it appears that the decrease in maximal voluntary contraction torque (−20.4 ± 2.9%, $p < 0.001$) was related to both neural and contractile impairment. Overall, these findings indicate that the balance between excitation and inhibition affecting the motoneuron pool remains constant during a sustained contraction where myoelectrical activity is controlled via an EMG biofeedback or let free to vary.

1. Introduction

Maintaining a submaximal level of force induces acute adaptations within the neuromuscular system (Ljubisavljevic et al., 1996; Hunter et al., 2002; Kouzaki et al., 2002; Place et al., 2005). For example, during a sustained submaximal isometric contraction an increase in surface electromyography (EMG) of the working muscles is classically observed (Lloyd, 1971; Gamet and Maton, 1989; Ebenbichler et al., 1998; Rochette et al., 2003). This rise in electrical activity under the recording electrodes reflects an increase in the neural drive (Gandevia, 2001; Suzuki et al., 2002) that is necessary to compensate for the force loss of the active motor units (Adam and De Luca, 2003) and thus allows task continuation.

The electrically-induced Hoffmann-reflex (*H*-reflex) is widely used to estimate alterations in the excitability of the α-motoneurons through the Ia afferents reflex pathway, which in turn depends on the facilitation of the synaptic transmission and changes in pre- and post-synaptic inhibitions (Schieppati, 1987). Interestingly, no consensus has emerged about changes in *H*-reflex during sustained submaximal isometric contractions. Indeed, the *H*-reflex amplitude has been shown either to increase (Löscher et al., 1996a; Patikas et al., 2006) or decrease (Duchateau et al., 2002; Walton et al., 2002; Kuchinad et al., 2004) during fatigue. These discrepancies can not be attributed to changes in use of muscle groups, as plantar flexors have been used in most of these works (Löscher et al., 1996a; Walton et al., 2002; Kuchinad et al., 2004; Patikas et al., 2006). However, the study of *H*-reflex plasticity during fatiguing contractions has always been performed while sustaining a submaximal torque. This study aimed to assess *H*-reflex plasticity during a sustained contraction where voluntary EMG activity is controlled via an EMG biofeedback. Averaged EMG activity from gastrocnemius lateralis (GL) and gastrocnemius medialis (GM) muscles was kept constant, whereas soleus (SOL) EMG activity was free to vary. In a recent study, we showed that the activation pattern of a synergist may vary if its EMG activity is not included in the biofeedback (Place et al., 2006). As muscle torque decreases when EMG activity is sustained (Place et al., 2006, 2007b), load sharing between the different synergists may also vary during the task, which can influence muscle performance. Therefore we assessed the strategy adopted by the central nervous system to allow continuation of the required task.

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2. Materials and methods

2.1. Subjects

Experiments were performed on 12 healthy males (age: 28.0 ± 4.8 yr; height: 174.6 ± 6.3 cm; mass: 68.8 ± 7.5 kg, mean ± SD) with no known neurological disease. The procedures were conducted according to the Declaration of Helsinki. Prior to the study, each subject gave written consent and the University of Burgundy Committee on Human Research approved the study protocol.

2.2. Experimental setup

All experiments were performed on the calf muscles because of the easy accessibility of the posterior tibial nerve and the selectivity of stimulation for the *H*-reflex (Schieppati, 1987).

2.2.1. Torque measurements

All measurements were taken on the left leg muscles. Subjects wore a shoe that was firmly secured to the footplate of the isokinetic dynamometer (Biodex, Shirley, NY) and were examined in the supine position with the hip and knee joints flexed at 120° and the ankle flexed at 90° (180° = full extension). To minimize hip and thigh motion during the contractions, and therefore to avoid the contribution of muscles other than the plantar flexors (e.g. knee extensors and hip flexors), straps were fastened across the chest and pelvis. The foot was also secured to the footplate by two straps. One strap was placed around the ankle and the second strap was placed around the foot, 1–2 cm proximal to the metatarsophalangeal joint of the toes. The alignment between the center of rotation of the dynamometer shaft and the axis of the ankle joint was checked at the beginning of each session. Particular care was taken in monitoring the posture of the subjects and in avoiding head rotations during the test to maintain constant corticovestibular influences on the excitability of the motor pool and limit afferent feedback from other peripheral receptors, i.e. Golgi tendon organs, cutaneous and joint afferents (Schieppati, 1987; Misiaszek, 2003).

2.2.2. Electromyography

After careful preparation of the skin (shaving, abrading, and cleaning with alcohol) to obtain low-impedance (<5 kΩ), pairs of silver–chloride circular (recording diameter of 10 mm) surface electrodes (Controle Graphique Medical, Brie–Comte–Robert, France) with an interelectrode distance (center-to-center) of 20 mm were placed along the mid-dorsal line of the leg, at a location corresponding to 2/3 of the line between the medial condylis of the femur to the medial malleolus for the SOL. For the GL and GM muscles, electrodes were fixed lengthwise over the middle of the muscle belly (De Luca, 1997). The location of the recording electrodes sites were carefully adjusted in pilot testing by eliciting at a given intensity the greatest compound muscle action potential (*M*-wave) amplitude for each muscle by tibial nerve stimulation. This procedure was performed to avoid the innervation zone and therefore to obtain the optimal amplitude of EMG responses (Merletti et al., 2001). The EMG activity of tibialis anterior (TA) was also measured to quantify antagonist activation during the sustained contraction and to ensure that the electrophysiological responses from plantar flexor muscles induced by tibial nerve stimulation were not contaminated by concomitant activation of TA. For this muscle, the electrodes were positioned at 1/3 of the line of the fibula and the tip of the medial malleolus (Hermens et al., 2000). The reference electrode was fixed in a central position on the same leg. Myoelectrical signals were amplified with a bandwidth frequency ranging from 15 Hz to 5 kHz (common mode rejection ratio = 90 dB; impedance = 100 MΩ and gain = 1000). The EMG and mechanical signals were digitized on-line (sampling frequency: 2 kHz) and stored for analysis with commercially available software (Tida, Heka Elektronik, Lambrecht/Pfalz, Germany).

