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ORIGINAL ARTICLE

Neural mechanisms of strength increase after one-week motor imagery training

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Abstract

The neural mechanisms explaining strength increase following mental training by motor imagery (MI) are not clearly understood. While gains are mostly attributed to cortical reorganization, the sub-cortical adaptations have never been investigated. The present study investigated the effects of MI training on muscle force capacity and the related spinal and supraspinal mechanisms. Eighteen young healthy participants (mean age: 22.5 ± 2.6) took part in the experiment. They were distributed into two groups: a control group ($n = 9$) and an MI training group ($n = 9$). The MI group performed seven consecutive sessions (one per day) of imagined maximal isometric plantar flexion (4 blocks of 25 trials per session). The control group did not engage in any physical or mental training. Both groups were tested for the isometric maximal plantar flexion torque (MVC) and the rate of torque development (RTD) before and after the training session. In addition, soleus and medial gastrocnemius spinal and supraspinal adaptations were assessed through the recording of H-reflexes and V-waves, with electrical stimulations of the posterior tibial nerve evoked at rest and during MVC, respectively. After one week, only the MI training group increased both plantar flexion MVC and RTD. The enhancement of muscle torque capacity was accompanied by significant increase of electromyographic activity and V-wave during MVC and of H-reflex at rest. The increased cortical descending neural drive and the excitability of spinal networks at rest could explain the greater RTD and MVC after one week of MI training.

Keywords: *Rate of force development, triceps surae, H-reflex, V-wave, EMG, maximal isometric torque*

Highlights

- Short-term mental training significantly improves plantar flexors' maximal force and rate of force development.
- The strength increase following mental training is linked with a greater cortical descending command.
- The strength increase following mental training is linked with an increase of resting spinal excitability.

Introduction

Motor imagery (MI) is the internal simulation of movement without corresponding motor output (Decety, 1996). Functional imagery studies showed that MI and actual movement share similar cortical activations (Gérardin et al., 2000, Lotze et al., 1999, Mellet et coll. 1998, Roth et al., 1996), particularly over the motor areas (Grèzes & Decety, 2001; Kilintari, Narayana, Babajani-Feremi, Rezaie, & Papanicolaou, 2016). Furthermore, many investigations using transcranial magnetic stimulation found an increased corticospinal excitability compared to rest (Facchini, Muellbacher, Battaglia, Boroojerdi, & Hallett, 2002; Mouthon, Ruffieux, Wälchli, Keller, & Taube, 2015; Rozand, Lebon, Papaxanthis, & Lepers, 2014). Regarding sub-cortical structures, results appear more controversial. Through H-reflex technique, some authors reported an increase in spinal excitability during MI (Bonnet, Decety, Jeannerod, & Requin, 1997; Cowley, Clark, & Ploutz-Snyder, 2008; Hale, Raglin, & Koceja, 2003), while no changes (Aoyama & Kaneko, 2011; Kasai, Kawai, Kawanishi, & Yahagi, 1997; Mouthon et al., 2015;

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Yahagi, Shimura, & Kasai, 1996) or even a decrease (Oishi, Kimura, Yasukawa, Yoneda, & Maeshima, 1994) have been reported by others. Nonetheless, recent findings showed that MI could activate spinal interneurons with low excitability threshold, in the absence of observable H-reflex changes (Grosprêtre, Lebon, Papaxanthis, & Martin, 2016).

However, the majority of the literature investigated online effects of MI, while this modality is mostly used in training-based approaches. Indeed, over the past decades, MI was considered as a complementary method in rehabilitation (Malouin & Richards, 2010), motor learning (Gentili & Papaxanthis, 2015) and sport performance (Lebon, Collet, & Guillot, 2010). The enhancement of motor performance after MI training in healthy participants (Ranganathan, Siemionow, Liu, Sahgal, & Yue, 2004) and patients (DiRienzo et al., 2014) was then mainly attributed to cerebral plasticity. However, sub-cortical adaptations cannot be ruled out, since changes in spinal excitability are considered as a key component of muscle strength increase after training (Aagaard, Simonsen, Andersen, Magnusson, & Dyhre-Poulsen, 2002). In a recent review, Ruffino, Papaxanthis, and Lebon (2017) suggested a model of neural adaptations following MI practice that includes spinal plasticity. However, to date, the contributions of spinal and supraspinal mechanisms to the increase in motor performance following a sustained use of MI have never been investigated.

The present study attempts for the first time to investigate whether strength gains following a prolonged MI training period are related to neural plasticity at spinal and/or supraspinal levels. To probe neural adaptations, V-wave and H-reflex are used as markers of descending neural drive and spinal excitability, respectively. While H-reflex allows to test both rest and active changes at the spinal level, V-wave is an index of the amount of supraspinal neural drive addressed to the motoneuronal pool during voluntary contraction. To determine the effect of MI training on muscle torque capacities, the classical peak of maximal isometric torque (MVC) is measured, as well as the rate of torque development (RTD) that is better correlated related to performance in functional daily tasks (Maffiuletti et al., 2016). While the impact of a whole MI training on RTD has never been investigated, we hypothesize that this index would be more sensitive to such training modality than the maximal force. Thus, we expected that MI training would increase torque capacities, with concomitant changes in descending neural drive (V-wave) and spinal excitability (H-reflexes).

