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NEURAL PLASTICITY DURING MOTOR LEARNING WITH MOTOR IMAGERY PRACTICE: REVIEW AND PERSPECTIVES

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Abstract—In the last decade, many studies confirmed the benefits of mental practice with motor imagery. In this review we first aimed to compile data issued from fundamental and clinical investigations and to provide the key-components for the optimization of motor imagery strategy. We focused on transcranial magnetic stimulation studies, supported by brain imaging research, that sustain the current hypothesis of a functional link between cortical reorganization and behavioral improvement. As perspectives, we suggest a model of neural adaptation following mental practice, in which synapse conductivity and inhibitory mechanisms at the spinal level may also play an important role. © 2016 IBRO. Published by Elsevier Ltd. All rights reserved.

Keywords: Motor imagery, TMS, Learning, Plasticity.

Contents

INTRODUCTION

Motor skills, such as playing piano, basketball, or writing, are developed through extensive practice over several years. Movement learning involves several interconnected components: processing and collecting sensory inputs relevant to action, applying a series of decision-making strategies that define movement parameters (e.g., direction, duration, force), and activating feed-forward, reactive, and biomechanical control processes during motor performance (Wolpert and Flanagan, 2001). Two experimental paradigms are frequently used to study the neural processes underlying motor skill learning (Doyon and Benali, 2005; Shadmehr et al., 2010 for a review): (1) motor sequence learning with the incremental acquisition of movements in a specific behavior and (2) adaptation learning with the compensation for changes in the body or environmental dynamics. In both paradigms, several phases can be distinguished: (i) a fast phase, in which performance improvement occurs within the first training session; (ii) a consolidation phase, in which an enhancement of performance occurs at least 6 h after the first practice session; (iii) a slow phase, in which further gains can be achieved across several training sessions; (iv) an automatic stage, in which the motor task is performed automatically with poor cognitive demand; and (v) a retention state, in which the motor performance can be executed in the absence of any practice after a long delay (Doyon and Benali, 2005; Halsband and Lange, 2006).

Physical practice is undeniably vital for the acquisition and the consolidation of new motor skills (Robertson et al., 2004). Two well-assessed complementary methods for motor skill learning are action observation (Mattar and Gribble, 2005; Naish et al., 2014 for a review) and motor imagery – MI (Pascual-Leone et al., 1995; Gentili et al., 2010; Gentili and Papaxanthis, 2015; Schuster et al., 2011). During action observation, visual information implicitly activates the so-called *mirror neuron* system (e.g., Iacoboni et al., 1999; Buccino et al., 2001) and may improve the observer's motor planning process (Pozzo et al., 2006; Sciutti et al., 2012). On the other hand, MI is the explicit or implicit mental representation of action without concomitant movements. Implicit MI is commonly involved in mental rotation tasks, while explicit MI is used when ones is *specifically* instructed to mentally simulate an action. Different modalities frame

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MI: kinesthetic (based on sensory information normally generated during actual movement), haptic (using cutaneous information to recreate the interaction with external objects), visual (with external and internal perspectives), or auditory. One can use these modalities independently or combine them to potentiate the activation of the sensorimotor system during MI. Mental practice by means of MI is increasingly used for motor learning in healthy people (Dickstein and Deutsch, 2007) or for motor rehabilitation in patients (Malouin et al., 2013a).

Over the past twenty years, many studies have provided relevant information about the neurophysiological mechanisms underlying MI. Nonetheless, the neural stages (cortical, subcortical and spinal) involved in MI process are mainly probed separately. It is not clear yet whether motor learning with MI equally affects central and peripheral neural structures. This review aims to present recent findings on the neural aspects following MI practice, to provide guidelines about the strategy for motor learning with MI, and to suggest a model of neural adaptation as a perspective for future research. We particularly discussed data from transcranial magnetic stimulation (TMS) studies, supported by those recorded during brain imaging research. TMS is a reliable and non-invasive tool used in fundamental and clinical research to probe the level of corticospinal excitability during MI and the cortical plasticity after MI practice.

WHAT DO BEHAVIORAL AND COGNITIVE NEUROSCIENCES REVEAL ABOUT MI?

For many years now, scientists have tried to understand the functional and neural similarities between mental and actual movements. The mental chronometry paradigm, aiming to correlate the temporal content of actual and mental actions, has been extensively used. The results showed that the duration of both movements is conventionally equivalent (see Guillot and Collet, 2005 for a review). Regarding the neurophysiological component, previous reviews, mainly focusing on fMRI data, have excellently presented the neural link between mental and actual states (Hétu et al., 2013). However, single-neuron recording studies showed specific activations during MI in comparison to actual movement (Amador and Fried, 2004; Leuthardt et al., 2004; Anderson et al., 2011). For example, Amador and Fried (2004) showed that the neurons in the supplementary motor area differentiated between actual and imagined movements.

To extent these results, we presented TMS studies that assessed the neural processes of MI and the mechanisms of neural modulation following mental practice with MI. This non-invasive technique with high temporal resolution presents many advantages to assess the level of corticospinal and intracortical excitability. TMS is extensively used in cognitive neuroscience to determine the involvement of brain areas and the temporal specificity. In the mid-80s, Barker et al. (1985) presented a technology designed to stimulate cortical areas that was less painful than electrical stimulation. The authors used a magnetic field to activate neurons located a few centimeters under the coil. A brief stimulation over the cortical representation of a body part in M1 activates the corticospinal track and induces a response in the corresponding contralateral muscle. This response is called a motor-evoked potential (MEP, see Loporto et al., 2011 for physiological and technical details). TMS can also be placed over other cortical areas to disrupt the activation of the targeted area and to explore the neural network underlying a specific behavior. Nowadays, this non-invasive technique is extensively used in fundamental and clinical studies and, by extension, in MI paradigms. A total of 164 articles, published between 1995 and 2016, were found through an online search with the PubMed (https://www.ncbi.nlm.nih.gov/pubmed/) and Google Scholar (https://scholar.google.fr/) databases, combining the terms "TMS" with "mental imagery", "motor imagery" or "mental practice". We selected all articles that presented mental/motor imagery and mental practice studies that used TMS as a technique to probe the underlying neurophysiological mechanisms (see Table A.1 in Appendix). Eighty-three TMS papers on this topic, i.e. 50%, have been published since 2010, showing the significant growing interest for this research field. When placed over M1, TMS elicited MEPs in the contralateral effector, a probe of corticospinal excitability, mostly during explicit mental imagery (78% of the papers; see Fig. 1) and very few during implicit mental imagery (2.4%). To our knowledge, only five studies (3%) measured corticospinal excitability before and after mental practice with MI, controlling cortical plasticity (Pascual-Leone et al., 1995; Bassolino et al., 2013; Leung et al., 2013; Avanzino et al., 2015; Volz et al., 2015). Finally, TMS placed over non-M1 areas in mental imagery studies were used to disrupt activity in this area and to assess its relevance to the mental task or to further understand the neural network (e.g., Ganis et al., 2000; Lebon et al., 2012b).