The EMG root mean square (RMS) biofeedback was provided by an integrated circuit, true RMS-to-DC converter (model AD536A, Analog Devices, USA; characteristics: maximal error for true RMS-to-DC conversion = 0.5%, bandwidth >450 kHz). This circuit instantaneously computed the true RMS level of the amplified EMG signal for three channels separately with an integration time of 375 ms; the EMG RMS of GL and GM muscles could be calculated and summed by the circuit. RMS (expressed in mV) was calculated as follows:

$$\mathrm{RMS}_{(t)} = \sqrt{\frac{1}{T}\int_{-T/2}^{+T/2} \mathrm{EMG}^2_{(t)} \cdot dt}$$

where T = 0.375 s and t = time variable.

In this study, the circuit displayed on a screen the summed EMG RMS of GL and GM muscles. The EMG RMS value obtained was displayed on a 15-in. monitor that was located 1 m in front of the subject.

2.2.3. Stimulation

The plantar flexor muscles were stimulated by delivering rectangular electrical pulses of 1-ms duration by means of a Digitimer stimulator (model DS7, Hertfordshire, UK). The self-adhesive cathode (8-mm diameter, Ag–AgCL) was located over the tibial nerve in the popliteal fossa and the anode, which was a large rectangular electrode (5 × 10 cm, Compex Medical SA), was placed on the anterior surface of the knee. The stimulation site resulting in the greatest *M*-wave amplitude was first located by a handheld cathode ball electrode (0.5-cm diameter). Once the stimulation site was determined, the stimulation electrode was firmly fixed to this site with rigid straps and taping.

2.2.4. Rate of perceived exertion

The rate of perceived exertion, an index of global effort, was assessed according to the Borg scale from 6 (very very easy) to 20 (task failure) (Borg, 1970) every 30 s during the exercise. The subjects were instructed to focus the assessment of effort on the calf muscles performing the task.

2.3. Experimental protocol

Testing procedure (detailed in Fig. 1) started with a recruitment curve to carefully search for the stimulus intensity necessary to obtain the maximal amplitude of the *H*-reflex (H_{max}) for SOL muscle; *H*-reflex amplitudes for GL and GM muscles were also recorded. Four stimuli were delivered at each intensity level, interspaced by 10 s between each pulse. Intensity was increased by 2 mA from the *H*-reflex threshold until maximal *M*-wave responses were obtained for SOL, GL and GM muscles. We found that the intensity eliciting SOL H_{max} also elicited GL and GM H_{max} in 8 (~67%) and 9 (75%) of the 12 sessions, respectively. In the remaining experiments, GL and GM *H*-reflexes were obtained in the ascending part of the recruitment curve, i.e. sensitive to excitation and/or inhibition mechanisms (Pierrot-Deseilligny and Mazevet, 2000), and were 84% and 87% of their maximal values, respectively. Consequently, we used SOL H_{max} intensity for all the *H*-reflexes elicited in this study to limit the number of stimulations during the sustained contraction. The H_{max} stimulation intensities ranged from 10 to 36 mA. The recruitment curve was followed by a warm-up including brief submaximal contractions of the plantar flexor and dorsiflexor muscles. Then three stimuli at supramaximal intensity

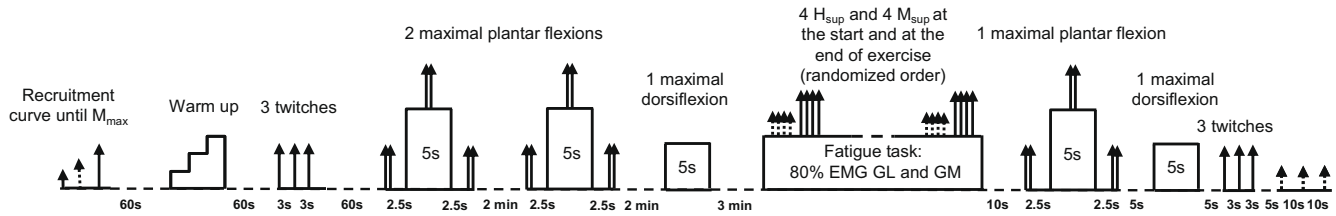

Fig. 1. Overview of the experimental protocol. H_{max} = peak-to-peak amplitude of the *H*-reflex evoked without any voluntary activation of the plantar flexor muscles; H_{sup} = peak-to-peak amplitude of the *H*-reflex evoked during the sustained contraction; M_{max} = peak-to-peak amplitude of the *M*-wave evoked without any voluntary activation of the plantar flexor muscles; M_{sup} = peak-to-peak amplitude of the *M*-wave evoked during the sustained contraction. ↑ Single twitch evoked at supramaximal intensity. ⇑ Doublet evoked at supramaximal intensity. ↕ *H*-reflex evoked at optimal (submaximal) intensity.

