BRAIN
RESEARCH
REVIEWS

Review

Cognitive motor processes: The role of motor imagery in the study of motor representations

Jörn Munzert[a,*], Britta Lorey[a,b], Karen Zentgraf[a,b]

[a]University of Giessen, Germany, Department of Psychology and Sport Science, Institute for Sport Science, Kugelberg 62, 35394 Giessen, Germany
[b]Bender Institute of Neuroimaging, University of Giessen, Otto-Behaghel-Str. 10H, 35394 Gießen, Germany

ARTICLE INFO

ABSTRACT

Motor imagery is viewed as a window to cognitive motor processes and particularly to motor control. Mental simulation theory [Jeannerod, M., 2001. Neural simulation of action: a unifying mechanism for motor cognition. NeuroImage 14, 103–109] stresses that cognitive motor processes such as motor imagery and action observation share the same representations as motor execution. This article presents an overview of motor imagery studies in cognitive psychology and neuroscience that support and extend predictions from mental simulation theory. In general, behavioral data as well as fMRI and TMS data demonstrate that motor areas in the brain play an important role in motor imagery. After discussing results on a close overlap between mental and actual performance durations, the review focuses specifically on studies reporting an activation of primary motor cortex during motor imagery. This focus is extended to studies on motor imagery in patients. Motor imagery is also analyzed in more applied fields such as mental training procedures in patients and athletes. These findings support the notion that mental training procedures can be applied as a therapeutic tool in rehabilitation and in applications for power training.

© 2009 Elsevier B.V. All rights reserved.

Contents

* Corresponding author. Fax: +49 641 9925209.
  E-mail address: joern.munzert@sport.uni-giessen.de (J. Munzert).

1.   Introduction: motor imagery as a window for observing neural processes of action performance

Motor imagery has been studied in both applied cognitive psychology and neurophysiology. However, up to now, these two disparate fields have paid little attention to each other's research, although research on the use of imagery procedures in applied cognitive psychology might well help to find categories with which to evaluate the results of basic research on motor imagery within neurophysiology. Nonetheless, before we can ask what applied cognitive psychology and neurophysiology can learn about imagery from each other, we have to review what each paradigm has uncovered. We shall focus on neurophysiological data collected during the last decade that has delivered new and partly surprising results that can contribute to the discussion on the underlying mechanisms of motor imagery (Crammond, 1997; Decety, 1996a; Guillot and Collet, 2005; Jeannerod, 1994, 2001; Lotze and Halsband, 2006). The main objective of these studies was to understand the generation and maintenance of motor imagery and its impact on later motor performance. As a result, motor imagery has come a long way since earlier discussions in more applied fields. It now promises new insights into underlying mechanisms, and is considered to support future attempts to improve the application of mental training procedures in applied fields.

We shall first define motor imagery and show how its subprocesses can be a source of variations in the imagery process depending on which instructions are given for imagery tasks. The second section will focus on behavioral outcomes by analyzing the results of mental chronometry studies using either explicit or implicit imagery instructions. Section 3 will analyze the neural basis of motor imagery with particular emphasis on activation of the primary motor cortex. Subsequently, Section 4 will also examine results on neural activation during motor imagery in patient studies on motor imagery after strokes and in Parkinson's disease. Finally, Section 5 examines applications of motor imagery in different applied fields such as sports, rehabilitation, and power training.

Imagery can be defined as a perception-like process in the absence of any external stimulus input (Annett, 1995; Farah, 1984; Kosslyn, 1987; Kosslyn et al., 2001). Farah (1984) has proposed a computational model that describes several distinguishable components of an imagery process starting with the retrieval of information from long-term memory. Although developed originally for visual imagery, her model adapts smoothly to motor imagery. In Farah's view, information about a motor act has to be processed from long-term to working memory. This process of *image generation* constitutes

the perception-like process in the strict sense. The image cannot just be *transformed* within working memory (e.g., by rotating a visual image or changing the intensity of an imagined hand grip); it can also be *maintained* as emphasized by Kosslyn (1987; 1994). Moreover, the image can be *inspected* with the aim of detecting details in order to compare specific aspects with former percepts or to deliver a verbal report on imagined sensations.

Whereas images can probably refer to all senses, dynamic images of the motor act focus typically on kinesthetic or visual information (Annett, 1995). In the latter, a distinction is also made between first-person and third-person perspectives. Participants are able to distinguish both processes, kinesthetic and visual, and also imagine features from other modalities such as acoustic input. However, that does not imply that they occur only in one sensory modality isolated from the others. In the sports domain, athletes often use more than one modality when reporting their images. Slalom skiers might report not only visual and kinesthetic images but also acoustic representations of the movement rhythm reflecting the dynamic onset of the grip of the ski. Experienced musicians might report acoustic, tactile, and kinesthetic information from their images. Indeed, many people can switch between modalities either voluntarily or when obliged by task instructions.