Materials and methods

Eighteen healthy young adults gave written informed consent to participate in the present study. Participants were randomly distributed into two groups: the control group ($n = 9$; 4 males and 5 females, age: 23.2 ± 2.8 years; height: 1.68 ± 0.03 m; weight: 62.7 ± 10.1 kg) and the MI training group ($n = 9$; 5 males and 4 females, age: 22.2 ± 2.6 years; height: 1.73 ± 0.07 m; weight: 66.1 ± 8.7 kg). All participants had no history or current clinical signs of neurological and physical disorders and committed not to engage in any training or exercise programme during the whole duration of the study. None of them were specifically involved in intense sport activities. All experimental procedures were performed in accordance with the latest version of the declaration of Helsinki and approved by the local Ethics Committee.

Overview of the experimental design

The training group carried out one week of MI training, while the control group did not perform any exercise during the week. MI training was accomplished daily during a whole week, i.e. 7 consecutive sessions of about 20 min. The same physiological variables, pre- and post- training, were measured in both groups. For the MI training group, pre- and post-training measurements were achieved before the first MI training session and the day after the last MI training session, respectively. Participants were familiarized to MI technique during the inclusion visit at the laboratory, as well as during the first experimental session.

Each experimental session for the pre- and post-measurements was organized as follow: after the experimenter positioned the electromyographic electrodes (see below for details), the participants sat on an isokinetic dynamometer. The position of ankle, knee and hip joints was set at 90°, with the foot firmly strapped on the pedal of the ergometer. First, the optimal posterior tibial nerve stimulation site was found to record H-reflexes and M-waves responses of soleus and medial gastrocnemius muscles at rest. Then, after a warm-up including 8–10 submaximal contractions, the participants performed eight maximal isometric voluntary contractions (MVC) of plantar flexion with the right foot, separated by at least 1-min rest. In order to record the maximal RTD, the following instructions were given to the participants before they performed each MVC: “reach the force peak as quickly as possible by pushing hard and fast on the pedal and maintain the maximal force until the experimenter tells you to stop”. During each plateau of isometric MVC, one superimposed H-reflex (×4) or M-wave (×4) was randomly evoked. Maximal isometric voluntary torque of the dorsiflexor muscles was also measured by asking the participants to perform two maximal dorsi-flexions.

MI training

Participants in the MI training group were first initiated to MI practice during a familiarization session and completed the revised version of the Movement Imagery Questionnaire (MIQ-R) to determine self-estimation of MI ability. The initial mean MIQ-R score was 46.9 ± 3.5 (maximum score: 56), indicating a good imagery capacity. Participants performed the first and last training sessions in the laboratory to monitor muscle electrophysiological signals during MI. Each training session lasted 20 min and involved 4 series of 25 imagined maximal isometric contractions of the plantar flexors of the right leg. To provide the optimal conditions of concentration and motivation during the training, short sessions (no more than 20 min) are usually recommended in healthy participants (Driskell, Copper, & Moran, 1994). In the present study, each imagined contraction lasted 5 s, followed by 5 s of rest; series were separated by 1-min rest.

Participants were instructed to imagine pressing maximally on the pedal of the ergometer and to evoke the corresponding sensation of muscle contraction. They were requested to feel the intensity of muscle contraction normally elicited during actual performance (kinesthetic modality). Each imagined trial was preceded by two oral signals given by the experimenter: "get ready" and "go", and it was stopped by a stop signal.

To determine if MI induced changes in muscular activity, background electromyography (EMG) of soleus (SOL) and medial gastrocnemius (MG) muscles was recorded continuously during the first and last MI training sessions (performed in the laboratory). For the sessions 2–6, participants were asked to train themselves daily at home by using an audio file with the recorded voice of the same experimenter. This file gave first the basic instructions about position and environmental constraints, then it gave the verbal "get ready","go" and "stop" signals for the whole session, with respect to the timings of the imagined contractions. In healthy active young participants, home-based training can provide comparable results to supervised training, particularly if the imagined movement is simple and has been experienced before (Malouin & Richards, 2010).

A survey was given to the participants to indicate the time of the training and to rate the quality of their training for each session, with a quote from 1 (poor) to 7 (excellent). None of the participants of the training group reported missing any of the training sessions. During the training week, the self-estimated imagery (mean: 5.6 ± 1.2 out of 7) did not show any significant fluctuation from one day to another ($F_{6,48} = 1.284$, $p = .282$).