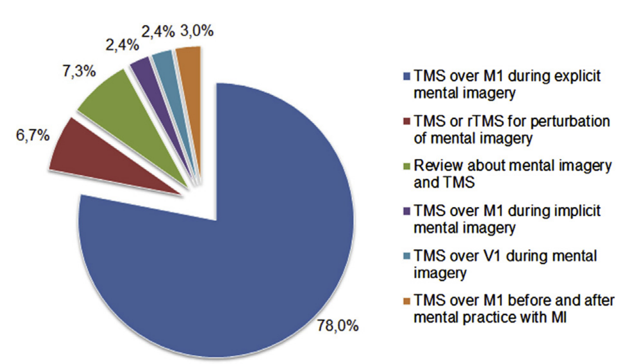

Fig. 1. Graphic distribution of transcranial magnetic stimulation (TMS) studies in mental imagery research. Mental imagery embraces motor imagery that includes all sensorimotor information that one can experience when interacting with the environment and non-motor imagery that involves any other activities that do not affect one's motor behavior (e.g., mental picturing or mental rotation of letters). Explicit and implicit mental imagery is the mental representation that one experiences consciously and unconsciously, respectively. Mental practice is the repetition of mental representations used for learning, training and rehabilitation. M1 = primary motor cortex; V1 = primary visual cortex; rTMS = repetitive TMS.

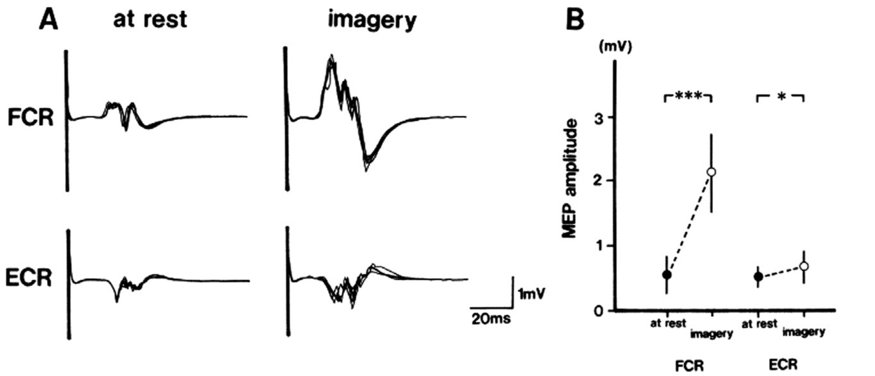

Fig. 2. Muscle-specificity of corticospinal excitability. Motor-evoked potentials increased in flexor carpi radialis (FCR), but not in extensor carpi radialis (ECR), during imagery of hand flexion (courtesy of Kasai et al. (1997)).

Single-pulse TMS over M1 is the main stimulation type used in this field of research. Peak-to-peak amplitude of the MEP is the most commonly reported measurement and is used as a marker of corticospinal excitability at the time of stimulation (Rossini et al., 1999). An increase in the amplitude of the MEP recorded in the relaxed contralateral muscle is generally observed during MI when compared to rest (Fig. 2). This increase reflects a facilitation of the corticospinal track, which is produced by a decrease in the cortical motor threshold of the corresponding muscle and/or a greater number of recruited motor neurons (Kasai et al., 1997; Yahagi and Kasai, 1998). These corticospinal facilitatory effects indicate that MI can induce online synaptic adaptations in M1, leading to rapid shifts in output representation patterns (Rossi and Rossini, 2004). It must be noted that this facilitation is muscle-specific (Fadiga et al., 1998; Yahagi and Kasai, 1998, 1999; Rossini et al., 1999; Tremblay et al., 2001; Facchini et al., 2002; Stinear and Byblow, 2003, 2004), time-specific (Fadiga et al., 1998; Hashimoto and Rothwell, 1999; Stinear and Byblow, 2003, 2004; Stinear et al., 2006b; Levin et al., 2004), and content-specific (Yahagi and Kasai, 1998; Li et al., 2004; Stinear et al., 2006a; Mizuguchi et al., 2013). Indeed, MEP amplitude increases only in the muscles that were functionally related to the imagined movement (Marconi et al., 2007) and for the period during which participants imagine the movement. This muscle and time specificity is even more pronounced when the imagery ability is greater (Lebon et al., 2012a), i.e. when behavioral and psychophysiological measurements during MI mimics those during actual execution. Furthermore, kinesthetic imagery is more often used in MI paradigms, since it activates the motor cortex to a greater extent than visual imagery (Stinear et al., 2006a). This is consistent with studies using different neurophysiological techniques (e.g., Guillot et al., 2009b for fMRI data and Stecklow et al., 2010 for EEG data).

Paired-pulse TMS was also used to assess short-interval intracortical inhibition during MI (SICI, described in Kujirai et al. (1993)). In this technique, two TMS pulses are triggered over M1 with a single coil. The first subthreshold stimulus activates low-threshold inhibitory inter-neurons. It is followed by a second suprathreshold stimulus (between 1 and 5 ms) that makes the pyramidal neurons fire. The percentage of SICI is measured by dividing the MEP amplitude elicited by the paired pulse with the MEP amplitude elicited by the single suprathreshold pulse. A decrease in SICI was observed when subjects imagined finger movements, although no contraction was recorded or expected (Abbruzzese et al., 1999; Stinear and Byblow, 2004; Kumru et al., 2008; Liepert and Neveling, 2009). This reduction of inhibition within M1 could explain corticospinal facilitation during MI (Ridding et al., 1995).

Recently, double-cone coil TMS protocols provided insights into inter-hemisphere processes. For example, Lebon et al. (2012b) stimulated the right inferior parietal lobule (rIPL) 12 ms prior to the contralateral M1. The authors used the neuronavigated technique (TMS combined with MRI data) to spot rIPL and the optimal scalp position in M1 (motor hotspot). They observed during MI a decrease in MEP amplitude after the double stimulation, when compared to MEP amplitude after a single TMS over M1. These results support the idea that rIPL forms part of a distinct inhibitory network that may prevent unwanted movement during imagery tasks. However, this inhibitory process may also involve other cortical and subcortical areas (see Guillot et al., 2012 for a review). For example, Lotze et al. (1999) found a differential activation in the cerebellum during MI and actual execution: the greater activation of the posterior lobe during MI may be involved in movement inhibition while imagining.