The imagery modality also has to be treated independently with respect to the authorship of the imagined movement. One can imagine one's own performance or that of another person. It has become widely accepted practice to use the term motor imagery to refer to an image that the participant experiences as if he or she were performing the action voluntarily (Annett, 1995; Lotze and Halsband, 2006). This can imply the use of different modalities. Instructions for motor imagery tasks often focus on kinesthetic images; that is, on the somatosensory feelings that a participant experiences when performing a movement him- or herself. However, kinesthetic sensations are not exclusive to motor imagery; they may also occur when imaging another person's movement. This is supported by findings from studies revealing activations of somatosensory areas during movement observation as well (Zentgraf et al., 2005). Motor imagery may be based on kinesthetic and visual imagery from a first-person perspective. Although the third-person perspective on the own person is not part of motor imagery, participants find it quite easy to generate. However, it does not produce the feeling as if the participant is actually performing the movement at that very moment in time.

Experimental procedures contain either explicit or implicit processes of image generation (cf. de Lange et al., 2008). They differ generally in terms of the amount of explicit imagery processing and particularly in terms of the subprocesses of

Table 1 – Brain imaging studies revealing M1 activity during motor imagery

Authors	Task	Method	Specific results
Beisteiner et al., 1995	Button press task, lifting both index fingers	EEG	Lateralization of motor cortex activity with imagery
Leonardo et al., 1995	Sequential finger-to-thumb opposition	fMRI	M1 activation for 2 out of 5 participants
Lang et al., 1996	(I) Hand movements	EEG	Lateralization of M1 activity with imagery
	(II) Self-paced finger flexion	MEG	Dipole strength about 50% of execution
Porro et al., 1996	Sequential finger-to-thumb opposition	fMRI	M1 activity (low level); partly S1 activity
Roth et al., 1996	Sequential finger-to-thumb opposition	fMRI	Lateralization of M1 activity (4 out of 6 participants)
Pfurtscheller and Neuper, 1997	Left- or right-hand movements	EEG	Contralateral M1 activity; ipsilateral M1 activity in 2 out of 3 participants
Schnitzler et al., 1997	Object manipulating finger movements	MEG	M1 activity, but no S1 activity
Krams et al., 1998	Selective key press	PET	M1 activity with movement preparation
Luft et al., 1998	Sequential finger-to-thumb opposition	fMRI	Bilateral activation of M1 (3 participants)
Lotze et al., 1999	Right- and left-hand movements	fMRI	Higher lateralization of M1 activity in execution than in motor imagery; reduced (70%) S1 activity
Neuper et al., 1999	Right- and left-hand movements	EEG	Lateralized activation over M1 was used for neurofeedback
Pfurtscheller et al., 1999	Right- or left-hand movements	EEG	Onset of M1 activity after about 250 ms
Porro et al., 2000	Sequential finger-to-thumb opposition	fMRI	Bilateral activation of M1
Miyai et al., 2001	Walking	NIRS, fMRI	Imagery of gait and gait-related flexion of feet activated M1
Nyberg et al., 2001	Imaginary encoding of different actions	fMRI	M1 activity revealed by contrast of imaginary and verbal encoding
Ruby and Decety, 2001	Verbally or visually instructed object manipulation	fMRI	Left M1 activation for first- and third-person perspective; left S1 activity for contrast of first- and third-person perspective
Boecker et al., 2002	Sequential key-press tasks with increasing length	PET	Contralateral activity of M1 and S1; ipsilateral activity of M1
Stippich et al., 2002	Tongue, finger, and toe movements	fMRI	Somatotopic activation of M1 during imagery
Kuhtz-Buschbeck et al., 2003	Compression of a foam block Sequential finger-to-thumb opposition	fMRI	Weak M1 activation for simple and complex task
Lotze et al., 2003	Playing violin (Mozart, KV 216)/left-hand movements only	fMRI	Different M1 activation for amateurs and experts; S1 activity stronger for amateurs
Malouin et al., 2003	Locomotor tasks	PET	Activation of leg area for MI-rest
Nair et al., 2003	Uni- or bimanual sequential finger-to-thumb opposition	fMRI	Right imagery: 6 out of 8 participants contralateral M1 activation; left imagery: 6 out of 8 participants contra- and/or ipsilateral M1 activation; bimanual imagery: 7 out of 8 participants left and/or right M1 activation
Caldara et al., 2004	Fixed sequence of key presses	EEG	Comparable amount of M1 activation for execution and imagery
Dechent et al., 2004	Sequential finger-to-thumb opposition	fMRI	Time course analysis revealed a small and significant initial increase of M1 activity
Galdo-Álvarez and Carrillo de la Peña, 2004	Right- or left-hand movements	EEG	Similar time onset of LRPs for execution and imagery
Gemignani et al., 2004	Sequential finger-to-thumb opposition	fMRI	Contrast of imagery+execution vs. execution only increased contralateral (+23%) and ipsilateral (+78%) M1 activation
Lacourse et al., 2004	Sequential button press task	fMRI	Mental practice decreased activation extent and increased activation intensity in contralateral M1 and decreased ipsilateral M1; activation similar to that in physical practice, but with weaker magnitude
Rodriguez et al., 2004	Phasic finger flexion	fMRI	Ratio of .75 of M1 voxels activated compared with execution
	Button press	EEG	Similar latencies and waveforms, but smaller amplitudes for LRPs in MI compared with execution
Solodkin et al., 2004	Sequential finger-to-thumb opposition	fMRI	M1 and S1 activity during motor imagery, but not during visual movement imagery
Alkadhi et al., 2005	Flexion/extension of the right foot	fMRI	M1 activity in 4 out of 8 healthy participants
Cramer et al., 2005	Attempted and imagined plantar flexion of the right foot	fMRI	Stronger activation of left primary sensorimotor cortex for attempted compared with imagined movement; stronger activation of right precentral gyrus for imagined compared with attempted right foot movement