Mechanical recordings

The instantaneous muscle torque (N.m) was recorded using an isokinetic dynamometer (Biodex System 3, Shirley, NY). The axis of the dynamometer was aligned with the external malleolus of the right leg. The foot was firmly strapped to the pedal to avoid any ankle extension during the experiment. The trunk was stabilized by two crossover shoulder harnesses. Mechanical signals were digitized on-line (sampling frequency: 5 kHz) and stored for analysis with Tida software (Heka Elektronik, Lambrecht/Pfalz, Germany).

Electromyographic recordings

EMG activity was recorded from two triceps surae muscles (SOL and MG) and from one muscle of the tibial compartment (tibialis anterior, TA). After shaving and dry-cleaning the skin with alcohol to keep low impedance (<5 kΩ), EMG signals were obtained by using two silver-chloride surface electrodes (8 mm diameter, center-to-center distance: 2 cm) placed over the muscle bellies following SENIAM recommendations (Hermens, Freriks, Disselhorst-Klug, & Rau, 2000). The common reference electrode was placed in a central position between the stimulation and recording sites. Electrode placements were marked on the skin to ensure same positioning between the pre- and post-test sessions.

EMG signals were amplified (gain = 1000) and filtered with a bandwidth frequency ranging from 15 to 1 kHz. EMG was digitized on-line (sampling frequency: 5 kHz) and stored for analysis with Tida software (Heka Elektronik, Lambrecht/Pfalz, Germany).

Posterior tibial nerve stimulation

Single rectangular pulses (1 ms width) were delivered to the posterior tibial nerve (PTN) by a Digitimer stimulator (model DS7, Hertfordshire, UK) to evoke H-reflex in the triceps surae muscles. A self-adhesive cathode (8 mm diameter, Ag-AgCl) was placed in the popliteal fossa and an anode (5 × 10 cm, Medicompex SA, Ecublens, Switzerland) was placed over the patella. The optimal stimulation site was first located by a hand-held cathode ball electrode (0.5-cm diameter). Then, the stimulation electrode was firmly fixed with straps. The intensity of stimulation was increased, with 2-mA increment and 4 pulses per intensity, starting from resting H-reflex threshold and ending when the M-wave was no longer increased. The intensity was then increased by 20% (supramaximal intensity) to record the maximal M-wave (Mmax). This whole procedure was performed during both the pre- and the post-experimental sessions.

Two intensities were then determined from recruitment curves to evoke resting and superimposed electrophysiological responses. First, the intensity used to record H-reflexes was the one that elicited maximal H-reflex (noted H_{max} at rest and H_{sup} during MVC) in SOL muscle, which is generally associated with a small M wave (noted M_{atH} at rest and M_{atHsup} during MVC). Variations of M_{atH} amplitude in SOL and MG muscles were useful to detect eventual modifications in PTN stimulation during the experiment. The second intensity, which was supramaximal, provided maximal M-waves of SOL and MG muscles (M_{max} at rest and M_{sup} during MVC). Contrary to M_{max} (M-wave at rest), M_{sup} (M-wave during MVC) is followed by a reflexive response, called V-wave, which is used as an index of the supraspinal descending neural drive. V-wave is the results of a collision occurring in motor axons between the antidromic impulse generated by the stimulation and the descending neural drive. This phenomenon allows to record a reflexive response reflecting the proportion of alpha-motoneurons activated by the electrical stimulus for which the collision is effective, i.e. those which are activated by the voluntary descending motor command (Grospretre & Martin, 2014). The superimposed responses during MVC were evoked by manually triggering the stimulations once the participant's torque reached the plateau of its maximal value. Participants were asked to maintain the contraction during and after the stimulation.

Data analysis

The mechanical signal during the contraction ramp, i.e. from the baseline to the plateau of maximal produced torque was analyzed during each MVC. To avoid confounding effects relying on dynamometer noise, contraction onset was set at 2% of the corresponding MVC (Granacher, Gruber, & Gollhofer, 2009). As it is recommended to analyze multiple time periods to provide a more accurate description of the rising torque, three consecutive portions of the contraction ramp were analyzed: from 0 to 50 ms, 50 to 100 ms and 100 to 200 ms (Maffiuletti et al., 2016). The RTD was calculated as the slope of the torque–time curve in each portion (N.m/s). To best fit to the related force-generating capacity (Maffiuletti et al., 2016), each RTD value was then normalized to the corresponding MVC value.

Root mean square of the EMG activities of the three muscles (SOL, MG and TA) was determined during four periods for each MVC: 0–50, 50–100, 100–200 ms, and during a 500 ms window in the plateau of the maximal torque prior to posterior tibial nerve stimulation. For SOL and MG muscles, RMS values were normalized to the corresponding maximal superimposed M-wave (RMS/M_{sup}). Coactivation levels were estimated by TA RMS during maximal plantar flexion expressed as a percentage of TA RMS during maximal dorsi-flexion.