Finally, another TMS technique, known as cortical mapping, is able to assess the cortical (re)organization of M1 during a specific task or after an event (motor learning or injury, see Tyc and Boyadjian, 2006, for a review). In this technique, a TMS map is generated by measuring the amplitude of MEPs evoked at an identified scalp site and quantifying the intensity and volume of the activation (e.g., Brasil-Neto et al., 1993; Thickbroom et al., 1999). A grid is positioned over M1 and centered on the motor hotspot of the targeted muscle. Each point of the grid is stimulated via the TMS coil and the potential response is measured at the periphery. Note that the number of, and the distance between, stimulation sites vary across studies. Up to now, very few studies have used this technique to assess cortical organization during MI (e.g., Vargas et al., 2004; Marconi et al., 2007; Bassolino et al., 2013). For example, Marconi et al. (2007) mapped out the cortical representation of hand and forearm muscles while imagining (or observing) repeated opposition of the thumb and the little finger. TMS mapping of the right and left hemisphere was performed when participants imagined or observed movements of the left and right hand, respectively. The authors used a grid, with 49 points equally spaced by 1.5 cm, along the medio-lateral and the antero-posterior axes. They measured the mean map area, defined as the number of scalp positions stimulation of which evoked

MEPs in the studied muscle, and the mean map volume, set as the sum of MEP amplitude from all sites showing MEPs in all participants. They found that MI and action observation increased map area and map volume, when compared to rest, in the prime mover (Opponens Pollicis) and in the synergist muscles (forearm muscles) only. The effect was even more marked in the left hemisphere. The authors also observed a functional overlap in the cortical representation of different muscles across tasks (rest, MI and action observation; see Fig. 6 in Marconi et al., 2007). They concluded that both MI and action observation do not change single muscle motor responses and that the hand/forearm muscle maps extensively overlap during motor-cognitive tasks. Interestingly, Vargas et al. (2004) demonstrated that the cortical map reflects the interference between the hand posture and the mental simulation of a hand movement. When the posture was compatible with the imagined movement, the cortical map area in M1 was more extended when compared to rest. The inverse pattern was observed for posture incompatible with MI. This modulation seems to result from the interaction between the facilitatory effects driven by MI and the hand-shaping effects driven by proprioceptive information (Vargas et al., 2004). This increase in excitability may relate to the fast phase of motor learning, when one explicitly focuses on the components of the movement.

The above-referenced papers suggest that the motor cortex integrates internal (e.g., kinesthetic, haptic) and external (e.g., visual, contextual) information to create a neural representation of the simulated action. These components may explain the benefits of MI during motor learning.

MOTOR LEARNING WITH MI TRAINING

The literature in sport psychology has provided several years ago relevant information about the positive effects of MI practice on motor performance (see Feltz and Landers, 1983; Driskell et al., 1994, for meta-analysis). Athletes and musicians extensively use mental practice, in addition to physical practice, to improve their dexterity (Jeannerod, 2006). Mental practice with MI improves several aspects of motor performance, such as muscle strength (see, Yue and Cole, 1992; Ranganathan et al., 2004), movement speed, accuracy and variability (Pascual-Leone et al., 1995; Gentili et al., 2006, 2010; Gentili and Papaxanthis, 2015). Recently, Schuster et al. (2011) reported the characteristics of successful MI interventions in five disciplines (sport, medicine, psychology, education and music) from 133 studies. Benefits after MI training occurred mostly in motor and strength-related tasks, and with participants of both genders, aged between 20 and 29 years (see Tables 3–7 in Schuster et al., 2011, for an overview of MI training studies). Interestingly, MI benefits rely on specific characteristics such as the imagery modality (kinesthetic or visual), the isochrony between imagined and actual execution, or the environment in which the intervention is performed. Several models offer a detailed description of the key-components of MI content (e.g., the PETTLEP model, Holmes and Collins, 2001; the MIIMS model, Guillot and Collet, 2008). For example, Holmes and Collins (2001) introduced the PETTLEP framework, building on findings in the functional neuroscientific research literature and experience in sport psychology. This method aims to facilitate designing MI interventions for athletes, and comprises seven components (physical, environment, task, timing, learning, emotion and perspective). All published experiments using the PETTLEP model indicated a positive effect of MI practice on performance (e.g., Smith et al., 2008; Wakefield and Smith, 2009; Wright and Smith, 2009).

Despite the fact that extensive proof exists demonstrating the positive effects of mental training on motor performance, little is known about the neural origins of this benefit. The lack of information may be due to the complexity of the motor tasks (e.g., mostly whole-body movements) and the reported variables (such as successful attempts at basketball shoots, rather than analytical data from movement kinematics and EMG). To fill this gap, recent studies, especially over the past five years, have focused on simpler tasks involving distal muscle movements and have used behavioral and physiological recordings (e.g., mental chronometry, kinematics, electrooculography) to infer modulations of the nervous system. For example, Gentili et al. (2006, 2010) conducted a couple of experiments in which mental training aimed to improve movement speed. Both experimental designs involved a target-aiming sequence (from 1 to 11) that required arm movements. The aim of the experiment was to reach with the index the targets from 1 to 11 as fast as possible (Fig. 3A). Participants were instructed to actually perform the sequence (PP Group), to imagine themselves performing it (MP Group), to train their eyes on the target without moving their arm or imagining moving it (AC Group), or to remain at rest (PC Group). In post-test sessions, hand movement duration and peak acceleration decreased and increased, respectively, only after physical and MI practice (Fig. 3B). Interestingly, the authors also observed a partial learning generalization, namely an enhancement of motor performance for the non-training sequence (from target 10 to 1). Finally, trial-by-trial recordings showed that gains during mental practice followed a similar asymptotic learning curve as seen during physical training (Gentili et al., 2010). Recently, Gentili and Papaxanthis (2015) demonstrated the superiority of the dominant arm in motor learning with mental practice for the same speed/accuracy trade-off task. The performance increase was smaller in the non-dominant arm following acute MI training. The specific adaptations during motor learning with mental practice have to be considered in further MI research/intervention.