Table 1 (*continued*)

Authors	Task	Method	Specific results
Neuper et al., 2005	Clenching a ball	EEG	Only motor but not visual imagery produced action-like activity over M1 area
Osman et al., 2005	Finger and toe tapping	EEG	Similar overall topography, normal for hands and paradoxical for feet
Carrillo-de-la-Peña et al., 2006	Button press (hand) and foot-flexion	EEG	Similar LRPs for execution and imagination; opposite polarity of LRPs for foot-flexions
Sacco et al., 2006	Sequences of tango steps	fMRI	M1 and S1 activity in the pretest; greater activation of M1 and S1 after active/mental training
Michelon et al., 2006	Rotational hand movement	fMRI	11/12 participants showed M1 activity on a single region level; contralateral activation of M1 for all participants
Szameitat et al., 2007	Everyday movements	fMRI	Homuncular representation in primary sensorimotor cortices
Guillot et al., 2008	Sequential finger movements	fMRI	Significant M1 activation in poor imagers but not in good imagers
Munzert et al., 2008	Gymnastic-like movements	fMRI	10/10 participants showed M1 activity
Orr et al., 2008	Ankle flexion	fMRI	M1 activation during MI, but not during observation
Sharma et al., 2008	Sequential finger-to-thumb opposition	fMRI	Activation of BA 4a and 4p; activation of BA 4p more robust and close to ME
Wriessnegger et al., 2008	Finger tapping	NIRS	Later onset and weaker M1 activation for MI compared to ME
Yoo et al., 2008	Squeezing the right fist	rtfMRI	Increasing M1 activity after real-time feedback

imagery that necessarily afford explicit processing. This can be demonstrated prototypically for self-assessment imagery scales, experimental protocols for fMRI and TMS studies on motor imagery, and mental rotation tasks (see Table 1 for an overview). Participants completing the Movement Imagery Questionnaire (Hall and Martin, 1997) are asked to first execute a defined movement sequence and then to imagine it either visually or kinesthetically before subsequently rating the ease/difficulty of image generation. This procedure contains explicit instructions asking for either kinesthetic or visual imagery of own movements along with explicit verbal reports about the image. Both behavioral and neurophysiological experiments also administer explicit instructions for motor imagery. For example, a participant may be asked to imagine a gymnastic movement previously demonstrated by a model (Zentgraf et al., 2005). However, in contrast to self-assessment scales, the outcome of imagery processes is examined indirectly through learning or neural activation measures. Classic experiments on mental training follow the same logic: participants are asked explicitly to imagine an action, but the analysis of the movement outcome is not based on a correspondingly explicit examination of the imagery. Furthermore, one can also use tasks that are considered to require imagery, but neither direct instruction for motor imagery nor scaling of vividness of imagery. One example for the latter is the mental rotation paradigm in which participants classify the identity of stimuli with different orientations, a process that calls for mental imagery processes (Kosslyn, 1994; de Lange et al., 2008; Parsons, 1994). In this case, time-consuming imagery processes are measured, implying no direct verbal report about the process or its product. It has to be stressed that manipulation checks are hardly ever performed to ensure whether participants really use implicit strategies in either mental rotation tasks or classic motor imagery experiments. Because it is clear that the accompanying experimental protocols do not necessarily imply explicit strategies, participants may well use different strategies to solve the imagery tasks.