For the MI training group, background EMG RMS of both SOL and MG muscles was determined at rest and during MI, in PRE- and POST-training measurements, and expressed as a ratio of the corresponding maximal M-wave (RMS/M_{max}). This ensured that the background level of muscular activity at rest was modified neither after MI training nor during MI.

For each muscle, the averaged peak-to-peak amplitude of each response was calculated and the following ratios were determined: $H_{\text{max}}/M_{\text{max}}$, $M_{\text{atHmax}}/M_{\text{max}}$, $H_{\text{sup}}/M_{\text{sup}}$, $M_{\text{atHsup}}/M_{\text{sup}}$ and V/M_{sup} and considered as dependent variables for statistical analysis.

Statistical analysis

All data are expressed by their mean ± standard deviation. The normality and the homogeneity of the data were verified by the Shapiro–Wilk test ($p < .05$) and the Levene test, respectively, in order to ensure that classical analysis of variance (ANOVA) could be used.

For all dependent variables at rest and during MVC repeated measure (rm) ANOVAs were performed, with *time* (PRE vs. POST) as within-subjects factor and *group* (Training vs. control) as between-subjects factor. Separate analyses were performed for each tested muscle.

When a main or an interaction effect was found, a post-hoc analysis was performed using an honest significant difference Tukey's test. Pearson's correlations (r coefficient) were assessed between the variation in performance (MVC, RFD) and the electrophysiological variables (H-reflex, V-waves, EMG–RMS) with P obtained in the Bravais-Pearson table (degree of freedom = 7). Statistical analysis was performed using STATISTICA (8.0 version, Statsoft, Tulsa, Okhlaoma, USA). Level of significance was fixed at $p < .05$.

Results

Maximal voluntary contractions

A significant interaction effect (Figure 1(A)) between *time* and *group* was found on MVC torques ($F_{1,16} =$

6.121, $p = .024$). Only the MI group significantly increased MVC torque (+9.64 ± 4.9%; $p = .012$); no changes were noticed for the control group (+3.04 ± 3.6%; $p = .821$).

No significant changes in background EMG activities (recorded at rest or during MI) were detected before, during or after MI training ($p > .40$ and $\eta_p^2 < 0.05$ for all comparisons). On the contrary, a significant interaction was found between *time* and *group* for normalized EMG during the plateau of MVC in both SOL ($F_{1,16} = 5.005$, $p = .039$) and MG muscles ($F_{1,16} = 6.138$, $p = .024$). In the MI training group, RMS/M_{sup} increased significantly for SOL ($p = .037$, Figure 1(C)) and MG ($p = .013$, Figure 1(D)), while it remained unchanged in the control group. Antagonist co-activation level did not show any significant change after the one-week period ($F_{1,16} = 0.304$, $p = .588$, Figure 1(B)).

Rate of torque development

A significant *group* × *time* interaction was found for the normalized RTD (RTD/MVC) during the three phases of the torque–time curve (Figure 2). The normalized RTD significantly increased for the MI training group by +17.6 ± 11.3% ($p = .04$) at 0–50 ms, by +22.2 ± 8.8% at 50–100 ms ($p = .01$) and by +20.1 ± 10.7% at 100–200 ms ($p = .01$), while it remained unchanged for the control group ($p > .5$).

Significant *time* × *group* interactions were found for the RMS/M_{sup} of SOL and MG muscles in the three time periods (all $p < .05$). MI training group significantly increased SOL and MG RMS/M_{sup} activity from PRE to POST in all time periods, while it remained unchanged for the control group (Figure 2).

Evoked responses

Figure 3 depicts typical recruitment curves of resting H-reflexes and M-waves from one participant of each group.

No significant main (*time* and *group*) or interaction effects were found for any of the M-waves (M_{atH} or maximal M) recorded in SOL and MG muscles at rest and during MVC. On the contrary, a significant *time* × *group* interaction was found for $H_{\max}/M_{\max}$ in SOL ($F_{1,16} = 7.296$, $p = .016$) and MG muscles ($F_{1,16} = 6.739$, $p = .019$). $H_{\max}/M_{\max}$ significantly increased after MI training by +19.3 ± 7.2% ($p = .037$) and by +60.1 ± 17.8% ($p = .038$) in SOL and MG, respectively; whereas it remained unchanged ($p = .616$ and $p = .903$ in SOL and MG, respectively) for the control group (Figure 4 (A,D)).