Optimal strategy for motor learning with MI

The different models (PETTLEP or MIIMS) consider the parameters for which MI is efficient (see above). Recent findings provided additional information aimed to perfect the optimal strategy for motor learning with MI. Heremans et al. (2011) investigated the functional role of eye movements during MI practice of a speed-

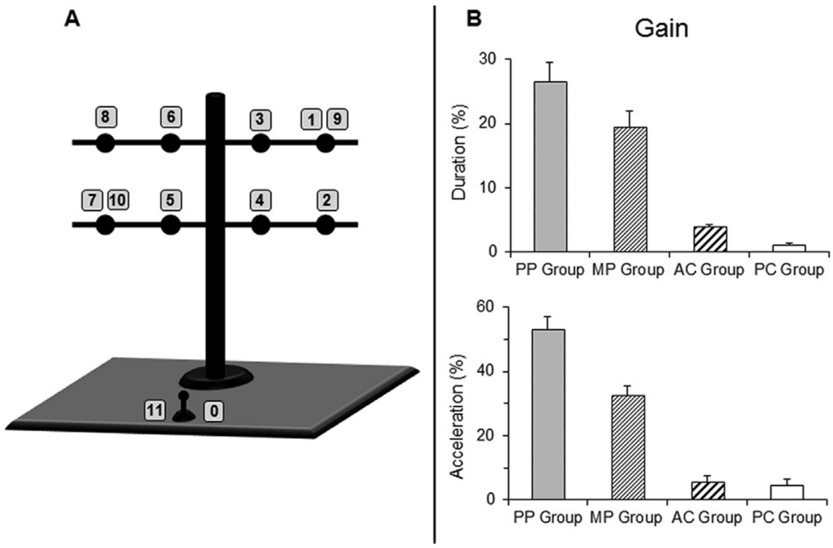

Fig. 3. Improvement of motor performance after motor imagery practice. The material and results of Gentili et al.'s study (2006) are graphically represented here. (A) Material: the aim of the study was to reach with the index the targets from 1 to 11 as fast as possible. (B) Results: the approximate gains observed in the study are represented. The authors found a decrease of movement duration and an increase of peak acceleration, only for the Physical (PP) and the Mental Practice (MP) group. AC: active control group; PC: passive control group.

accuracy task (Fitts' task). During a four-day training, participants were required to imagine themselves aiming at several targets with their non-dominant hand, either with their eyes fixed or with no particular instructions about eye movements in order to measure their spontaneous eye-movement behavior. A third control group received no training. The results showed that movement duration decreased over time in all groups. Task accuracy and efficiency, however, was enhanced to a greater extent after MI training, and even more when participants followed the trajectory with their eyes while imagining. The authors concluded that eye movements during MI practice affected the spatial parameters of the trained movement only, thus confirming previous results that reported no effects of eye movements on temporal parameters (Gueugneau et al., 2008; Debarnot et al., 2011). Indeed, Gueugneau et al. (2008) found that eye movements during MI were not necessary to preserve the temporal similarities with actual movement production. Interestingly, Heremans et al. (2011) tested the intermanual transfer of MI practice by measuring the performance of the untrained (dominant) hand. They found that the greatest performance gains appeared for the group of MI practice accompanied by eye movement. The authors concluded that eye movements during MI practice have an effect on the central movement representation of a coordination pattern. Altogether, during the learning process with MI practice, the central nervous system may integrate eye movements as an input to the internal predictive model, and thus facilitate the accuracy of MI. The benefits of mental practice may partially stem from the so-called efferent copy, reflected in the activations of the motor cortex. On the basis of an efferent copy of the motor command and the actual state of the limb, the brain can predict the future state of the limb – predicting the consequences of a motor command is called a forward model – and thus improve motor performance and recall movement parameters once instructed to actually perform the action (Wolpert and Flanagan, 2001).

Interestingly, some studies highlighted the positive effects of sleep after MI practice on memory consolidation (Debarnot et al., 2009a, b, 2010, 2011). For example, Debarnot and colleagues found that a night's sleep (2009a) and a daytime nap following MI (2011) elicited improvement in performance (accuracy and movement duration) in a finger sequence task, reflecting a significant offline consolidation process. By contrast, a comparable interval of time during the daytime (without intervening sleep) did not result in any performance gains. Overall, these results reinforce the idea that performance improvement following MI are somewhat sleep-dependent, thus suggesting that a night's sleep after MI practice results in similar motor memory consolidation as when following physical practice.

Another important parameter to consider before starting a mental training is the duration of the session. Indeed, Gentili et al. (2010) showed that the concentration of the subjects decreases after 60 imagined movements' repetitions. Although a mental training session does not appear to induce neuromuscular fatigue (Rozand et al., 2014), a recent study demonstrated that a prolonged motor imagery session decrease the motor imagery accuracy (Rozand et al., 2016). The authors observed an increase of imagined movement duration, after 100 repetitions, and this augmentation could be explained by the emergence of mental fatigue. Surprisingly, the fatigue was not observed when actual movements were inserted between imagined movements. These results provide valuable information on the maximum number of imagined repetitions and on the prevention of mental fatigue during MI practice.

Finally, the design of MI intervention is of importance regarding the potential benefits of mental practice. Debarnot et al. (2015) compared variable and constant MI practice on visuomotor task performance. They found that alternating the test task with similar imagined movements but with different sequences induced a greater consolidation and a better transfer to novel sequence, after a night's sleep. In addition, motor learning with MI appears to provide greater benefit in complex tasks than in simple ones (Allami et al., 2008). These authors observed greater motor performance enhancement when the difficulty of the task increased, promoting greater potential gain.

A variable MI intervention oriented for complex motor tasks and performed preferentially during late morning or mid-afternoon may be the optimal strategy to achieve the greatest benefits. The consolidation process may be prominent after a night's sleep, supporting the neural plasticity hypothesis induced by mental practice. To further support the benefits of MI training, it is of importance to probe the cognitive changes associated with behavioral modulations in healthy subjects and patients.

COMBINATION OF MI WITH OTHER INTERVENTIONS

Above, we reviewed the benefits of mental practice with MI on performance improvement. Some authors also focused on the combination of MI with different interventions, to further understand the contribution of such techniques to cortical reorganization and motor learning.

MI combined with physical practice

There is now growing evidence that a combination of MI and movement execution induces greater, if not equivalent, changes than mental or physical training alone (e.g. Jackson et al., 2004; Vergeer and Roberts, 2006; Allami et al., 2008; Avanzino et al., 2009; Smith et al., 2008, 2009). For example, Frank et al. (2014), studying novice golfers, compared their putting performances and their mental representation structures following physical, mental or combined training. The authors suggested that "mental practice promotes the cognitive adaptation process during motor learning, leading to more elaborate representations than physical practice only". To provide important information about the repartition and the proportion of actual or imagined movements during motor learning, Allami et al. (2008) compared, for a fixed number of trials, different percentages of imagined movements (0%, 25%, 50%, and 75%) completed by actual execution for the remaining trials. The authors found that the greater the number of imagined movements (distribution of 50% and 75% imagined trials), the greater the motor improvement, especially when the task was difficult.