These observations prompt us to introduce a working model for the use of imagery modalities in mental training and motor imagery experiments. We assume that imagery modalities are not distinct and isolated processes, but that they are linked together as a function of both the task and the participant's experience and can be weighted for different purposes by applying different manipulations. An experimental motor imagery instruction emphasizing the kinesthetic modality will encourage participants to shift their attention to this modality. This is not to imply that other representations are not present, but that the kinesthetic modality will be weighted strongly. Every experimental setting for mental imagery has to draw on similar assumptions, because they all instruct participants verbally to imagine a specific movement. However, the imaging process cannot be observed, and can be measured only indirectly via its behavioral or neural outcome. We specify the underlying assumptions in two ways: first, we assume that imagery modalities are linked closely and cannot be separated in absolute terms. Second, we view instructions as a means to focus individuals' attention on a specific modality and thereby to weight this modality during the imaging process. It has been demonstrated that the focus of attention during motor action actually does modulate neural activity in motor areas (Binkofski et al., 2002).

Imagery research has demonstrated strikingly that visual imagery and perception (Farah, 1984; Kosslyn, 1994) as well as motor imagery and motor execution (Jeannerod, 1994, 2001) share similar neural representations. This led Jeannerod (2001) to propose a concept of functional equivalence between motor imagery and motor execution. He views motor images as being based on neural processes for motor execution that are inhibited at a certain stage of processing. However, this overlap of neural representations is not just found between motor imagery and motor execution. It also emerges when other cognitive motor processes such as movement observation, action planning, and action verbalization are compared with motor execution. Jeannerod (2001) coined the term S

states to describe all those processes taken to be covert stages of action that share common representations with motor execution. It can be argued that S states simulate, to some degree, the real action. Mental simulation theory provides convincing arguments for processes that underlie mental training and explain neural activation during motor imagery as well as behavioral outcomes of mental training. The basic idea is that a neural motor network is activated while imaging motor actions (Jeannerod, 2001). This activation includes not only premotor and motor areas such as PMC, SMA, and M1 but also subcortical areas of the cerebellum (Lotze et al., 1999) and the basal ganglia (Bonda et al., 1995).

Conceiving motor imagery as an S state involves two general hypotheses: first, common neural representations can be anticipated between motor imagery and motor execution along with similar motor-relevant physiological responses (Guillot and Collet, 2005). The present review focuses on neurophysiological results. Nonetheless, changes to autonomic nervous system responses have also been reported to be similar in both motor imagery and motor execution (Decety et al., 1993; Wuyam et al., 1995). Second, differences can be anticipated between motor imagery and motor execution reflecting the fact that motor imagery is the covert stage of an action, whereas motor execution also implies additional processes for the overt behavior stage. Hence, correspondences as well as differences between motor imagery and motor execution should be found on both a behavioral and a neural level.

2. Behavioral outcomes of motor imagery

2.1. Similarity of mental and actual durations of movements

A strong argument for the relevance of motor representations in motor imagery comes from the similar durations found when participants perform the same movements either actively or mentally (Decety, 1996b; Jeannerod, 1994). This argument starts by assuming that durations will be similar if both active and mental performance rely on the same motor representation. According to mental simulation theory, this implies an activation of motor processes for mental simulation as well.

Decety et al. (1989) conducted an influential study of actual and mental durations of movements by examining walking distances of 5 m, 10 m, and 15 m. They found high correlations between mean active and mean mental durations. A closer inspection of the data also revealed very similar means. Although using means for statistical analyses has the drawback of canceling out errors within a participant that have different signs, this study was nonetheless the first to provide evidence for mental simulation theory based on an analysis of actual and mental durations. It also revealed dissociations between actual and mental durations when participants had to carry 25-kg loads while walking (see, also, Cerritelli et al., 2000): actual walking times were not influenced by the additional load, whereas mental durations were increased. Actual and mental durations for walking on a horizontal, an uphill, or a downhill track at different speeds

were very similar for all conditions, even though durations often differed markedly between conditions (Courtine et al., 2004). A further study revealed no effects on the accuracy of mental durations for either order of active and mental tasks or the time delay between active and mental tasks (Papaxanthis et al., 2002a). In addition, several studies demonstrated a similar effect of exposure to microgravity on both active and mental durations (Papaxanthis et al., 2003).