(1.5 times the maximum *M*-wave stimulus intensity) were delivered at 3-s intervals and the mean value of the three recorded *M*-wave amplitudes was considered as the maximal *M*-wave amplitude (M_{max}) value for each muscle; the mechanical response was considered as the twitch. The supramaximal intensities ranged from 40 to 100 mA. Then subjects were asked to perform two maximal voluntary contractions (MVC) with the plantar flexor muscles with doublet (paired stimuli separated by 10 ms) delivered 2.5 s before, over the isometric plateau and 2.5 s after the MVC to assess peak doublet amplitude and maximal voluntary activation level. One MVC with the dorsiflexor was then performed; each MVC lasted 5 s and was separated by a 2-min rest period. After that, the EMG feedback of gastrocnemius muscle was carefully adjusted to a level measured at 80% MVC and subjects had to sustain the contraction; 8 potentials (4 H_{sup} and 4 M_{sup}, i.e. evoked at the same intensity as H_{max} and M_{max} but superimposed onto the voluntary contraction, respectively) were randomly evoked (at ~3 s-interval (Patikas et al., 2006) to limit duration of the stimulation period) at the start of the exercise (namely "start") and when subjects reached a rate of perceived exertion of 19 on the 6–20 Borg scale (namely "end"); the order of the stimulation intensity (either the 4 H_{sup} first or the 4 M_{sup} first) was maintained throughout the exercise. The sustained contraction was stopped a few seconds after the last tibial nerve stimulation. Immediately at task termination subjects performed a superimposed MVC with the plantar flexor muscles with doublet elicited before and after the contraction, followed by a MVC of the dorsiflexor muscles. The experimental session ended with three supramaximal stimuli interspaced by 3 s (M_{max} intensity) and three submaximal stimuli interspaced by 10 s (H_{max} intensity) delivered on the tibial nerve. The exercise was performed at a relatively high intensity (EMG level measured at 80% MVC) as pilot experiments showed a significant and consistent decrease in SOL activation at this target level.

2.4. Data analysis

2.4.1. MVC, EMG activity and muscle activation

MVC torque was considered as the peak torque attained during the contraction. EMG of SOL, GL, GM and TA muscles during the plantar flexors MVC was quantified as the RMS for a 0.5 s interval at peak force (250 ms-interval either side of the peak force). Maximal RMS values for SOL, GL, GM muscles were then normalized to the RMS of the *M*-wave for the respective muscles, in order to obtain RMS/RMS_M ratio. This normalization procedure accounted for peripheral influences including neuromuscular propagation failure and changes in impedance from the EMG recordings. Averaged RMS/RMS_M ratio has also been calculated and corresponded to the mean of the ratios obtained for SOL, GL and GM muscles during maximal plantar flexion. Maximal RMS of the TA muscle was quantified for the dorsiflexors MVC. TA RMS calculated during the plantar flexors MVC was then normalized to that calculated when this muscle acted as an agonist, i.e. during the maximal dorsiflexion. During the sustained contraction, RMS activity of SOL, GL, GM and TA muscles were calculated over a 2-s period (Lévénez et al., 2005) before the first train of four stimulation and after the second train of four stimulation, both at the start and towards the latter stage of the exercise (namely "start1", "start2", "end1" and "end2", respectively). All the RMS of the EMG signal obtained during the sustained contraction were normalized to that determined during the MVC performed before the fatiguing contraction. Maximal voluntary activation level was estimated according to the following formula, i.e. voluntary activation level = [1 − (superimposed doublet amplitude × voluntary torque level just before the superimposed doublet/maximal voluntary torque)/potentiated doublet amplitude] × 100 (Strojnik and Komi, 1998). It has recently been shown that the twitch interpolation technique may overestimate the level of central fatigue, as intramuscular processes can account for the increased superimposed doublet amplitude (Place et al., 2008]. Therefore the value of maximal voluntary activation level should be interpreted cautiously.

2.4.2. Evoked potentials

The average EMG signal for all trials in SOL, GL and GM muscles was used to determine peak-to-peak amplitude of (1) *H*-reflexes (H_{max} and H_{sup}), (2) small *M*-waves preceding H_{max} and H_{sup} (i.e. $M_{H_{max}}$ and $M_{H_{sup}}$, respectively) and maximal *M*-waves (M_{max} and M_{sup}). Here the *M*-waves accompanying the *H* responses were used to ensure that stimulation conditions remained constant throughout the whole experiment (Duclay and Martin, 2005). Peak-to-peak duration of *M*-wave was also determined to assess eventual neuromuscular propagation impairment after exercise. In order to calculate RMS/RMS_M ratio (see above) the RMS of the *M*-wave was determined during the time interval corresponding to the area above baseline, i.e. 0 mV (Place et al., 2006). The following ratios were then calculated for respective muscles: $M_{H_{max}}/M_{max}$, $M_{H_{sup}}/M_{sup}$, H_{max}/M_{max} and H_{sup}/M_{sup} (Duclay and Martin, 2005). Indeed, the use of these ratios provides information about the stability of the recording conditions (see Section 4.3 for more details).

2.4.3. Contractile properties

The three trials for mechanical parameters (single stimulus) were averaged and further analysed. The following variables were analysed from the twitch response: peak twitch, time to peak twitch and half-relaxation time. Peak torque was also analysed for the doublet (peak doublet). In order to standardize postactivation potentiation between subjects before exercise, peak doublet elicited before (unpotentiated) and after (potentiated) the first MVC of the plantar flexor muscles was considered for analysis.