Such a combined intervention is predominant in rehabilitation studies, in which patients follow the conventional recovery process. In these studies, the experimental group is instructed to mentally rehearse the movements of their affected limb and the control group to perform a neutral cognitive task (Guillot et al., 2009a, with burn patients; Page et al., 2001; Jackson et al., 2004; Malouin et al., 2004, with stroke patients; see Braun et al., 2006, and Malouin et al., 2013a for reviews). In the majority of the studies mentioned above, combined intervention led to superior motor recovery. However, this positive outcome needs to be put into perspective. Malouin et al. (2013a) published a critical review of the factors influencing benefits derived from mental training, in terms of adherence to the training, the dose of MI intervention, the relaxation component, the outcomes measured, the group heterogeneity, the selection of patients and the nature of MI instructions. The benefits of MI delivery will only be relevant, especially in a clinical environment, once all the components have been clearly described and their respective efficacy understood. To achieve a better performance with MI practice, Malouin et al. (2013a) recommended first familiarizing the participants with MI. It seems also interesting to associate MI with physical practice and to add sessions of self-practice to increase the number of repetitions.

MI combined with action observation

During the 90s, a group of Italian scientists discovered mirror neurons in the motor cortex of monkeys. These neurons are activated both during actual execution and during observation of the same task (Gallese et al., 1996; Rizzolatti et al., 1996). In human studies, it has been found that MEPs in hand muscles increased when subjects observed hand movements of another subject (e.g., Fadiga et al., 1995; Maeda et al., 2002). Interestingly, MI and action observation encompass similar neural processes, such as muscle-specificity. Gangitano et al. (2001) showed that an increase in MEPs was closely related to the different phases of hand flexion/extension: greater MEPs in hand flexor muscles only during observation of the flexion phase. Interestingly, Sakamoto et al. (2009) found that the combination of MI and observation increased MEPs to a greater extent. This effect was only observed when the two interventions were congruent. More recently, Wright et al. (2014) showed that the facilitation of corticospinal excitability during the combined condition was muscle-specific, i.e., only present in the muscle involved in the task.

In their review, Vogt et al. (2013) highlighted the benefits of combining MI and action observation for motor performance, but also noticed that only few studies explored their interaction. The authors suggested three kinds of combination. First, during congruent MI and action observation, the observer imagines the action, while observing a third person performing the same type of action. This combination may represent the most practically relevant scenario, and seems to induce stronger activations in a number of execution-related areas (Macuga and Frey, 2012). Secondly, one could imagine an action in response to an observed movement, a combination called coordinative MI and observation, also known as joint action. This approach would reflect, to a greater extent, daily interactions during which a reaction more than an imitation is expected. Finally, conflicting MI and action observation may be used to further understand the biases effect of MI on observed actions, and inversely. These different types of combination could offer a novel approach, with a view to finding other applications in sport, occupational therapy, and neurorehabilitation (Vogt et al., 2013).

MI combined with cortical stimulation

In the case of motor impairment following central or peripheral damage, functional rehabilitation through physical execution is challenging and demanding. One solution is to 'boost' activation of the motor network and to potentiate functional reorganization. Recent techniques, such as repetitive TMS and transcranial direct current stimulation (TDCS), are relevant enough to potentiate M1 and facilitate neuroplasticity during motor (re)learning (Reis and Fritsch, 2011). TDCS is a non-invasive brain stimulation technique that applies a weak direct electrical current via the scalp to modulate cortical excitability in the human brain in a painless and reversible way (Nitsche and Paulus, 2000). The current can either hyperpolarize (cathodal stimulation) or depolarize (anodal stimulation) neuronal membranes. Foerster et al. (2013) investigated the association of MI practice and TDCS on motor performance improvement. MI sessions were accompanied with sham or active anodal stimulation over the right supplementary motor area, right premotor area, right cerebellum, right M1 or left dorsolateral prefrontal cortex. The authors observed greater motor improvement in the left (non-dominant) hemibody after mental practice with anodal stimulation only over right M1 and left dorsolateral prefrontal cortex. These findings highlight the importance of the activation of those areas in the long-term potentiation-like processes associated with motor learning following mental practice. More recently, Saimpont et al. (2016) also studied the combination between MI practice and TDCS, on a finger tapping task. As for the previous study, the application of electrical stimulation by TDCS during MI practice induced greater effect than MI practice alone or TDCS alone. More interestingly, these effects remained observable 90 min after the end of training. Although the combination of MI with cortical stimulation did not contribute to a larger number of publications, interest in this intervention may help to further understand the neural mechanisms underlying MI and to determine the most relevant way to enhance motor performance following mental practice with MI.

CORTICAL PLASTICITY FOLLOWING MI PRACTICE

Cortical representations over a lifetime are not fixed but highly dynamic (Sanes et al., 1988; Buonomano and Merzenich, 1998; Rossini et al., 2003). In response to peripheral and central inputs and outputs, the architecture of neural connections is continuously being reorganized. Therefore, experience can modify brain structure (Mulder, 2007) and constitutes an important component in learning and, more especially, during recovery after neural damage. The decrease of afferent information sent to the brain, following disuse or impairment (e.g. deafferentation), induces a reduction in size of the muscle topographical representation in the somatosensory (Merzenich et al., 1983) and motor cortex (Avanzino et al., 2011). These findings have been replicated extensively (see Allard et al., 1991; Brasil-Neto et al., 1993; Merzenich and Jenkins, 1993). Sensorimotor adaptations during MI training reveal the integration of information from the environment to construct and modulate in real-time the motor program, even in the absence of voluntary movement. Michel et al. (2013) showed that prism adaptation also occurred when participants imagined arm pointing movements. This was testified by significant after-effects following prism exposure associated with mental practice. Using force field perturbation, Anwar et al. (2011), Anwar and Khan (2013) found that MI training induced greater after-effects and reduced muscle co-contraction. The authors suggested that MI training may facilitate motor learning and could be used to increase the rate of adaptation. These findings indirectly demonstrate cortical plasticity due to mental practice. In this following section, we specifically focused on corticospinal reorganization related to mental practice in healthy participants and patients.

Cortical plasticity in the healthy population

Pascual-Leone et al. (1995) were the first to show cortical reorganization induced by mental practice. Their study is still widely quoted when reporting MI benefits on motor performance. The authors used the TMS technique to map the primary motor cortex area targeting the contralateral hand muscles before and after a 5-day learning period. The task relevant to our topic consisted in repeating a 5-finger exercise on the piano in time with a metronome. During 2-h practice sessions, participants were instructed to either actually perform the task or to visualize their fingers performing the exercise and to imagine the sound. The performance of each participant was tested daily and followed by TMS mapping. After 5 days of training, both groups showed progressive skill improvement, testified by the reduced number of errors and the reduced variability in the intervals between key presses. Similarly, cortical representation of long finger flexor and extensor muscles in contralateral M1 increased after actual and mental practice (Fig. 4). This finding suggests that mental training with MI produces cortical changes comparable to those elicited through physical practice (Pascual-Leone et al., 1995). An extension of this experiment is discussed below.

