REVIEW ARTICLE

Motor imagery and cortico-spinal excitability: A review

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Abstract

Motor imagery (MI) has received a lot of interest during the last decades as its chronic or acute use has demonstrated several effects on improving sport performances or skills. The development of neuroimagery techniques also helped further our understanding of the neural correlates underlying MI. While some authors showed that MI, motor execution and action observation activated similar motor cortical regions, transcranial magnetic stimulation (TMS) studies brought great insights on the role of the primary motor cortex and on the activation of the cortico-spinal pathway during MI. After defining MI and describing the TMS technique, a short report of MI activities only at cortical level is provided. Then, a main focus on the specificities of cortico-spinal modulations during MI, investigated by TMS, is provided. Finally, a brief overview of subcortical mechanisms gives importance to the activation of peripheral neural structures during MI.

Keywords: Transcranial magnetic stimulation, motor control, neuroscience, performance

1. Introduction

1.1. Motor Imagery

According to Denis (1985, p. 4), motor imagery (MI) is "the mental simulation of an overt action, without any corresponding motor outputs". This simulation can involve only a visual projection of the movement (visual imagery), but also sensations normally generated during actual execution (kinaesthetic imagery). The particularity of MI, which makes it of interest to researchers involved in motor learning and rehabilitation, is the neural similarity with voluntary actual movement. Numerous cortical processes involved in actual contractions were found to be also involved in MI, such as the activation of supplementary motor area (SMA), premotor and primary motor cortices (Decety et al., 1994; Lotze et al., 1999). As well, numerous studies showed that MI can activate cortico-spinal pathways although no motor output is produced (e.g., Facchini, Muellbacher, Battaglia, Boroojerdi, & Hallett, 2002; Fadiga et al., 1999; Munzert, Lorey, & Zentgraf, 2009). The scientific interest for this topic really emerged during the last decade of the twentieth century, as the technical and methodological advances in cortical stimulation allowed increasing our knowledge about the neural mechanisms. This paper reviews mainly the modulations of cortico-spinal excitability, and its specificities, during kinaesthetic MI.

1.2. Transcranial magnetic stimulation

The cortico-spinal pathway is represented with two major connections: from the pyramidal cells of the cortex to the spinal motoneurons and from the spinal motoneurons to the muscles. Pyramidal cells in the primary motor cortex (M1) represent the final output of the brain, eliciting the voluntary descending drive along the pyramidal track. This motor command reaches alpha motoneurons in the spinal cord, where peripheral nerves represent the final pathway towards the muscles.

Transcranial magnetic stimulation (TMS) is a noninvasive technique that consists of delivering an electromagnetic field, through a coil placed over the head, to stimulate superficial cortical areas. When the coil is placed over M1, the rapidly changing magnetic field induces an electric current in the underlying cortical tissue, causes the neurons to depolarise and activates the cortico-spinal system to produce a muscular contraction in the contralateral side. The muscle activation is then measured by

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surface electromyography (EMG) electrodes to provide a marker of cortico-spinal excitability at the time of stimulation (Petersen, Pyndt, & Nielsen, 2003), the response being called a motor evoked potential (MEP).

Particular care should be taken regarding the experimental setting of TMS studies, the stimulation being focal (1 to 3 cm^2) and sensitive to coil orientation. First, the stimulation site, corresponding to the cortical representation of the contralateral muscle, needs to be located. The "hot spot" is marked when TMS of constant intensity elicits the greatest MEPs in the targeted muscle. It is of importance to monitor the subjects' head throughout the experiment to ensure the stability of the coil over the stimulation site and to maintain constant cortico-vestibular influence on the excitability of the motor pool (Kobayashi & Pascual-Leone, 2003). Then, the resting motor threshold (rMT) is measured. The rMT is the stimulation intensity that elicits at least four responses out of eight greater than 50 µV (Kobayashi & Pascual-Leone, 2003). Classically, test intensity used during the experimental conditions for MI studies is set between 110 and 120% of rMT (Loporto, McAlliser, Williams, Hardwick, & Holmes, 2011). Mean MEP amplitude obtained during MI is usually compared to ones during control conditions (e.g. at rest or when fixating on a cross). Larger MEPs indicate the activation of the cortico-spinal track when imaging (see Figure 1). This criterion can be used to ensure that subjects imagine the movement at the time TMS is triggered (Rozand, Lebon, Papaxanthis, & Lepers, 2014). However, particular care should be taken to monitor the control task and ensure constant stimulus conditions. For instance the observation of the considered limb, even in static position, can already induce a modulation of MEP amplitude compared to another cognitive task (Wright, Williams, & Holmes, 2014). This should be considered when comparing MI effects and a control condition.