2.4.4. Statistical analyses

Normality of the data was checked and confirmed using the Kolmogorov–Smirnov test. Separate one-factor [TIME (pre vs. post)] ANOVAs with repeated measures were used to compare MVC torque (for both maximal plantar flexion and dorsiflexion), maximal

voluntary activation level, twitch contractile properties, peak doublet and TA maximal EMG. Separate two-factor [TIME (pre vs. post) × MUSCLE (SOL vs. GL vs. GM)) ANOVA with repeated measures was used to compare RMS/RMS$_M$ ratios and duration of the *M*-wave. Separate two-factor [TIME (pre vs. start vs. end vs. post) × MUSCLE (SOL vs. GL vs. GM) ANOVAs with repeated measures were performed to compare H_{max}, H_{sup}, M_{max}, M_{sup}, $M_{H_{max}}/M_{max}$, $M_{H_{sup}}/M_{sup}$, H_{max}/M_{max} and H_{sup}/M_{sup}. A two-factor [TIME (start1 vs. start2 vs. end1 vs. end2) × MUSCLE (SOL vs. GL vs. GM vs. TA)] ANOVA with repeated measures was conducted to compare EMG activity throughout the sustained contraction. A one-factor ANOVA (time) with repeated measures was used to compare the torque at 0%, 1%, 3%, 5%, 10%, 15%, 20%, 25%, 30%, 35%, 40%, 45%, 50%, 60%, 70%, 80%, 90% and 100% of the endurance time (Place et al., 2007b). Post-hoc analyses (Tukey) were used to test for differences among pairs of means when appropriate. Pearson correlation coefficients were used to assess the relation between two independent variables when appropriate. The statistical analyses were performed by using Statistica software for Windows (Statsoft, version 6.1, Statistica, Tulsa, OK). A significance level of $p < 0.05$ was used to identify statistical significance. All data are reported as mean ± standard error (SE).

3. Results

3.1. Evoked potentials

As no significant differences were observed during the course of the sustained contraction, start and end data were averaged (namely "during exercise", Table 1 and Fig. 2) for H_{sup}, M_{sup} and $M_{H_{sup}}/M_{sup}$. H_{max} measured in passive condition and H_{sup} measured during the sustained contraction were significantly ($p < 0.001$) greater in SOL muscle compared to GL and GM muscles (Table 1).

Table 1
Changes in *H*-reflex and *M*-wave amplitude evoked before (at rest), during (with voluntary activation) and after (at rest) the sustained contraction for the three plantar flexor muscles investigated.

	SOL	GL	GM
Before exercise			
H_{max} (mV)[b]	3.57 ± 0.53	1.27 ± 0.36	1.18 ± 0.24
$M_{H_{max}}/M_{max}$ (a.u.)[a]	0.08 ± 0.01	0.48 ± 0.16	0.45 ± 0.11
M_{max} (mV)	6.24 ± 0.50	6.45 ± 0.72	7.54 ± 1.0
During exercise			
H_{sup} (mV)[b,c]	4.50 ± 0.70	2.35 ± 0.54	2.88 ± 0.60
$M_{H_{sup}}/M_{sup}$ (a.u.)[a]	0.18 ± 0.08	0.36 ± 0.13	0.49 ± 0.10
M_{sup} (mV)	7.97 ± 0.96	7.08 ± 0.71	8.29 ± 1.19
After exercise			
H_{max} (mV)[b]	3.12 ± 0.54	1.37 ± 0.43	1.26 ± 0.21
$M_{H_{max}}/M_{max}$ (a.u.)[a]	0.15 ± 0.03	0.51 ± 0.17	0.45 ± 0.11
M_{max} (mV)	5.83 ± 0.66	7.13 ± 0.94	7.18 ± 0.87

As no changes were observed during the fatiguing task, data collected at the start and at the end of the contraction were pooled. SOL = soleus muscle; GL = gastrocnemius lateralis and GM = gastrocnemius medialis. H_{max} = peak-to-peak amplitude of the *H*-reflex evoked without any voluntary activation of the plantar flexor muscles; H_{sup} = peak-to-peak amplitude of the *H*-reflex evoked during the sustained contraction; M_{max} = peak-to-peak amplitude of the *M*-wave evoked without any voluntary activation of the plantar flexor muscles; M_{sup} = peak-to-peak amplitude of the *M*-wave evoked during the sustained contraction; $M_{H_{max}}/M_{max}$ = peak-to-peak amplitude of the *M*-wave accompanying the *H*-reflex over the *M*-wave amplitude, both evoked without any voluntary activation of the plantar flexor muscles; $M_{H_{sup}}/M_{sup}$ = peak-to-peak amplitude of the *M*-wave accompanying the *H*-reflex over the *M*-wave amplitude, both evoked during the sustained contraction. Values are mean ± SE.

[a] SOL muscle significantly different from GL and GM muscles, $p < 0.05$.
[b] SOL muscle significantly different from GL and GM muscles, $p < 0.001$.
[c] H_{sup} significantly different from H_{max} measured before and after exercise, $p < 0.01$.