To support these findings, Avanzino et al. (2015) tested cortical plasticity in M1 following mental practice, using the paired associative stimulation (PAS) technique. This intervention consists in repeating the combination of peripheral nerve stimulation and TMS. The inter-stimulus interval of 10 and 25 ms reduces (long-term depression-like plasticity, LTD) and increases (long-term potentiation-like plasticity, LTP) corticospinal excitability, respectively (Stefan et al., 2000, 2002; Ziemann, 2004). Participants were instructed to actually or mentally repeat finger opposition as quickly as possible during an acute training session. Speed rate increased after both physical and MI practice. The authors observed a reversal of the PAS25 effect from LTP-like plasticity to LTD-like plasticity following physical and MI practice. Interestingly, LTD-like plasticity (PAS10 protocol) increased after physical practice, while it was occluded after MI practice. These results reveal that, in addition to cortical reorganization, MI practice strengthened the synaptic connectivity (see Rosenkranz et al., 2007 for actual motor learning).

Imaging studies (PET and fMRI) assessing the hemodynamic changes in the brain further support cortical reorganization following MI practice. For example, Jackson et al. (2003) used a PET scan to demonstrate that learning a sequential motor task through MI and physical practice induces similar cerebral functional changes, i.e., increased activation of the orbitofrontal cortex and a decrease in the cerebellum. Moreover, the findings concord with the hypothesis that MI practice

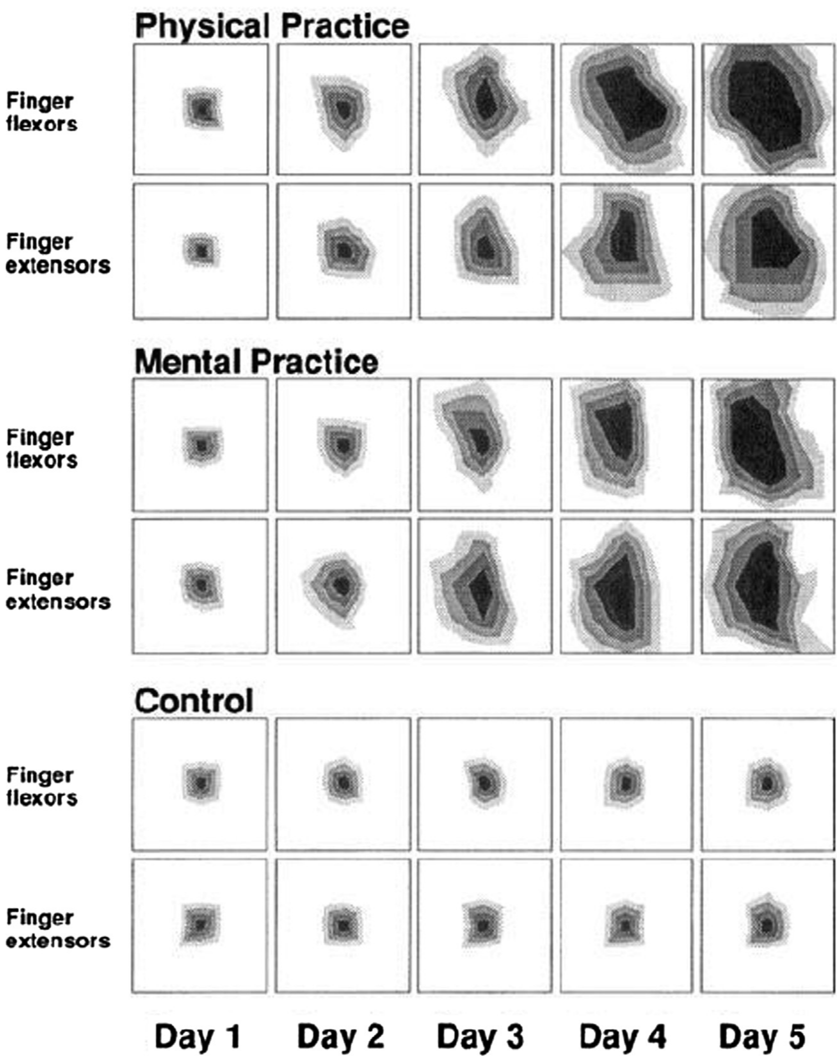

Fig. 4. M1 plasticity after mental practice measured by TMS. After physical and mental practice of finger-sequence task, the authors observed a larger cortical map representing the long finger flexor and extensor muscles in contralateral M1 (courtesy of Pascual-Leone et al. (1995)).

improves performance, at least initially, by acting on the preparation and anticipation of movements rather than on execution per se (Jackson et al., 2003). Interestingly, Lafleur et al. (2002) observed changes bilaterally in the dorsal premotor cortex and cerebellum, and in the left inferior parietal lobule during the early phase of physical learning. However, after the end of training, most of these brain regions (e.g., cerebellum and dorsal premotor cortex) were no longer significantly activated, suggesting that they are critical for establishing the cognitive strategies and motor routines involved in early sequence learning (Lafleur et al., 2002). On the contrary, cortical activation after practice increased bilaterally in the medial orbitofrontal cortex and striatum, as well as in the left rostral portion of the anterior cingulate and a different region of the inferior parietal lobule. The authors suggested that these structures play an important role in the development of a long-lasting representation of the movement sequence. Interestingly, a similar pattern of dynamic changes was observed in both phases of learning during MI practice. This latter finding suggests that the cerebral plasticity occurring during incremental acquisition of a motor sequence executed physically is reflected in the covert production of this skilled behavior using MI (Lafleur et al., 2002). Similar results were observed by Lacourse et al. (2004). The authors compared the functional reorganization of the cortex after one week of intensive training of mental and physical sequential movements. Following MI practice, motor performance improvement was accompanied by activations of the cerebellar, premotor and striatal areas, while physical practice showed increased activation in the striatal area and decreased activation in the cerebellum. The principle of functional equivalence (Jeannerod, 1994) appears to extend from novel learning to skilled learning phases for both upper and lower limb movements (Lacourse et al., 2005).