In addition, PRE- to- POST-training increases in MVC were significantly correlated to changes in SOL and MG $H_{\max}/M_{\max}$ (SOL: $r = 0.72$, $p < .05$;

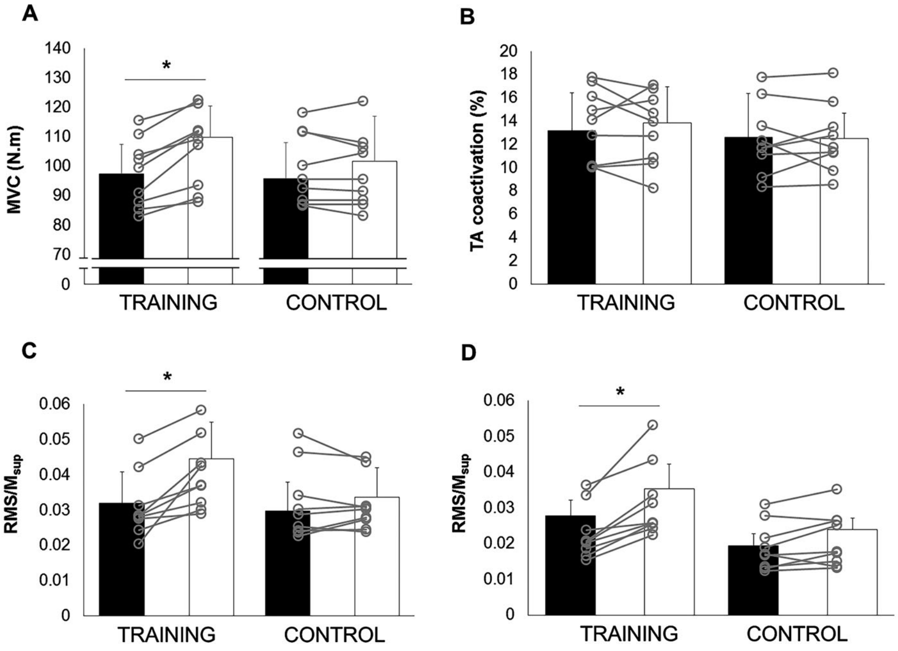

Figure 1. Maximal peak torques and normalized EMG activities. Data recorded before (black bars) and after (white bars) the one-week period, for the training ($n = 9$) and control ($n = 9$) groups. (A) Maximal voluntary contraction (MVC). (B) Co-activation level of the antagonist tibialis anterior (TA) muscle. (C) Normalized EMG activity in soleus muscle (SOL). (D) Normalized EMG activity in medial gastrocnemius (MG) muscle. Grey bars indicate individual performance.*: Significantly higher than values before training at $p < .05$.

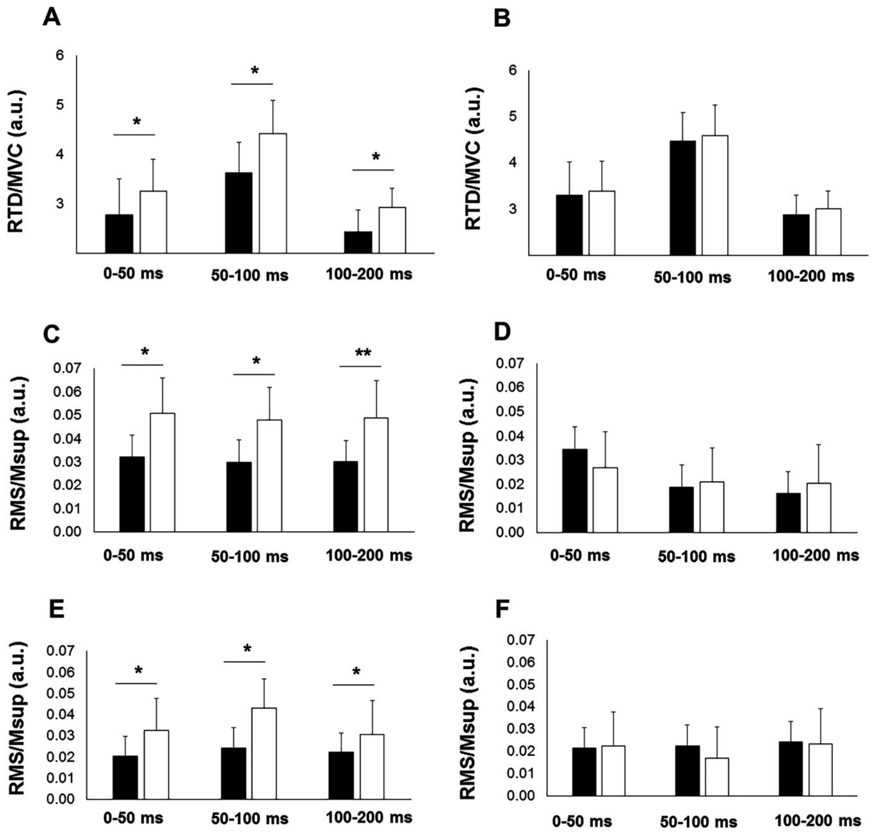

Figure 2. Maximal rates of torque development (RTD) and associated EMG activities. The RTD (normalized by the corresponding MVC) was obtained during the rise of the torque–time curve from onset to 50 ms (0–50 ms), 50 to 100 ms and 100 to 200 ms, before (black bars) and after (white bars) the one-week period for the training group (A) and the control group (B). Similarly, soleus (SOL) and medial gastrocnemius (MG) RMS/M_{sup} corresponding to these three periods are depicted for the training group (C and E, for SOL and MG respectively) and for the control group (D and F). *, **: Significant differences between PRE and POST at $p < .05$ and $p < .01$, respectively.