In this review, we first provide a brief overview of cortical activations during MI to describe the general neural pattern. For this latter, fMRI and EEG are more appropriate to provide an insight of cortical activities in the whole cortex, whereas TMS modifies the state of excitability of one targeted structure. Then, we review studies using TMS and its contribution to the knowledge of neural mechanisms underlying MI.

2. Motor imagery and cortical activity

TMS studies mainly bring relevant information about the excitability of one of the components of the nervous system, the cortico-spinal network. When this technique is used to probe cortical mechanisms, it needs complementary insights from



Figure 1. General picture of transcranial magnetic stimulation during motor imagery.

Dotted and plain lines represent the activation of cortico-spinal tracks during motor imagery and at rest, respectively. The amplitude of the electromyographic response increases during motor imagery in comparison to rest.

other recording methods. First, EEG is of interest due to its high temporal resolution. During MI, a decrease in the somatosensory potential evoked by electrical stimulation of the median nerve was observed (Cheron & Borenstein, 1992). Highdensity EEG dynamics represents a useful electrophysiological tool to investigate the brain state during MI (Yi et al., 2014). The main limit of EEG technique is its poor spatial resolution when investigating the cortical network activated during MI. To that aim, one of the most spatially accurate techniques to investigate cortical activation is fMRI, particularly while no movement is produced in the scanner like during MI. Second, contrary to TMS which is mostly used to assess the excitability of one structure, i.e. M1 and its related cortico-spinal pathway, fMRI allows to investigate the activation of other, superficial and deeper, areas, such as the parietal or frontal cortices or the basal ganglia. Many authors showed that some cortical areas involved in actual contraction could also be activated during MI (Jeannerod, 2001; Munzert et al., 2009). For instance, SMA, and premotor, cingular and parietal cortices were reported to be activated during MI (Tyszka, Grafton, Chew, Woods, & Colletti, 1994). However, the activation of these areas could differ between actual contraction and MI. The superficial part of the SMA seems to be activated only during MI, whereas actual contraction leads to an activation of a deeper part (Gerardin et al., 2000). Other structures involved in MI, such as the cerebellum or the parietal cortex were shown to be activated differently to actual contraction (Lotze et al., 1999).

More recent studies demonstrated an activation of M1 during MI (Munzert et al., 2009). This activity was observed independently of the corticalisation of the body part involved in the imagined movement. Indeed, M1 activation was apparent for MI of finger movements (Gueugneau et al., 2013; Guillot et al., 2009), for MI of wrist movements (Hashimoto & Rothwell, 1999; Kasai, Kawai, Kawanishi, & Yahagi, 1997) and for MI of foot movements (Tremblay, Tremblay, & Colcer, 2001). However, these studies involving simple mono-articular movements, other authors also found similar results during MI of more complex actions, such as locomotion (Malouin, Richards, Jackson, Dumas, & Doyon, 2003) or everyday life actions (Szameitat, Shen, & Sterr, 2007).

Few studies reported a similar activity, in terms of magnitude, between MI and actual contraction (e.g., Caldara et al., 2004). Nevertheless, a majority of the authors demonstrated that cortical activation during MI still remains weaker than during actual movement (e.g., Ehrsson, Geyer, & Naito, 2003; Porro et al., 1996). The magnitude of M1 activity recorded during MI may depend on several factors, such as the motor repertory or the level of expertise of the subject in the considered task (Guillot et al., 2008) or the ability to practice MI (Lacourse, Turner, Randolph-Orr, Schandler, & Cohen, 2004).

Although the fMRI technique provides a great spatial accuracy to assess the activation of the cortical map involved in a specific task, and EEG provides a great temporal resolution about brain state changes, the TMS technique helps to further investigate the neural mechanisms underlying MI. Particularly, TMS focuses on the activation of M1 and of the whole cortico-spinal pathway. For instance, giving its high temporal resolution, TMS facilitates the assessment of timing aspects of MI.

3. Cortico-spinal modulations during motor imagery

Numerous studies using TMS reported an increase of MEP amplitude during MI compared to rest, for upper and lower limb movements (e.g., Facchini et al., 2002; Fadiga et al., 1999; Munzert et al., 2009), reflecting an increase in the cortico-spinal excitability. It was shown that MEP threshold was lowered during MI, which can be partly explained by an increase of neurons responsiveness to magnetic stimulation (Facchini et al., 2002; Kasai et al., 1997; Yahagi & Kasai, 1998) and/or a decrease of intracortical inhibition (Stinear & Byblow, 2004). During MI of hand movement, some authors also reported a spread of cortical areas controlling *abductor digiti minimi* and *opponens pollicis* muscles (Marconi, Pecchioli, Koch, & Caltagirone, 2007). This result brings evidence that cortical cell responsiveness may increase during MI, allowing to recruit more neural structures when discharging a magnetic pulse.