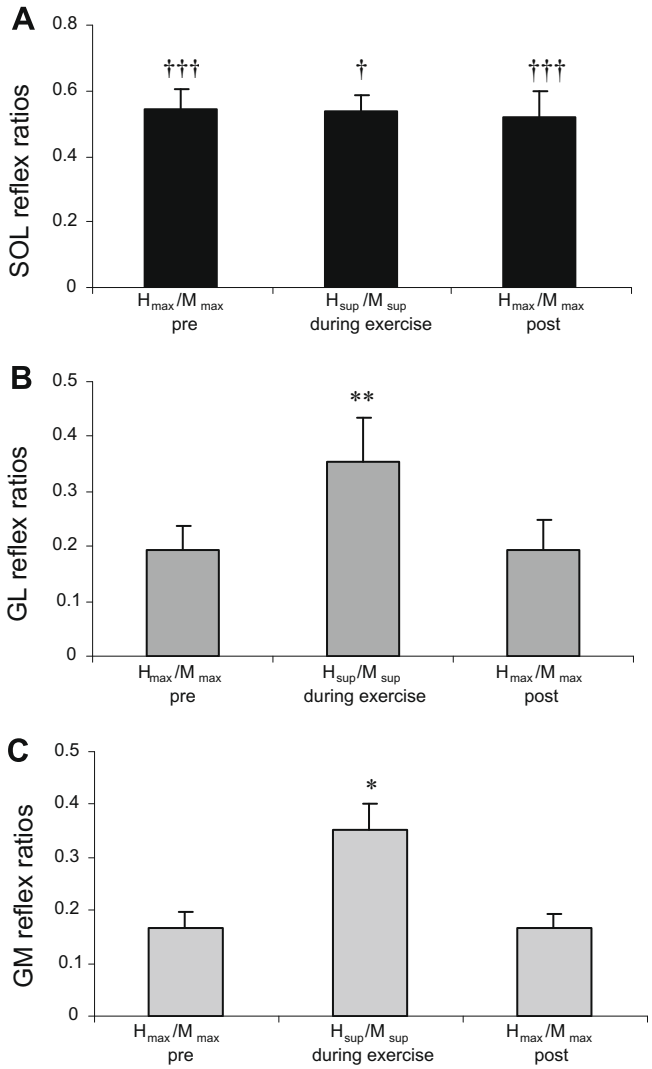

Fig. 2. *H*-reflex amplitude/*M*-wave amplitude evoked before (H_{max}/M_{max} pre), during (H_{sup}/M_{sup} during exercise) and after (H_{max}/M_{max} post) the sustained contraction for (A) soleus (SOL) muscle, (B) gastrocnemius lateralis (GL) muscle and (C) gastrocnemius medialis (GM) muscle. As no change has been observed during the contraction, the values measured at the start and at the end of the exercise have been averaged. SOL muscle significantly different from GL and GM muscles: $^{\dagger}p < 0.05$; $^{\dagger\dagger\dagger}p < 0.001$. H_{sup}/M_{sup} significantly different from H_{max}/M_{max} before and after fatigue: $^{*}p < 0.05$; $^{**}p < 0.01$. Note the different scale for SOL muscle. Values are mean ± SE.

Furthermore, H_{sup} was significantly ($p < 0.01$) potentiated as compared to H_{max} measured before or after exercise. No time effect ($p > 0.05$) was found when considering the ratios $M_{H_{max}}/M_{max}$ or $M_{H_{sup}}/M_{sup}$, suggesting that stimulus conditions were stable during the whole experiment (Table 1). However, a muscle effect followed by a post-hoc analysis revealed that these ratios were significantly ($p < 0.05$) higher for SOL muscle in comparison to GL and GM muscles. M_{max} and M_{sup} were not statistically different ($p > 0.05$), did not change during the course of the experiments ($p > 0.05$), and no differences were found between SOL, GL and GM muscles ($p > 0.05$, Table 1).

As for H_{max} and H_{sup}, H_{max}/M_{max} and H_{sup}/M_{sup} were significantly ($p < 0.05$) greater in SOL muscle as compared with GL and GM muscles. No significant ($p > 0.05$) difference was observed in H_{max}/M_{max} before and after exercise. Similarly, H_{sup}/M_{sup} did not show any changes during the course of the contraction for any muscles and the values during exercise have been averaged for clarity reasons (Fig. 2). H_{sup}/M_{sup} was 0.50 ± 0.05% and

0.58 ± 0.04% for SOL, 0.37 ± 0.10% and 0.34 ± 0.06% for GL and 0.35 ± 0.05% and 0.36 ± 0.05% for GM muscle, at the start and at the end of the sustained contraction, respectively. H_{sup}/M_{sup} during exercise was significantly potentiated compared to H_{max}/M_{max} for GL and GM muscles.

3.2. Time course of EMG activity during fatigue

EMG activity was constant for GL and GM muscle (from 58.2 ± 5.4% to 61.8 ± 6.1% maximal RMS for GL muscle and from 61.2 ± 4.4% to 57.5 ± 3.3% maximal RMS for GM muscle, which gives an averaged summed RMS of 59.7 ± 4.8% maximal RMS for these two muscles during exercise) throughout the sustained contraction (Fig. 3A). In contrast, EMG activity of the SOL muscle decreased significantly ($p < 0.001$) during the course of the exercise (from 65.5 ± 6.4% to 42.3 ± 3.8% maximal RMS, $p < 0.05$, Fig. 3A). No change in EMG activity was observed for TA muscle during the contraction (from 5.7 ± 0.7% to 5.0 ± 0.7% maximal RMS on average, $p > 0.05$). EMG activity remained constant ($p > 0.05$) for all the muscles investigated during the time period necessary for the collection of the 4 H_{sup} and the 4 M_{sup}, both at the beginning (start1 and start2) and the latter stages (end1 and end2) of the contraction. Interestingly, we found a significant ($p < 0.001$) strong correlation between the reduction in SOL EMG activity and the mechanical torque decrease at the end of the contraction (Fig. 3B) for 9 of the 12 subjects participating in the experiments.

A representative recording of voluntary and evoked EMG activity is provided in Fig. 4. Despite different voluntary EMG activity behavior between the three plantar flexor muscles, H_{sup} and M_{sup} remained unchanged during the course of the contraction for SOL, GL and GM muscles.