MG: $r = 0.86$, $p < .01$). The participants with the greatest MVC increase after MI training showed the greatest increase of H-reflex amplitude at rest. Similarly, the PRE-to-POST increase in maximal RTD obtained in each subject (in the 50–100 ms windows) was significantly correlated to the increase in H-reflex for both SOL ($r = 0.73$, $p < .05$) and MG ($r = 0.77$, $p < .05$).

During MVC, H_{sup}/M_{sup} did not show any main or interaction effect neither for the SOL ($p > .030$ for all comparisons, Figure 4(B)) nor for the MG ($p > .80$ for all comparisons, see Figure 4(E)).

The descending neural command, assessed with the V/M_{sup} ratio, was significantly modulated after MI training. A significant *time* × *group* interaction was found in SOL ($F_{1,16} = 6.532$, $p = .021$) and MG muscles ($F_{1,16} = 5.683$, $p = .029$). MI training group significantly increased V/M_{sup} ratio by +91.9 ± 45.9% in SOL ($p = .037$) and by +44.6 ± 34.1% in MG ($p = .016$). These increases were significantly correlated to the increases of MVC for both muscles (SOL: $r = 0.73$, $p < .05$; MG: $r = 0.71$, $p < .05$).

Discussion

The present study investigated for the first time the effects of one-week MI training on muscle torque capacity and the related contribution of supraspinal and spinal mechanisms. An increase of isometric torque and RTD was observed after one-week of MI training. This greater performance was accompanied by greater EMG activity recorded in both SOL and MG muscles. In parallel to this increase, spinal and supraspinal adaptations were also observed, as evidenced by greater H-reflexes at rest and greater V-waves for both muscles.

Increase in maximal torque and RTD

In the present study, the MI training group increased their plantar flexor MVC (+9.64 ± 4.9%), contrary to the control group. These results may appear in the usual range for MVC increase, large gains already being reported with such training modality (e.g. Yue & Cole, 1992: +22%; Zijdewind et al. 2003: +36%). Interestingly, the present study also showed

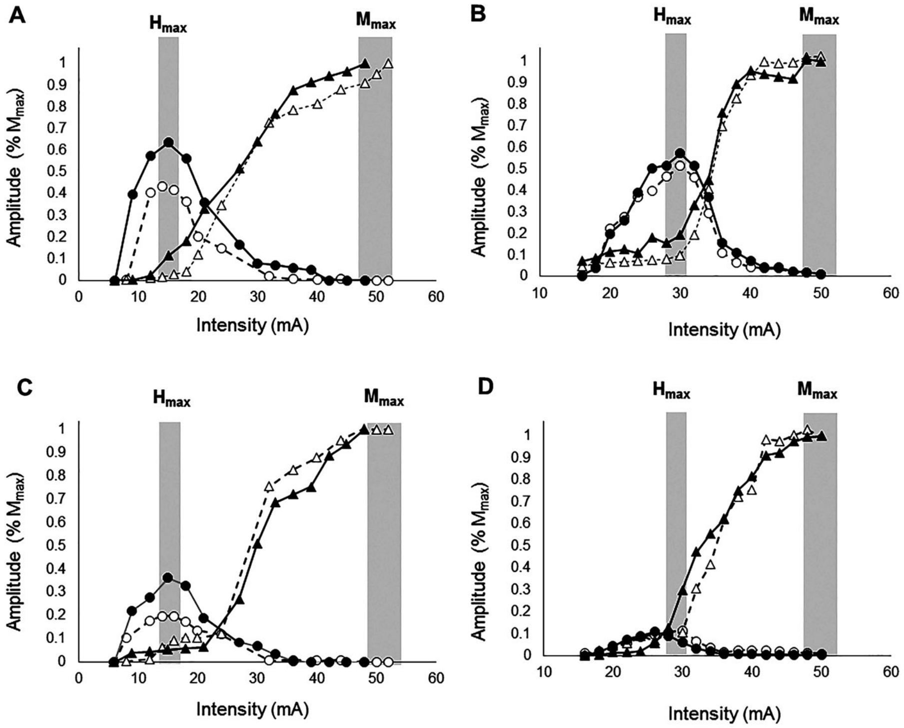

Figure 3. Representative recordings of soleus and medial gastrocnemius resting H-reflexes and M-waves. Representative recordings of the whole soleus recruitment curves (response amplitude plotted against stimulus intensity) of H-reflex responses (circles) and M-waves (triangles) recorded before (white dots) and after (black dots) the week, for one trained participants (A) and one control participant (B). Grey areas represent the intensities taken for H_{max} and M_{max} analysis. Response amplitudes are normalized by the corresponding maximal M-wave (M_{max}). Results of the medial gastrocnemius are similarly depicted for the same trained subject (C) and control participant (D).