3.1. Spatial aspects

The increase of cortico-spinal excitability is specific to the muscle involved in the imagined movement. For instance, an increase of MEP amplitude in the biceps brachii muscle was observed during MI of elbow flexion but not during MI of elbow extension, and inversely for the triceps brachii muscle (Fadiga et al., 1999). During MI of knee extension, MEPs in knee extensor, but not knee flexor, muscles were greater compared to rest (Tremblay et al., 2001). Regarding fine movements involving distal muscles, MI of index abduction increased MEP of first dorsal interosseus but not MEP of abductor digiti minimi neither MEP in forearm muscles such as extensor carpi radialis (Rossini, Rossi, Pasqualetti, & Tecchio, 1999). As well, MI of thumb opposition towards the base of the little finger only increased MEP of muscles involved specifically dedicated to this movement (opponens pollicis) and synergists muscles (first dorsal interosseus) contrary to other intrinsic hand muscles such as abductor digiti minimi (Marconi et al., 2007). In a same way, MI of thumb abduction also increased cortico-spinal excitability of the abductor pollicis brevis but not of the first dorsal interosseus (Facchini et al., 2002) nor of the abductor digiti minimi (Stinear, Byblow, Steyvers, Levin, & Swinnen, 2006). Finally, the muscle-specific modulation was observed in both hemispheres, independently of subjects' lateral dominance (Facchini et al., 2002).

3.2. Temporal aspects

One of the main advantages of TMS relies in its high temporal resolution. Therefore, TMS is used to assess the time course of the cortico-spinal excitability changes during MI. Several authors showed that the temporal parameters of the actual movement were also preserved during MI. For instance, Fadiga et al. (1999) demonstrated that during imagined repetitive flexion-extension of the elbow, MEPs of *biceps brachii* muscle only increased during the flexion phase of the imagined movement. Similar results were obtained during repetitive hand closing and opening while measuring MEPs in the *opponens* *pollicis* muscle (Fadiga et al., 1999), and during rhythmic wrist flexion/extension while measuring MEPs of *flexor carpi radialis* (Hashimoto & Rothwell, 1999; Levin, Steyvers, Wenderoth, Li, & Swinnen, 2004). During actual repetitive movements in time with a metronome, it was previously shown by recording EMG activity of the considered muscle that this latter was activated slightly before the beep and was not activated between two beeps (Stinear & Byblow, 2003). The temporal specificity of repetitive MI of thumb movements was assessed with the same experimental paradigm by delivering TMS impulses before the beep, when the muscle is active in actual trials (ON phase) and between two beeps, when the muscle is silent in actual trials (OFF phase). An increase of cortico-spinal excitability was observed during the ON, but not the OFF, phase of imagined movements (Lebon, Byblow, Collet, Guillot, & Stinear, 2012; Stinear et al., 2006). These results suggested that cortico-spinal activity during MI of repetitive movements mimicked the time specificity of actual movements.

3.3. Gradual aspects

Interestingly, some authors investigated whether the magnitude of cortico-spinal facilitation induced by MI was proportional to the participation of the targeted muscle in the imagined task. Thus, even if the level of cortico-spinal excitability during MI is less than that during actual movement, its modulation according to several level of activation is qualitatively similar in both conditions. For instance, MEP amplitude of the *first dorsal interosseus* muscle is greater during the specific action associated to this muscle (index flexion) than that during synergistic actions (index extension or index abduction), during both actual and imagined movements (Yahagi & Kasai, 1998). When studying finger mechanical responses induced by the magnetic stimulation, i.e. the peak torque of the targeted limb, Li, Latash, and Zatsiorsky (2004) showed a similar synergistic behaviour during MI and actual contractions. Thus, the peak torque of index flexion evoked by TMS was greater during MI of maximal index contraction alone than that during MI of maximal contraction of all fingers (Li, Latash, et al., 2004). In fact, this neural mechanism, called "enslaving", reflects biomechanical coupling between fingers during actual movement (Slobounov, Johnston, Chiang, & Ray, 2002). However, even if MI activation patterns mimicked actual contraction, it remains some limits regarding quantitative aspects of MI activation. Park and Li (2011) showed that MEP amplitude was not modulated according to the level of imagined contraction force (from 10% to 60% of maximum

voluntary contraction), contrary to actual contractions (Kobayashi & Pascual-Leone, 2003).

3.4. Contextual aspects

Like actual contraction, MI is influenced by subjects' motor skills or environmental factors. Participants with high MI ability showed a greater increase of the cortico-spinal excitability (Williams, Pearce, Loporto, Morris, & Holmes, 2012) and respected the temporal and spatial specificity of this activation (Lebon et al., 2012). Independently of subjects' capacity, it was also previously shown that MEPs of the right hand are likely more facilitated for righthanded subjects during MI of right-hand movements (Marconi et al., 2007). However, a facilitation of left-hand muscle MEP was not always observed for left-handed subjects when they imagine a movement of the left hand (Yahagi & Kasai, 1999). Fadiga et al. (1999) suggested that MI processes were dominant in left hemisphere for right-handed subjects.