Dynamic changes in motor behavior may be reinforced by sensorimotor inputs evoked by overt activation performed after mental practice. In the study by Pascual-Leone et al. (1995), the MI group showed a significant increase in performance after 5 days of training, but this improvement was even greater for the physical group. However, no neurophysiological differences were observed between the two groups after 5 days of training. The difference between behavioral and neurophysiological data might be explained by the limits of the TMS technique to identify fine neural changes that could explain performance differences. Studies using PET (Lafleur et al., 2002; Jackson et al., 2003) or fMRI (Lacourse et al., 2004) observed small but distinct differences in intensity and location of brain activations between physical and MI training. These differences in activation and performance may arise from the absence of sensory feedback while imagining. Pascual-Leone et al. (1995) showed an equivalent performance between a physical and an MI group, when the latter performed a 2-h physical practice at the end of the fifth day of MI practice. This highlights the importance of additional sensory feedback for the consolidation of neural modifications induced by mental training. When participants were unable to move after imagining, no such cortical modulations were observed (Crews and Kamen, 2006). Bassolino et al. (2013) showed that the cortical map of the first dorsal interosseous muscle, assessed by TMS, was reduced after 10 h of immobilization of the hand and the forearm, even if participants imagined moving their hand during the immobilization period. This result supports the hypothesis of an afference-dependent relationship between MI practice and cortical plasticity. In contrast, Clark et al. (2015) recently showed that MI training reduced strength loss and decreased the attenuation of voluntary activation normally induced by a four-week immobilization of the wrist. The difference in the results in the studies of Bassolino et al. (2013) and Clark et al. (2015) may be due to the type of movements, object grasping in the first and grip force with a high level of muscle contraction in the second study. Recent studies have shown gradual activation of the corticospinal track with an increasing level of imagined contractions (Mizuguchi et al., 2013 and Helm et al., 2015). Activation of the motor cortical regions via strong imagined contractions may attenuate weakness and modulate neurophysiological responses, by maintaining normal levels of inhibition (Clark et al., 2015).

Cortical plasticity during motor recovery

Richardson (1964, 1967) first discussed the possibility of using mental practice through MI as a viable technique for physiotherapists in the motor rehabilitation process. Recently, several review articles listed MI interventions in various forms of neurological disorder (for example, stroke, Parkinson's disease, spinal cord injury, amputation) and discussed the benefits of mental training in motor performance improvement (Jackson et al., 2001; Braun et al., 2006; Sharma et al., 2006; de Vries and Mulder, 2007; Dickstein and Deutsch, 2007; Mulder, 2007; Garrison et al., 2010; Malouin et al., 2013b) or presented changes in MI ability associated with motor impairment (Simmons et al., 2008; Malouin and Richards, 2010; Guillot et al., 2012). In numerous studies, MI rehearsals induced greater motor improvement or at least a reduction of the decline.

In this review, we have focused specifically on the engagement of the motor network during MI in patients and the cortical reorganization facilitated by mental practice after impairment. While it is well-established that MI training induces neural plasticity during the recovery period, less is known about the origin of this modulation and its link with motor rehabilitation. Kaneko et al. (2003) studied, in eight orthopedic patients, corticospinal and spinal excitability after immobilization with splints for 3–6 weeks, at rest, while imagining, or during 10% maximum voluntary contraction. After immobilization, the authors reported a decrease of MEP amplitude during MI, without changes in spinal excitability. This result suggests that a cortical reorganization following immobilization may impact the capacity to reactivate M1 during MI. More recently, Hovington and Brouwer (2010) assessed the engagement of the corticospinal network in stroke patients during MI accompanied by visual or auditory cues, or both. The authors showed that cued MI facilitated MEPs associated with healthy and paretic muscles related to the imagined task. These findings suggest that MI may integrate the feedbacks induced by sensory cues to facilitate the cortical reorganization.

To better understand the plasticity of the corticospinal network, Cicinelli et al. (2006) mapped out finger representation in the affected and unaffected hemispheres (after stroke), at rest and while imagining. The authors found that MI induced an enhancement of the finger map area and volume in both hemispheres in a way that partly corrected the abnormal asymmetry between affected and non-affected hands seen in the rest condition. These findings indicate that these patients were able to recruit the corticospinal circuit relative to the prime mover when imagining, whatever the stroke lesion location. However, an inability to image any movement after stroke has been reported in specific patient cases. This cognitive impairment is known as 'chaotic motor imagery' (Sharma et al., 2006). The authors defined it "*as an inability to perform motor imagery accurately or, if having preserved accuracy, demonstration of temporal uncoupling*". Chaotic motor imagery may be limb-specific, affecting distal but not proximal movement in patients with parietal damage (Sirigu et al., 1996). It would be of interest to determine whether the inability to imagine movements in these patients reflects inactivation of the motor neural network. Indeed, it might be essential to determine the capacity of patients to generate properly actual movements and to evaluate the potential for cortical reorganization before integrating these patients into rehabilitation programs based on mental practice.

Few studies demonstrated the reorganization of M1 with TMS mapping at rest following disuse with no intervention. Liepert et al. (1995) showed a decrease in map areas at rest after disuse of the targeted muscle. The area reduction was correlated to the duration of immobilization. In contrast, Zanette et al. (1997) observed enhanced motor excitability (in area and volume) after upper limb immobilization in patients with unilateral wrist fracture. They hypothesized that the discrepancy between the two studies may be related to the persistence of pain, to the different durations of immobilization, or to the body part affected. In those cases, impairment at the periphery induces changes centrally. In the same way, injuries at the central level (such as stroke) induce reorganization of M1 and impairments at the periphery, even if the anatomical structures of the muscles are not damaged. Mapping M1 with TMS supplies valuable information about the motor cortical reorganization after stroke and the functional effects of rehabilitation programs (Traversa et al., 1997).

To our knowledge, no TMS experiment has reported the reorganization of the cortical map following mental practice in patients with motor impairments. Only Bassolino et al. (2013) mapped cortical changes after mental practice and action observation in healthy participants whose hand joints were immobilized for ten hours (see above for details). In contrast, studies using fMRI focused on these neurophysiological changes in patients (see Butler and Page, 2006; Page et al., 2009). One possible reason is that cortical mapping with TMS design is time-consuming (about 2 h) and, due to the demanding level of arousal and concentration, it might not be advisable for patients.

CONCLUSION AND PERSPECTIVES

This review provided relevant information, based on the latest researches, to optimize the benefits of mental practice with MI in motor learning. Such motor improvements were associated to brain modulation. While the TMS technique is presented as reliable technique to evaluate cortical reorganization, one has to keep in mind its limitations (Burke and Pierrot-Deseilligny, 2010). The peripheral response elicited by TMS is an indicator of corticospinal excitability at a specific time point, under defined conditions. It is worth noting that the projection from M1 to motoneurons is influenced by other projections, cortical and/or spinal. The results from TMS studies give a partial picture of the activated neurophysiological network during the mental simulation of action. To fully understand the general essence of MI, the association with other techniques is important (fMRI, PET, magnetoencephalography, oculometry, electroencephalography, etc.) and the interdisciplinarity is essential (e.g., neurophysiology, neuropsychology).