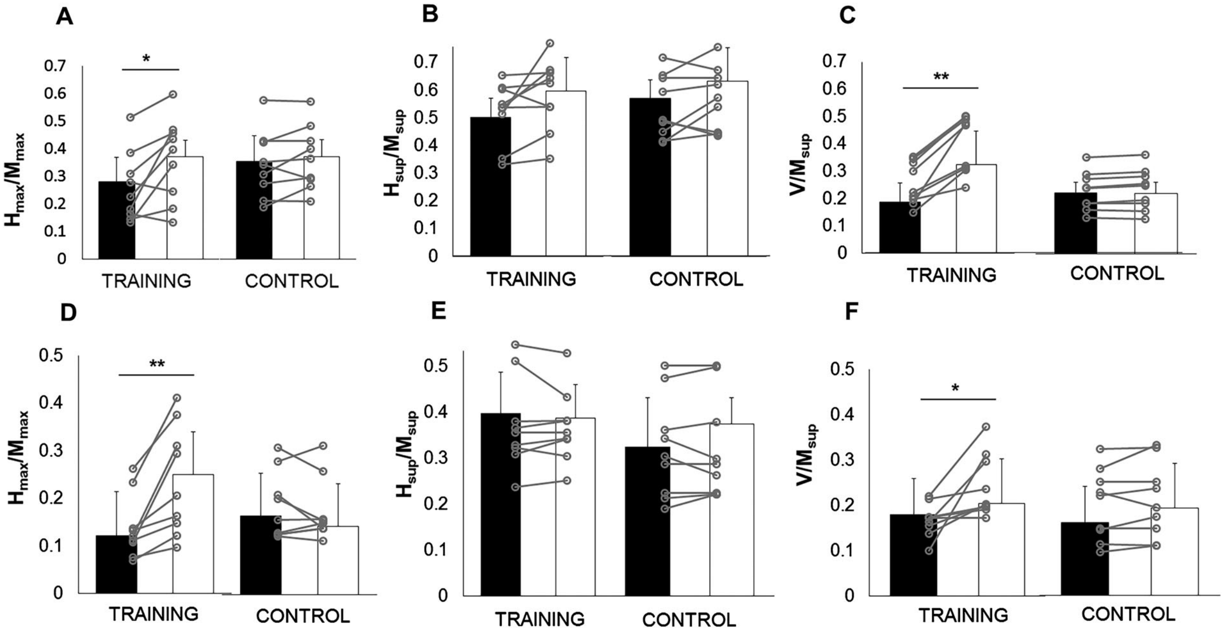

Figure 4. H_{max}/M_{max}, H_{sup}/M_{sup}, and V/M_{sup} ratios. EMG ratios of Soleus (A–C) and medial gastrocnemius (D–F) obtained at rest (H_{max}/M_{max}) and during the plateau of maximal voluntary plantar flexion (H_{sup}/M_{sup} and V/M_{sup}) before (black bars) and after the one-week period (white bars). Individual variations are represented by light grey lines and circles between bars. *, **: Significantly higher than values before training at $p < .05$ and $p < .01$ respectively.

an increase in RTD following MI training (+22.2 ± 8.8%) even more pronounced than the MVC increase. Interestingly, the RTD was more sensitive to training-induced changes in neuromuscular function than the plateau of isometric MVC and could be considered as a key component of sport performance and daily-life activities (Maffiuletti et al., 2016). The present findings confirmed the effectiveness of MI to improve strength capacity, although the benefits are lower than that following actual strength training, for which an increase of 20–30% for MVC and of 35–40% for RTD can be observed (Gruber & Gollhofer, 2004; Kubo, Kanehisa, Ito, & Fukunaga, 2001).

Based on the previous literature, the strength increase following MI training has been attributed to neural adaptations rather than muscular changes (Ranganathan et al., 2004; Yue & Cole, 1992), such as an optimization of the central command and a better coordination of muscles activations (Ranganathan et al., 2004). The present study showed no effect of MI training on tibialis anterior co-activation level, emphasizing the main contribution of the agonist activity to the strength gains. Indeed, the significant increase of RMS/Msup in both SOL and MG muscles of the training group, while M-waves remained constant from PRE to POST measurement, suggests a strong effect of MI training on the voluntary motor command. In line with the present results, many authors established a strong link between gains in RTD after physical training and such increase in agonist EMG activity (DelBalso & Cafarelli, 2007; DeRuiter et al., 2012).

The absence of background EMG change observed during the first as well as during the last MI session suggests that such an increase in central command is not related to specific muscle activity when performing the mental training. Moreover, the lack of M-wave amplitude modulation from PRE to POST indicates that MI training did not induce changes at the muscle level. Subsequently, the analysis of evoked responses to peripheral nerve stimulation should provide interesting clues regarding higher neural levels that contribute to the elaboration of the motor command, i.e. spinal and supraspinal levels.