Although some authors made the assumption that MI processes should not depend on the initial state of the body (Johnson, 2000), later results showed that sensorial information, such as proprioceptive feedback, influence cortico-spinal responses during MI. For instance, the link between imagery ability and proprioceptive information has already been established. By placing the subject's hand in a noncongruent position relative to the imagined movement, his MI ability decreased (Shenton, Schwoebel, & Coslett, 2004). Thus, the position of the considered segment during MI could influence cortico-spinal excitability (Mercier, Aballea, Vargas, Paillard, & Sirigu, 2008; Vargas et al., 2004), as the use of several body positions may induce variations on cortical activity observed using an fMRI technique (de Lange, Helmich, & Toni, 2006). In fact, it appeared that the biomechanical complexity of the imagined task according to the initial body position increased the amount and number of cortical areas involved during MI, suggesting that proprioceptive information are incorporated in the elaboration of the motor plan also for imagined motor tasks. Similar observations were noticed with TMS. For instance, the facilitation of opponens pollicis MEPs during MI of thumb abduction was greater when the hand was kept in a position compatible with the task than when in an incompatible position (Vargas et al., 2004). It was also previously found that neuromuscular fatigue, known to alter peripheral feedback, could influence MI capacities. This latter result suggests that mental representation of the action integrates the initial state of the neuromuscular system (Demougeot & Papaxanthis, 2011). Mizuguchi, Sakamoto, Muraoka, and Kanosue (2009) found that MEPs were enhanced during MI of gripping a foam ball when the object was passively held in a same way as the imagined contraction. They reported that tactile output may have influenced MI. However, in this last study results do not allow to distinguish the influence of tactile input generated by holding the object from the influence of proprioceptive feedback generated by the specific posture of the arm.

Another approach of interest is the combination of MI with other interventions. For example, action observation and MI encompass similar neural processes, such as spatial specificity of cortico-spinal modulation. Interestingly, this combination induced greater MEPs increase (for review, see Naish, Houston-Price, Bremner, & Holmes, 2014). It has been suggested that such combined approach may be more effective than MI alone to improve motor performance in sport, and neurorehabilitation (Wright et al., 2014).

4. Below the brain: missing clues

TMS provides a global index of cortico-spinal excitability but does not allow making a distinction between the several nervous levels. Thus, the use of different techniques is needed to investigate, for example, the spinal level independently. However, regarding lower nervous levels, results are more controversial in the literature than TMS studies. Indeed, an increase of finger flexors stretch reflex amplitude has already been reported (Li, Kamper, Stevens, & Rymer, 2004), as an increase of wrist flexor H-reflex (Gandevia, Wilson, Inglis, & Burke, 1997). These results suggest that MI increases spinal transmission efficiency. A modulation of spinal excitability of lower limb muscle has also been reported. Indeed, an increase of plantar flexor H-reflex amplitude was shown during MI compared to rest (Bonnet, Decety, Jeannerod, & Requin, 1997). Moreover, this increase seems to be proportional to the intensity of the imagined contraction (Cowley, Clark, & Ploutz-Snyder, 2008). On the contrary, Hashimoto and Rothwell (1999) did not find any change in H-reflex amplitude during MI of wrist flexion compared to rest. In some studies, a decrease of H-reflex was reported during MI compared to rest (Oishi, Kimura, Yasukawa, Yoneda, & Maeshima, 1994). However studies still remain under-represented in the literature to establish a consensus about spinal modulations during MI. This statement is even more complex when the methods used to assess spinal excitability differ among studies. For instance, some authors analysed variations in the electrically evoked H-reflex (Oishi et al., 1994) whereas others used a brief passive joint extension to elicit a stretch reflex (Li, Kamper, et al., 2004).

At the muscle level, some authors found a subliminal EMG activity during MI compared to rest, proportional to the level of imagined force (for review, see Guillot & Collet, 2005). However, other authors did not find any muscular activity during MI compared to rest (Gentili, Papaxanthis, & Pozzo, 2006). They suggested that background EMG activity during MI could easily be assimilated to small isometric actual contraction. Particularly during MEP recording, which can be modulated even by smallest levels of activation, particular care should be taken in monitoring muscle activity. These inconsistent results may also originate from methodological problems mainly, such as electrode type, distance between active fibres and electrodes or location of the muscle (see Guillot et al., 2007).