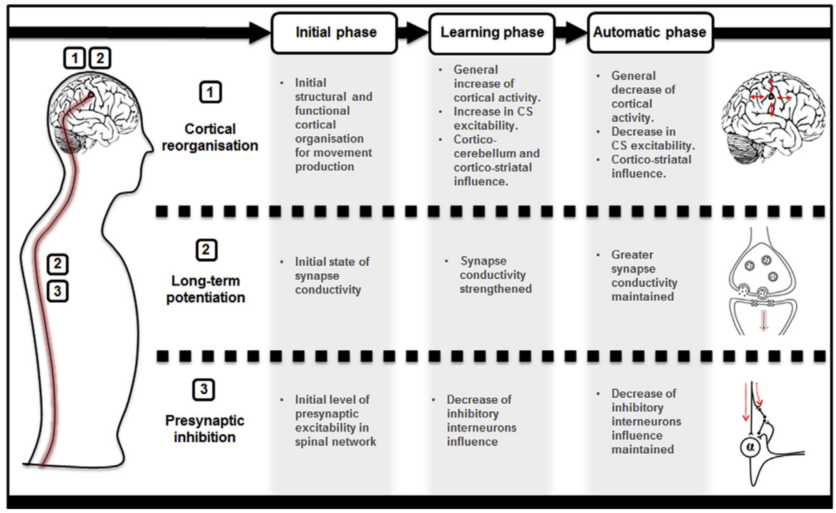

Fig. 5. Neural adaptation model of mental practice with motor imagery. The chart describes the three phases related to learning, from the initial phase to the automatic phase, in relation to three potential neurophysiological processes (cortical reorganization, long-term potentiation and presynaptic inhibition). The graphical representations on the right depict the three processes occurring at the cortical (1 and 2) and spinal (2 and 3) levels. The first picture shows the cortical map modulation (increase and decrease) within the primary motor cortex. The second picture shows the greater synapse sensitivity through the conduction of neurotransmitters. The third picture shows the decrease of presynaptic inhibition at the alpha-motoneuron level. The dotted red arrows illustrate the subliminal motor output generated during motor imagery and its influence on presynaptic interneurons.

In this review, we have illustrated motor improvement following MI practice and the concomitant reorganization of cortical structures. Interestingly, recent findings open up new prospects regarding neural adaptations occurring at the spinal level. Grosprêtre et al. (2016) showed that, during MI, a subliminal motor output was driven along the corticospinal track to reach spinal structures without activating alpha-motoneurons. While previous studies found disparate results regarding spinal excitability modulation (facilitation for Bonnet et al., 1997; Cowley et al., 2008; inhibition for Oishi et al., 1994), Grosprêtre et al. (2016) used two types of stimulation and two reliable techniques to ensure the potential effects of MI on spinal structures. Cervico-medullar-evoked potentials (CMEP) and Hoffmann (H) reflexes were elicited by stimulating the descending axons at the cervicomedullary junction and the peripheral nerve, respectively. Although both responses probe spinal excitability, CMEP is a direct measurement of the pyramido-motoneuronal junction (Taylor, 2006), and H-reflex provides information about the transmission between Ia afferences and alpha-motoneurons. When the targeted limb was kept in a constant position, CMEPs, but not H-reflexes, increased during MI in comparison to rest. This ensured that descending cortico-spinal tracks, but not alpha-motoneurons, were activated. Then, two techniques (passive muscle lengthening and H-reflex conditioning) were used to activate low-threshold pre-synaptic interneurons (e.g., Daniele and MacDermott, 2009; Duclay et al., 2011), known to reduce the amplitude of H-reflex at rest (Mizuno et al., 1971; Pinniger et al., 2001). In both conditions, the reduction of H-reflex was suppressed during MI, highlighting the effect of a subliminal motor output activating low-threshold spinal structures. The inhibition induced by pre-synaptic interneuron activation during lengthening is removed by the descending volleys generated during MI via other inhibitory interneurons (see Fig. 5 in Grosprêtre et al., 2016).

With this new evidence, we should consider neural adaptation following MI practice at a broader level. In addition to neural plasticity at the cortical level, the reinforcement of synapse conductivity and the decrease of pre-synaptic inhibition at the spinal level might also be part of neural modulation after MI practice. We suggest here a neural adaptation model for MI (Fig. 5):

- At the cortical level, both the cortical map representing trained muscles and the corticospinal excitability would increase during the first weeks of learning, then would decrease with performance stabilization in the automatic phase. At first, cortico-cerebellum and cortico-striatal networks are activated in the learning phase, while only the second one recalls the motor patterns when the movement is automatized, as confirmed by the different cortical activations associated with MI expertise (Guillot et al., 2008).
- At both cortical and spinal levels, the neural process of long-term potentiation may occur to strengthen the synapse (for review, see Nicoll et al., 1988). This mechanism is observed following rTMS in humans and animals (e.g., Wang et al., 1996; Post et al., 1999) or following high frequency stimulation and pairing in single neurons (e.g., Paulsen, 2000). The

subliminal motor output generated during MI may reinforce the sensibility and conductivity of synapses in the corticospinal tracks involved (Avanzino et al., 2015).

– At the spinal level, the decrease in presynaptic inhibition may also facilitate signal conductivity. The increasing influence of descending volleys on spinal structures is a key-component of motor expertise in specific activity (Tahayori and Koceja, 2012). After actual eccentric training, which exacerbates the influence of cortical volleys on presynaptic inhibitory interneurons, Duclay et al. (2008) showed a decrease in H-reflex amplitude. The descending motor output elicited during MI might induce similar changes in presynaptic inhibition.

In reference to most recent publications, we discussed the potential neural adaptations following mental practice with MI. Both cortical and spinal modulations may play a role in the motor learning process. While most studies focused on macroscopic cortical activations, a perspective of research would be to give considerations to synapse adaptation and spinal excitability during MI practice. Further investigation of these mechanisms may improve the understanding of MI benefits on motor performance.

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APPENDIX

Table A.1. List of publications using TMS to study mental imagery

TMS over M1 during explicit mental imagery	
1995	Izumi et al. Facilitatory effect of thinking about movement on motor-evoked potentials to transcranial magnetic stimulation of the brain. *Am J Phys Med Rehabil. 74:207–13.*
1996	Abbruzzese et al. The excitability of the human motor cortex increases during execution and mental imagination of sequential but not repetitive finger movements. *Exp Brain Res. 111:465–72.*
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TMS or rTMS for perturbation of mental imagery

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We classified the publications into 5 themes: (1) TMS over M1 during explicit mental imagery; (2) TMS or rTMS for perturbation of mental imagery; (3) Review about mental imagery and TMS; (4) TMS over M1 during implicit mental imagery; (5) TMS over V1 during mental imagery. TMS = transcranial magnetic stimulation; rTMS = repetitive TMS; M1 = primary motor cortex; V1 = primary visual cortex.

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