Spinal adaptations

A significant increase of resting spinal excitability was observed after MI training, as evidenced by higher $H_{\mathrm{max}}/M_{\mathrm{max}}$ ratio in both SOL and MG muscles. This increase could not be the result of changes in stimulation conditions onto the posterior tibial nerve, since no changes in M-waves accompanying H-reflexes (M_{atH}) was observed on both muscles (Grosprêtre & Martin, 2012). In addition, this H-reflex increase was positively correlated to the increase in MVC and maximal RTD, as previously seen after actual training (Holtermann, Roeleveld, Engstrøm, & Sand, 2007). The increase of spinal efficiency is crucial in the enhancement of the discharge rate of motor units needed to improve RTD performance (VanCutsem, Duchateau, & Hainaut, 1998). It has been suggested that repeating the same task or stimulating the same pathway for an extended period of time (e.g. days or years) can result in long-term structural changes in spinal circuits (Tahayori & Koceja, 2012).

However, when tested during MVC, the superimposed H-reflex (Hsup/Msup) remained unchanged. In fact, this differs with actual training, showing an effect on both resting and active spinal excitabilities (Holtermann et al., 2007). This result indicates that MI did not involve a global arousal of spinal circuitry but has impacted specific circuits. Indeed, while H_{sup} involves both pre- and post-synaptic mechanisms, H_{max} changes are more likely attributed to presynaptic mechanisms, acting at the level of Ia afferent-to-alpha-motoneuron synapse, and to the excitability of the motoneurons itself. Although a direct change in alpha-motoneuronal excitability after training cannot be totally ruled out, MI was recently shown to result in a sub-threshold cortical motor output that could modulate the activity of spinal structures that mediates presynaptic inhibition of Ia terminal onto alpha-motoneurons (Grosprêtre et al., 2016). It is known from animal experiments that such structures are more sensitive to weak stimuli in comparison to alpha-motoneurons (Daniele & MacDermott, 2009). It can be suggested that the H_{max} increase after MI training might be the result of a reduction of spinal presynaptic inhibition rather than a direct impact on alpha-motoneuronal output, although this assumption deserves further experiments to be confirmed.

Supraspinal adaptations

At higher levels, the increase in V/M_{sup} ratio suggests a supraspinal adaptation following MI training. The fact that MI and actual movement share similar activations on many brain regions may be one of the main clues that allows such neural plasticity (Decety et al., 1994; Grèzes & Decety, 2001; Lotze et al., 1999). Particularly, previous studies using functional magnetic resonance imaging have evidenced that the primary motor cortex was widely activated during MI (Munzert, Lorey, & Zentgraf, 2009). In addition, a large majority of studies using transcranial magnetic stimulation over M1 areas showed a greater motor evoked potential during MI compared to rest (see Grosprêtre, Ruffino, & Lebon, 2015, for review). In the present study, the V-wave amplitude was evaluated, as a reliable index to quantify the cortical neural drive addressed to the spinal motoneuronal pool (Grospretre & Martin, 2014) and found to increase by 40–90% after MI training. The activation of primary motor cortices during MI practice may then induce an increase in the ability to produce a great cortical descending command. Indeed, some authors suggested, by observing greater brain activations in motor regions and resting state connectivity with functional magnetic resonance, that MI training may strengthen brain-to-muscle command, inducing greater spinal motor unit recruitment and descending command (Zhang et al., 2014). In the present study, the supraspinal origin of V-wave modulation is supported by the absence of change in H_{sup} amplitude, reflecting spinal excitability during MVC (Gondin, Duclay, & Martin, 2006). Therefore, the cortical reorganization that is often suggested as the main factor of the strength gains observed after MI training (Ranganathan et al., 2004) may also result in an increase of the cortical output addressed to the spinal motoneuronal pool.

Conclusion

The present study provides new insights into neural plasticity following MI practice. While the majority of the literature reports an increase of evoked potentials or brain activations during MI compared to rest (online effect), the present results brings evidence that one week of daily MI practice can result in an increase of the supraspinal command and in the rest spinal excitability, which may explain the gains observed in maximal force and RTD. Thus, the study supports previous studies for the use of MI in motor rehabilitation (Malouin & Richards, 2010; Schuster et al., 2011). Additional experiments would be useful to investigate the persistence of such gains following MI training. Further investigations using conditioning stimulation paradigms could also help identifying and isolating the specific corticospinal circuits involved after MI practice. On a practical point of view, this experiment probed the relevance of a short-term MI training on strength capacities. In addition, investigating the plantar flexors is of particular interest since ankle injuries are among the most common traumas and often results in the immobilization of the considered limb, thus preventing from using conventional physical therapy in the early stage of rehabilitation. Using MI practice at this stage would help fasten the recovery period.

Disclosure statement

No potential conflict of interest was reported by the authors.

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