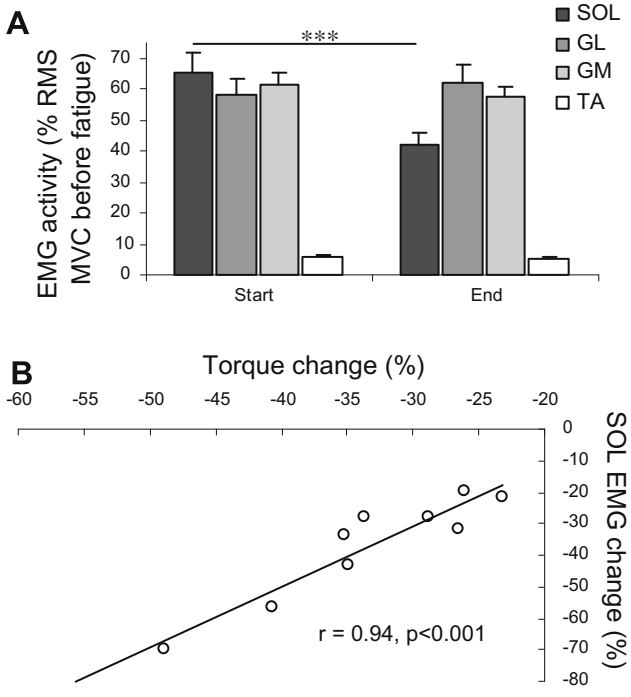

Fig. 3. (A) EMG RMS activity measured at the start and at the end of the sustained contraction for soleus (SOL), gastrocnemius lateralis (GL), gastrocnemius medialis (GM) and tibialis anterior (TA) muscles. (B) Relationship between the decrease in SOL EMG activity and the reduction in torque at the end of the exercise (start vs. end) for 9 of the 12 subjects. ***Start significantly different from end, $p < 0.001$. Values are mean ± SE.

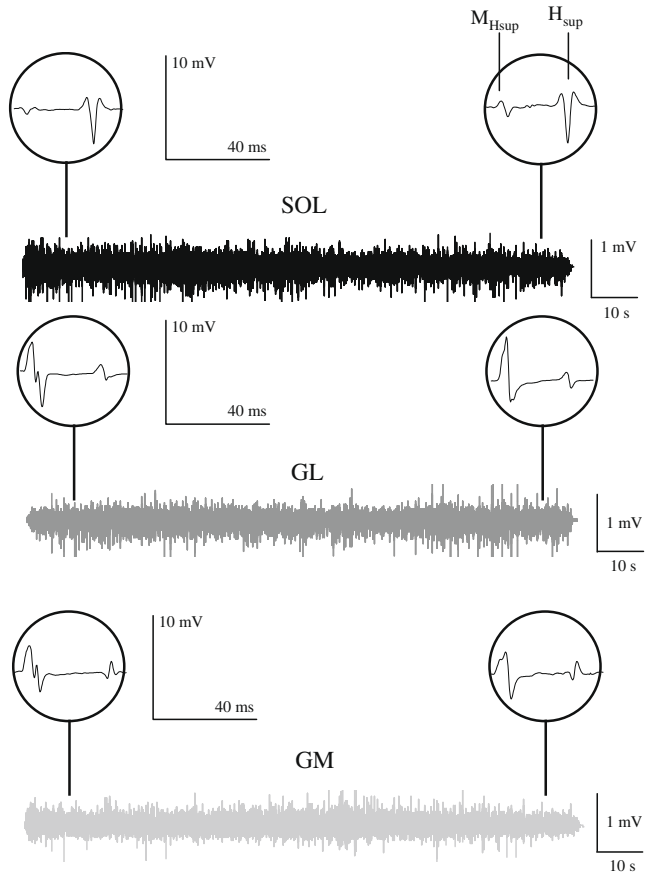

Fig. 4. Typical recordings of surface EMG activity and evoked responses of soleus (SOL), gastrocnemius lateralis (GL) and gastrocnemius medialis (GM) muscles during the sustained voluntary contraction.

3.3. Fatigue level measured after the sustained contraction

The time required to attain a rate of perceived exertion of 19 during the prolonged contraction was 112 ± 7 s; muscle torque at the start of the contraction was 80.7 ± 0.9% MVC torque and decreased significantly ($p < 0.001$) from 5% of endurance time to reach 53.8 ± 2.1% MVC torque at the end of the task. MVC torque decreased significantly ($p < 0.001$) from 136 ± 7 to 109 ± 6 N.m, i.e. a loss of 20.4 ± 2.9%. MVC loss was significantly correlated with averaged RMS/RMS_M reduction (Fig. 5A) and peak twitch change (Fig. 5B).

Central activation was depressed after the fatiguing task, as revealed by the slight but significant ($p < 0.05$) decrease in maximal voluntary activation level (Table 2) and the reductions in RMS/RMS_M during MVC (range 18–27%). In contrast, peak twitch was significantly potentiated (+28.3 ± 3.6%, $p < 0.001$, Table 2) after the prolonged contraction as compared to before exercise; this potentiation was accompanied by a shortening of the time to peak twitch (−14.1 ± 5.5%, $p < 0.05$, Table 2) and no significant change in the half-relaxation time. *M*-wave amplitude did not change ($p > 0.05$) after exercise (Table 1). Similarly, *M*-wave duration was not altered at termination of the fatiguing task for any muscle (from 3.17 ± 0.38 to 3.14 ± 0.39 ms on average, $p > 0.05$). Contrary to peak twitch, peak doublet (either potentiated by a MVC or unpotentiated) remained unchanged after the fatiguing task (Table 2).

No difference was observed for the maximal dorsiflexion torque before and after exercise (43 ± 2 vs. 42 ± 2 N.m, respectively, $p > 0.05$), or in maximal EMG activity of TA muscle ($p > 0.05$).