As suggested by Jeannerod (2001), MI is a "nonexecuted action". Despite the fact that the primary motor cortical areas are activated, no movement is generated. Two theories may explain this phenomenon: (1) a complete inhibitory mechanism block the command initiated by the motor cortex (Guillot, Di Rienzo, Macintyre, Moran, & Collet, 2012) and/or (2) the cortical activation during MI is too weak to engage a muscle response but could still reach lower nervous level (Lebon, Rouffet, Collet, & Guillot, 2008). Yet, no consensus can be established regarding cortical or sub-cortical structures involved during MI. Further investigations are needed to further understand the neural mechanisms underlying MI. For instance, conditioning TMS techniques, has already highlighted that intracortical inhibition is partially removed during MI compared to rest, which could explain the MEP amplitude increase (Stinear & Byblow, 2004). However this removal was shown to be less than that during voluntary contraction. Therefore, we can speculate that even if a specific cortical mechanism inhibits the command during MI, a subliminal cortical output is still generated, but not strong enough to reach the muscle. It would be of interest to investigate in more details the activations of spinal inhibitory interneurons by H-reflex conditioning techniques, more sensitive than H-reflex only.

5. Conclusion and practical applications

It is now well established that MI activates cortical structures normally activated during the actual movement (Decety et al., 1994; Gerardin et al., 2000; Lotze et al., 1999). Although the activation of M1, generating the final motor command in the brain, was not always reported using fMRI technique (Tyszka et al., 1994), TMS studies helped to establish a strong statement about M1 and the cortico-spinal track activation during MI. An alternative way to probe the neural processes is also to combine brain imagery techniques, such as EEG or fMRI, to TMS. MI should then represent an intermediate state between actual contraction and rest (Li, Latash, et al., 2004), allowing to study motor command processes without feedback resulting from muscle contraction. To summarise, several studies using TMS showed that MI is temporally, spatially and gradually specific and does not induce a general activation increase of M1. From a methodological point of view, carefully set the time and the location of the TMS pulse during the imagined movement appears to be essential when studying cortico-spinal excitability during MI.

Using MI as a method to improve performance has been widely reported in different populations, such as healthy people, athletes or patients (for review about neurological disorders and MI, see Malouin, Jackson, & Richards, 2013). Results from TMS studies and other techniques help design the optimal MI training. For example, using kinaesthetic modality is more likely to activate the motor system, facilitating motor learning. Finally, the combination of MI with other interventions, such as action observation, is of interest to access the entire network underlying motor performance.

References

- Bonnet, M., Decety, J., Jeannerod, M., & Requin, J. (1997). Mental simulation of an action modulates the excitability of spinal reflex pathways in man. *Cognitive Brain Research*, 5, 221– 228. doi:10.1016/S0926-6410(96)00072-9
- Caldara, R., Deiber, M.-P., Andrey, C., Michel, C. M., Thut, G., & Hauert, C.-A. (2004). Actual and mental motor preparation and execution: A spatiotemporal ERP study. *Experimental Brain Research*, 159, 389–399. doi:10.1007/s00221-004-2101-0
- Cheron, G., & Borenstein, S. (1992). Mental movement simulation affects the N30 frontal component of the somatosensory evoked potential. *Electroencephalography and Clinical Neurophysi*ology, 84, 288–292. Retrieved from http://www.ncbi.nlm.nih. gov/pubmed/1375888
- Cowley, P. M., Clark, B. C., & Ploutz-Snyder, L. L. (2008). Kinesthetic motor imagery and spinal excitability: The effect of contraction intensity and spatial localization. *Clinical Neurophysiology : Official Journal of the International Federation of Clinical Neurophysiology*, 119, 1849–1856. doi:10.1016/j.clinph. 2008.04.004
- Decety, J., Perani, D., Jeannerod, M., Bettinardi, V., Tadary, B., Woods, R., ... Fazio, F. (1994). Mapping motor representations with positron emission tomography. *Nature*, 371, 600– 602. doi:10.1038/371600a0
- de Lange, F. P., Helmich, R. C., & Toni, I. (2006). Posture influences motor imagery: An fMRI study. *NeuroImage*, 33, 609–617. doi:10.1016/j.neuroimage.2006.07.017
- Demougeot, L., & Papaxanthis, C. (2011). Muscle fatigue affects mental simulation of action. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 31, 10712–10720. doi:10.1523/JNEUROSCI.6032-10.2011
- Denis, M. (1985). Visual imagery and the use of mental practice in the development of motor skills. *Canadian Journal of Applied Sport Sciences/Journal Canadien Des Sciences Appliquées Au Sport*, 10(4), 4S–16S. Retrieved from http://www.ncbi.nlm.nih.gov/ pubmed/3910301
- Ehrsson, H. H., Geyer, S., & Naito, E. (2003). Imagery of voluntary movement of fingers, toes, and tongue activates

corresponding body-part-specific motor representations. *Journal of Neurophysiology*, 90, 3304–3316. doi:10.1152/jn.01113.2002