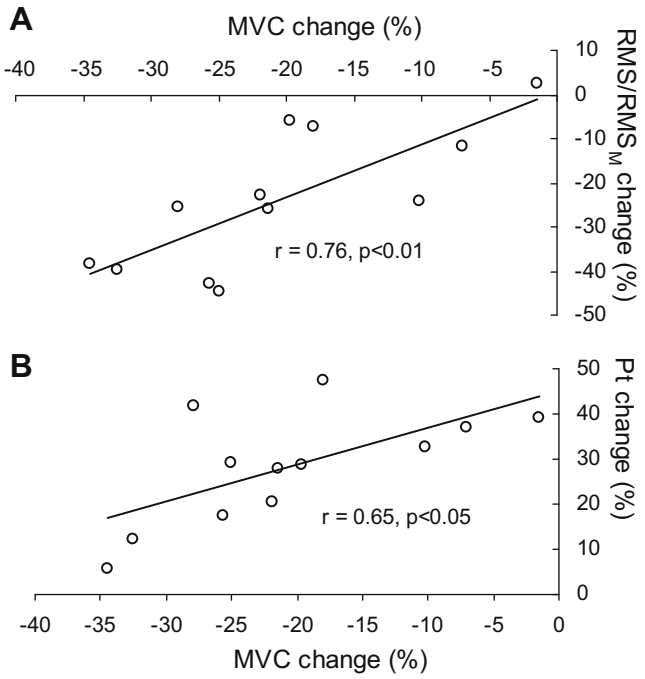

Fig. 5. Linear relations were found between maximal voluntary contraction torque (MVC) loss and the change in (A) RMS/RMS$_M$ averaged from soleus, gastrocnemius lateralis and gastrocnemius medialis muscles (n = 12) and (B) peak twitch (n = 12).

Table 2
Contractile properties and central activation measured before (Pre) and immediately after (Post) the sustained contraction.

	Pre	Post	Change (%)
Contractile properties			
Peak twitch (N.m)	16.9 ± 1.4	21.5 ± 1.6***	28.3 ± 3.6
Time to peak twitch (ms)	112.4 ± 6.1	95.3 ± 7.2*	−14.1 ± 5.5
Half-relaxation time (ms)	93.9 ± 6.3	104.4 ± 10.9	14.3 ± 14
Unpotentiated peak doublet (N.m)	36.3 ± 2.1	37.0 ± 2.3	1.6 ± 2.4
Potentiated peak doublet (N.m)	40.9 ± 2.3	38.7 ± 2.6	−5.4 ± 4.4
Central activation			
Voluntary activation level (%)	99.1 ± 0.47	96.5 ± 1.10*	−2.7 ± 1.8
SOL RMS/RMS$_M$ (a.u.)	0.145 ± 0.017	0.103 ± 0.016**	−27.0 ± 5.5
GL RMS/RMS$_M$ (a.u.)	0.116 ± 0.015	0.087 ± 0.013**	−19.6 ± 8.3
GM RMS/RMS$_M$ (a.u.)	0.094 ± 0.014	0.073 ± 0.011**	−17.9 ± 9.1

RMS/RMS$_M$ = EMG RMS normalized by respective M-wave RMS; SOL = soleus muscle; GL = gastrocnemius lateralis; GM = gastrocnemius medialis. Values are mean ± SE.
* Significantly different from pre, $p < 0.05$.
** Significantly different from pre, $p < 0.01$.
*** Significantly different from pre, $p < 0.001$.

4. Discussion

The main purpose of this study was to investigate the balance between the excitation and inhibition affecting the motoneuron pool during a sustained contraction where voluntary EMG activity is controlled via an EMG biofeedback. Our main finding was that despite a different activation pattern between plantar flexors during fatigue (constant EMG activity for the gastrocnemius muscle vs. decrease in EMG activity for the SOL muscle), evoked potentials remained constant for the three plantar flexor muscles during fatigue.

4.1. Activation pattern of the plantar flexors during the sustained contraction

In this work, we chose to provide subjects with an EMG biofeedback from GL and GM muscles only. Interestingly, we observed that EMG activity for the three plantar flexors was not different when starting the contraction despite SOL not being included in the biofeedback. This result suggests that the central nervous system is not able to differentiate central drive between different plantar flexor muscles when starting the contraction. It confirms the results that our group recently reported for knee extensor muscles (Place et al., 2006). However, in contrast to what we observed in quadriceps muscle (Place et al., 2006), maintaining EMG activity of the bi-articular gastrocnemius allowed EMG of the mono-articular SOL to decrease during the course of the sustained contraction. In this study, it is interesting to note that the electrical activity of the fatigue-resistant SOL muscle (not included in the biofeedback to the subjects) decreased during the contraction whereas EMG activity of gastrocnemius (included in the biofeedback), which contains much more fast-twitch fibres (Johnson et al., 1973), remained constant. Schieppati et al. (1990) showed that Ia-mediated inhibitions from gastrocnemius muscle to soleus do not occur when the muscle is voluntarily contracted and therefore cannot explain the reduction in SOL activation. Thus, the decrease in SOL EMG activity may be thought of as a strategy used by the CNS to progressively reduce the activity of this muscle. Load sharing strategies, such as alternate muscle activity during low-force contraction, have already been observed (Tamaki et al., 1998; Kouzaki et al., 2002) and have been found to attenuate muscle fatigue (Kouzaki and Shinohara, 2006). Ciubotariu et al. (2004) showed that the pain-induced decrease in GL and GM EMG activity was compensated by an increased SOL activation at the start of a sustained contraction at 80% MVC. Similarly, Akima et al. (2002) provided evidence that activation strategy during repeated contractions could be modified if one of the synergist was prefatigued. These various examples show that CNS adapts to allow continuation of a required task and in our study the decrease in SOL activation was interpreted as an economical process. As a result, we found that the decrease in SOL activation correlated with the reduction in muscle torque during the prolonged contraction (Fig. 3B), which is in accordance with the suboptimal mechanical contribution of gastrocnemii to the plantar flexor torque at a flexed knee angle (Cresswell et al., 1995). Finally, the constant EMG activity of TA during the task indicates that antagonistic activation did not significantly contribute to the observed torque reduction.