- Facchini, S., Muellbacher, W., Battaglia, F., Boroojerdi, B., & Hallett, M. (2002). Focal enhancement of motor cortex excitability during motor imagery: A transcranial magnetic stimulation study. *Acta Neurologica Scandinavica*, 105(3), 146– 151. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/ 11886355
- Fadiga, L., Buccino, G., Craighero, L., Fogassi, L., Gallese, V., & Pavesi, G. (1999). Corticospinal excitability is specifically modulated by motor imagery: A magnetic stimulation study. *Neuropsychologia*, 37, 147–158. Retrieved from http://www. ncbi.nlm.nih.gov/pubmed/10080372
- Gandevia, S. C., Wilson, L. R., Inglis, J. T., & Burke, D. (1997). Mental rehearsal of motor tasks recruits alpha-motoneurones but fails to recruit human fusimotor neurones selectively. *The Journal* of *Physiology*, 505, 259–266. Retrieved from http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1160109&tool=pm centrez&rendertype=abstract
- Gentili, R., Papaxanthis, C., & Pozzo, T. (2006). Improvement and generalization of arm motor performance through motor imagery practice. *Neuroscience*, 137, 761–772. doi:10.1016/j. neuroscience.2005.10.013
- Gerardin, E., Sirigu, A., Lehéricy, S., Poline, J. B., Gaymard, B., Marsault, C., ... Le Bihan, D. (2000). Partially overlapping neural networks for real and imagined hand movements. *Cerebral Cortex (New York, N.Y. : 1991), 10*, 1093–1104. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11053230
- Gueugneau, N., Bove, M., Avanzino, L., Jacquin, A., Pozzo, T., & Papaxanthis, C. (2013). Interhemispheric inhibition during mental actions of different complexity. *PLoS One*, 8(2), e56973. doi:10.1371/journal.pone.0056973
- Guillot, A., & Collet, C. (2005). Contribution from neurophysiological and psychological methods to the study of motor imagery. *Brain Research Reviews*, 50, 387–397. doi:10.1016/j. brainresrev.2005.09.004
- Guillot, A., Collet, C., Nguyen, V. A., Malouin, F., Richards, C., & Doyon, J. (2008). Functional neuroanatomical networks associated with expertise in motor imagery. *NeuroImage*, 41, 1471–1483. doi:10.1016/j.neuroimage.2008.03.042
- Guillot, A., Collet, C., Nguyen, V. A., Malouin, F., Richards, C., & Doyon, J. (2009). Brain activity during visual versus kinesthetic imagery: An fMRI study. *Human Brain Mapping*, 30, 2157–2172. doi:10.1002/hbm.20658
- Guillot, A., Di Rienzo, F., Macintyre, T., Moran, A., & Collet, C. (2012). Imagining is not doing but involves specific motor commands: A review of experimental data related to motor Inhibition. *Frontiers in Human Neuroscience*, 6, 247. doi:10.3389/ fnhum.2012.00247
- Guillot, A., Lebon, F., Rouffet, D., Champely, S., Doyon, J., & Collet, C. (2007). Muscular responses during motor imagery as a function of muscle contraction types. *International Journal of Psychophysiology*, 66(1), 18–27. doi:10.1016/j.ijpsycho.2007. 05.009
- Hashimoto, R., & Rothwell, J. C. (1999). Dynamic changes in corticospinal excitability during motor imagery. *Experimental Brain Research*, 125(1), 75–81. Retrieved from http://www.ncbi. nlm.nih.gov/pubmed/10100979
- Jeannerod, M. (2001). Neural simulation of action: A unifying mechanism for motor cognition. *NeuroImage*, 14(1 Pt 2), S103– S109. doi:10.1006/nimg.2001.0832
- Johnson, S. H. (2000). Thinking ahead: The case for motor imagery in prospective judgements of prehension. *Cognition*, 74(1), 33–70. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/10594309
- Kasai, T., Kawai, S., Kawanishi, M., & Yahagi, S. (1997). Evidence for facilitation of motor evoked potentials (MEPs) induced by motor imagery. *Brain Research*, 744(1), 147–150. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/9030424