4.2. Spinal reflex plasticity and task failure

Previous works have investigated the change in H-reflex during prolonged submaximal contraction. Some studies showed an increased reflex response in plantar flexors during sustained plantar flexion at 20% MVC (Löscher et al., 1996a; Patikas et al., 2006) and proposed that increased drive to the agonist α-motoneuron pool is an adaptation to facilitate recruitment of motor units during fatigue (Löscher et al., 1996a). In contrast, at higher contraction intensities (25–66% MVC), Kuchinad et al. (2004) observed a reduced H-reflex during exercise, but the H-reflex was evoked without any background activation and not normalized to M_{max}. Similarly, Duchateau et al. (2002) showed a decreased excitation to the α-motoneurons during sustained contraction with the abductor pollicis brevis muscle at 25% and 50% MVC, which were compensated by an enhancement of the central drive in order to keep a constant torque output. Thus no consensus has emerged during sustained contraction while focusing on force output, i.e. when EMG activity is not controlled. Indeed, a steady background of EMG activity while evoking H-reflexes is recommended to ensure that the pool of α-motoneurons remains steady (Stein, 1995). In this study, we limited EMG fluctuations and thus changes in the recording conditions during fatigue. Indeed, the use of the EMG biofeedback allowed us to assess the fatigue-induced changes in H-reflex amplitude in muscles whose EMG activity was kept

constant or free to vary. We found no change in GL, GM and SOL H_{sup}/M_{sup}, suggesting that a change in spinal excitability is not a prerequisite for a modification in the activation pattern during a sustained contraction. Nevertheless, caution should be taken as voluntary EMG reflects changes in activation of all motor units, whereas *H*-reflex is considered to reflect changes in the slow motor units mainly (Duchateau et al., 2002).

It is well recognized that factors such as postsynaptic reciprocal inhibitory mechanisms and presynaptic inhibition can modulate the amplitude of the *H*-reflex (Schieppati, 1987). In this study, we observed that H_{sup}/M_{sup} was potentiated when compared to H_{max}/M_{max} in GL and GM but not in SOL. This absence of potentiation in SOL may be explained by the activation of the antagonistic TA during exercise, which certainly increased the level of reciprocal inhibition and disfacilitated the *H*-reflex in SOL; indeed, TA is a pure antagonist to SOL and only partly antagonistic to the gastrocnemius. However, as TA EMG activity remained constant during the exercise (Fig. 3A), reciprocal inhibition may have played limited role in the absence of change in H_{sup}/M_{sup} and in the reduction in SOL EMG activity during the sustained contraction. Furthermore, any rise in the degree of presynaptic inhibition will alter the neurotransmitter release at the α-motoneurone synapse (Stein, 1995; Rudomin and Schmidt, 1999) and reduce the size of the reflex. During sustained submaximal contraction, the small diameter groups III and IV afferents have been suggested to inhibit *H*-reflex (Duchateau et al., 2002). However, the *H*-reflex may also be facilitated during a sustained submaximal contraction because of a decrease in postsynaptic recurrent inhibition (Löscher et al., 1996b). Taken all these factors together, our unchanged H_{sup}/M_{sup} values suggest that the balance of the excitations and inhibitions received by the α-motoneurons during the present exercise remained constant for SOL, GL and GM muscles.

Finally, it has been proposed that potentiated twitch or doublet should be preferred to non-potentiated ones to detect excitation–contraction failure (Kufel et al., 2002; Place et al., 2007a). Here neither M_{max} nor peak doublet (potentiated or not) were affected, suggesting that peripheral muscle excitability and excitation–contraction coupling were well preserved. Moreover, the non-potentiated twitch amplitude significantly increased following exercise and time to peak twitch was reduced. Fig. 5B suggests that the greater peak twitch potentiation, the better preserved MVC. In the absence of neuromuscular transmission changes indicated by the unchanged *M*-wave properties, this observation suggests that alteration in calcium handling played a role in the decreased maximal force generating capacity.

4.3. Methodology

As *H*-reflex can be influenced by recording conditions, it is important to follow several methodological requirements for accurate interpretation of the results (Zehr, 2002; Misiaszek, 2003). First, to prevent any problems arising from or caused by change in muscle length or background activation (Gerilovsky et al., 1989), we fixed both knee and ankle angles during all experiments and normalized every evoked potential to the respective M_{max} or M_{sup} elicited at the same level of voluntary activation (Frigon et al., 2007). Factors, which are acknowledged as stable indices of recording conditions, include the constancy of $M_{H_{max}}$ and the constancy of the maximal amplitude of the M_{max} (Zehr, 2002). Thus, we used the stimulation intensity that gave H_{max} to assess if the stimulation conditions were stable, which would not have been possible with the use of another stimulus intensity (e.g. 50% H_{max}). Results showed that neither $M_{H_{max}}$ (respectively, $M_{H_{sup}}$), nor M_{max} (respectively, M_{sup}) varied over the course of the experiment. Therefore, the absence of *H*-reflex variation cannot be attributed to changes in the position of the stimulation electrode with respect to the tibial nerve.

H-reflex values obtained in passive condition or during exercise were normalized to the maximal *M*-wave amplitude recorded in the same condition; indeed, the use of these ratios is a necessary prerequisite to assess spinal reflex plasticity (Duclay and Martin, 2005). Our results show as previously observed (Löscher et al., 1996a) that H_{max}/M_{max} ratio was also higher for SOL compared to GL and GM. This result can be easily explained as (i) stimulus intensity was optimized for SOL, (ii) SOL contains more muscle spindles than GL and GM (Voss, 1971) and (iii) SOL has more slow-twitch fibres compared to the gastrocnemius (Johnson et al., 1973); indeed, H_{max} is thought to result from the activation of the slow-twitch motor units (Buchthal and Schmalbruch, 1970).

In summary, present results indicate that (i) the balance between excitation and inhibition affecting the motoneuron pool remains constant during a sustained contraction where myoelectrical activity is controlled via an EMG biofeedback or let free to vary and (ii) the decrease in maximal torque generating capacity after a sustained submaximal plantar flexion is related to both central and peripheral, presumably intramuscular, processes.

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