- Kobayashi, M., & Pascual-Leone, A. (2003). Transcranial magnetic stimulation in neurology. *The Lancet. Neurology*, 2, 145–156. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/12849236
- Lacourse, M. G., Turner, J. A., Randolph-Orr, E., Schandler, S. L., & Cohen, M. J. (2004). Cerebral and cerebellar sensorimotor plasticity following motor imagery-based mental practice of a sequential movement. *Journal of Rehabilitation Research* and Development, 41, 505–524. Retrieved from http://www.ncbi. nlm.nih.gov/pubmed/15558380
- Lebon, F., Byblow, W. D., Collet, C., Guillot, A., & Stinear, C. M. (2012). The modulation of motor cortex excitability during motor imagery depends on imagery quality. *The European Journal of Neuroscience*, 35, 323–331. doi:10.1111/j.1460-9568. 2011.07938.x
- Lebon, F., Rouffet, D., Collet, C., & Guillot, A. (2008). Modulation of EMG power spectrum frequency during motor imagery. *Neuroscience Letters*, 435, 181–185. doi:10.1016/j.neulet.2008. 02.033
- Levin, O., Steyvers, M., Wenderoth, N., Li, Y., & Swinnen, S. P. (2004). Dynamical changes in corticospinal excitability during imagery of unimanual and bimanual wrist movements in humans: A transcranial magnetic stimulation study. *Neuroscience Letters*, 359, 185–189. doi:10.1016/j.neulet.2004.01.070
- Li, S., Kamper, D. G., Stevens, J. A., & Rymer, W. Z. (2004). The effect of motor imagery on spinal segmental excitability. *The Journal* of Neuroscience: The Official Journal of the Society for Neuroscience, 24, 9674–9680. doi:10.1523/JNEUROSCI.2781-04.2004
- Li, S., Latash, M. L., & Zatsiorsky, V. M. (2004). Effects of motor imagery on finger force responses to transcranial magnetic stimulation. *Cognitive Brain Research*, 20, 273–280. doi:10.1016/ j.cogbrainres.2004.03.003
- Loporto, M., McAllister, C., Williams, J., Hardwick, R., & Holmes, P. (2011). Investigating central mechanisms underlying the effects of action observation and imagery through transcranial magnetic stimulation. *Journal of Motor Behavior*, 43, 361–373. doi:10.1080/00222895.2011.604655
- Lotze, M., Montoya, P., Erb, M., Hülsmann, E., Flor, H., Klose, U., ... Grodd, W. (1999). Activation of cortical and cerebellar motor areas during executed and imagined hand movements: An fMRI study. *Journal of Cognitive Neuroscience*, 11(5), 491– 501. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/ 10511638
- Malouin, F., Jackson, P. L., & Richards, C. L. (2013). Towards the integration of mental practice in rehabilitation programs. A critical review. *Frontiers in Human Neuroscience*, 7(September), 576. doi:10.3389/fnhum.2013.00576
- Malouin, F., Richards, C. L., Jackson, P. L., Dumas, F., & Doyon, J. (2003). Brain activations during motor imagery of locomotor-related tasks: A PET study. *Human Brain Mapping*, 19(1), 47–62. doi:10.1002/hbm.10103
- Marconi, B., Pecchioli, C., Koch, G., & Caltagirone, C. (2007). Functional overlap between hand and forearm motor cortical representations during motor cognitive tasks. *Clinical Neurophysiology: Official Journal of the International Federation of Clinical Neurophysiology*, 118, 1767–1775. doi:10.1016/j. clinph.2007.04.028
- Mercier, C., Aballea, A., Vargas, C. D., Paillard, J., & Sirigu, A. (2008). Vision without proprioception modulates cortico-spinal excitability during hand motor imagery. *Cerebral Cortex (New York, N.Y.: 1991)*, 18, 272–277. doi:10.1093/cercor/bhm052
- Mizuguchi, N., Sakamoto, M., Muraoka, T., & Kanosue, K. (2009). Influence of touching an object on corticospinal excitability during motor imagery. *Experimental Brain Research*, 196, 529–535. doi:10.1007/s00221-009-1875-5
- Munzert, J., Lorey, B., & Zentgraf, K. (2009). Cognitive motor processes: The role of motor imagery in the study of motor representations. *Brain Research Reviews*, 60, 306–326. doi:10.1016/j.brainresrev.2008.12.024

- Naish, K. R., Houston-Price, C., Bremner, A. J., & Holmes, N. P. (2014). Effects of action observation on corticospinal excitability: Muscle specificity, direction, and timing of the mirror response. *Neuropsychologia*, 64C, 331–348. doi:10.1016/j. neuropsychologia.2014.09.034
- Oishi, K., Kimura, M., Yasukawa, M., Yoneda, T., & Maeshima, T. (1994). Amplitude reduction of H-reflex during mental movement simulation in elite athletes. *Behavioural Brain Research*, 62(1), 55–61. Retrieved from http://www.ncbi.nlm. nih.gov/pubmed/7917033
- Park, W.-H., & Li, S. (2011). No graded responses of finger muscles to TMS during motor imagery of isometric finger forces. *Neuroscience Letters*, 494, 255–259. doi:10.1016/j. neulet.2011.03.027
- Petersen, N. T., Pyndt, H. S., & Nielsen, J. B. (2003). Investigating human motor control by transcranial magnetic stimulation. *Experimental Brain Research*, 152(1), 1–16. doi:10.1007/s00221-003-1537-y
- Porro, C. A., Francescato, M. P., Cettolo, V., Diamond, M. E., Baraldi, P., Zuiani, C., ... di Prampero, P. E. (1996). Primary motor and sensory cortex activation during motor performance and motor imagery: A functional magnetic resonance imaging study. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 16, 7688–7698. Retrieved from http:// www.ncbi.nlm.nih.gov/pubmed/8922425
- Rossini, P. M., Rossi, S., Pasqualetti, P., & Tecchio, F. (1999). Corticospinal excitability modulation to hand muscles during movement imagery. *Cerebral Cortex (New York, N.Y. : 1991)*, 9, 161–167.
- Rozand, V., Lebon, F., Papaxanthis, C., & Lepers, R. (2014). Does a mental training session induce neuromuscular fatigue? *Medicine and Science in Sports and Exercise*, 46, 1981–1989. doi:10.1249/MSS.00000000000327
- Shenton, J. T., Schwoebel, J., & Coslett, H. B. (2004). Mental motor imagery and the body schema: Evidence for proprioceptive dominance. *Neuroscience Letters*, 370(1), 19–24. doi:10.1016/j.neulet.2004.07.053
- Slobounov, S., Johnston, J., Chiang, H., & Ray, W. (2002). Movement-related EEG potentials are force or end-effector dependent: Evidence from a multi-finger experiment. *Clinical Neurophysiology: Official Journal of the International Federation of Clinical Neurophysiology*, 113(7), 1125–1135. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/12088709
- Stinear, C. M., & Byblow, W. D. (2003). Motor imagery of phasic thumb abduction temporally and spatially modulates corticospinal excitability. *Clinical Neurophysiology*, *114*, 909–914. doi:10.1016/S1388-2457(02)00373-5
- Stinear, C. M., & Byblow, W. D. (2004). Modulation of corticospinal excitability and intracortical inhibition during motor imagery is task-dependent. *Experimental Brain Research*, 157, 351–358. doi:10.1007/s00221-004-1851-z
- Stinear, C. M., Byblow, W. D., Steyvers, M., Levin, O., & Swinnen, S. P. (2006). Kinesthetic, but not visual, motor imagery modulates corticomotor excitability. *Experimental Brain Research*, 168, 157–164. doi:10.1007/s00221-005-0078-y
- Szameitat, A. J., Shen, S., & Sterr, A. (2007). Motor imagery of complex everyday movements. An fMRI study. *NeuroImage*, 34, 702–713. doi:10.1016/j.neuroimage.2006.09.033
- Tremblay, F., Tremblay, L. E., & Colcer, D. E. (2001). Modulation of corticospinal excitability during imagined knee movements. *Journal of Rehabilitation Medicine*, 33(5), 230–204. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11585155
- Tyszka, J. M., Grafton, S. T., Chew, W., Woods, R. P., & Colletti, P. M. (1994). Parceling of mesial frontal motor areas during ideation and movement using functional magnetic resonance imaging at 1.5 tesla. *Annals of Neurology*, 35, 746– 749. doi:10.1002/ana.410350617

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- Vargas, C. D., Olivier, E., Craighero, L., Fadiga, L., Duhamel, J. R., & Sirigu, A. (2004). The influence of hand posture on corticospinal excitability during motor imagery: A transcranial magnetic stimulation study. *Cerebral Cortex (New York, N.Y.:* 1991), 14, 1200–1206. doi:10.1093/cercor/bhh080
- Williams, J., Pearce, A. J., Loporto, M., Morris, T., & Holmes, P. S. (2012). The relationship between corticospinal excitability during motor imagery and motor imagery ability. *Behavioural Brain Research*, 226, 369–375. doi:10.1016/j.bbr.2011.09.014
- Wright, D. J., Williams, J., & Holmes, P. S. (2014). Combined action observation and imagery facilitates corticospinal excitability. *Frontiers in Human Neuroscience*, 8, 951. doi:10.3389/ fnhum.2014.00951
- Yahagi, S., & Kasai, T. (1998). Facilitation of motor evoked potentials (MEPs) in first dorsal interosseous (FDI) muscle is

dependent on different motor images. *Electroencephalography* and Clinical Neurophysiology, 109, 409–417. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/9851298

- Yahagi, S., & Kasai, T. (1999). Motor evoked potentials induced by motor imagery reveal a functional asymmetry of cortical motor control in left- and right-handed human subjects. *Neuroscience Letters*, 276, 185–188. doi:10.1016/S0304-3940 (99)00823-X
- Yi, W., Qiu, S., Wang, K., Qi, H., Zhang, L., Zhou, P., ... Ming, D. (2014). Evaluation of EEG oscillatory patterns and cognitive process during simple and compound limb motor imagery. *PLoS One*, 9(12), e114853. doi:10.1371/journal.pone.0114853