A correspondence between actual and imagined durations has also been found for writing and drawing (Decety and Michel, 1989; Papaxanthis et al., 2002a). Moreover, task complexity (as conceptualized in Fitts' law) has also been shown to impact in the same way on both real and mental movements (Bakker et al., 2007; Decety and Jeannerod, 1996; Sirigu et al., 1995, 1996). Additional forces applied to arm movements bring about similar changes in both actual and mental durations (Gentili et al., 2004; Papaxanthis et al., 2002b). However, a comparison of Fitts' law in an older population versus younger controls revealed dissociations between active and mental durations in the aged: Imagined movements did not comply with Fitts' law, whereas actual movements did (Skoura et al., 2005). Schott and Munzert (2007) also reported dissociations between actual and mental durations for walking distances in over-80-year-olds. This might be due to a trend toward slightly diminished imagery capacity in the aged (Mulder et al., 2007). A similar dissociation was found for children with developmental coordination disorder (DCD). Their actual movements revealed a speed-accuracy tradeoff in line with Fitts' law, but their mental movements did not (Wilson et al., 2001).

Whereas this close relation between actual and mental durations can also be seen in pedalo boating (Munzert, 2002), other studies using even more complex tasks have delivered evidence for a dissociation between actual and mental durations. Such evidence comes specifically from tasks in the sports domain such as golf putting (Orliaguet and Coello, 1998), playing badminton rallies (Munzert, 2008), performing floor routines in gymnastics (Calmels and Fournier, 2001), and springboard diving by novices and intermediates—but not by experts (Reed, 2002). Although several factors have been discussed as being potentially responsible for the observed dissociation between actual and mental durations in these tasks, it has been suggested that they perturb the close relationship between motor execution and motor imagery rather than establishing different basic processes of motor imagery. It has been shown that differences between active and mental durations could be reduced by motor expertise (Munzert, 2008; Reed, 2002), that noise-induced arousal influenced both actual and mental durations by similar proportions (Ozel et al., 2004), and that muscle fatigue did not alter motor imagery accuracy (Guillot et al., 2005). Furthermore, first- and third-person perspectives did not differentially influence imagery of the complex movement pattern of a gymnastic vault (Calmels et al., 2006).

All these results indicate a close relationship between the timing of actual and mental durations. This relationship can be explained in an elegant and simple way by positing that motor imagery and motor execution are based on overlapping representations. At the time of the early studies on the mental chronometry of motor imagery (Decety et al., 1989; Jeannerod, 1994), such arguments seemed quite speculative. They

became accepted only after neuroimaging studies were published confirming a common neural basis of motor imagery and motor execution (Jeannerod, 2001). Nevertheless, the chronometry paradigm is still open to criticism. It relies on a voluntary decision by the participant to indicate the beginning and ending of motor imagery. One cannot always rule out the possibility that participants use strategies such as counting to fill the intervals, or that they rely on former experiences without forming vivid images. Nonetheless, some ingenious protocols address these concerns (Sharma et al., 2006; Sirigu et al., 1996), and their results further support the general effect found in other motor imagery studies.

2.2. Mental rotation paradigm

This section draws on behavioral, fMRI, and TMS studies to discuss the mental rotation paradigm. When similar objects with different orientations have to be compared, time for completion depends on the angular disparity between the objects. Higher disparity leads to longer reaction times (Shepard and Metzler, 1971), because participants rotate the objects mentally. The mental rotation paradigm has been applied not only for rotations of letters and 3D cubes but also for hands, legs, and whole-body figures (Cooper and Shepard, 1975; Jola and Mast, 2005; de Lange et al., 2006; Parsons, 1987, 1994).

It has been shown that motor constraints also influence the time course of decisions on the orientation of body parts. Longer reaction times were found for anatomically inaccurate body parts or positions (Petit and Harris, 2005; Petit et al., 2003; Sauner et al., 2006). Judging imagined prehension movements that varied in level of difficulty due to the opposition axis of the fingers revealed longer reaction times for difficult movements, showing that motor imagery reflects the biomechanics of the arm (Frak et al., 2001). A study with upper limb amputees revealed slower reaction times for inaccurate arm positions, slower reaction times compared with controls, and a strong impact of loss of the preferred limb (Nico et al., 2004). Similar results have been reported for patients with congenital hemiparesis (Steenbergen et al., 2007) and cerebral palsy (Mutsaarts et al., 2007). When only a decision for an adequate grip was required, hemiplegics demonstrated similar performance to healthy controls (Johnson, 2000). Body part laterality judgments are also impaired in patients with idiopathic cervical dystonia (Fiorio et al., 2007) and pain syndromes (Moseley, 2004; Schwoebel et al., 2001).

Sirigu and Duhamel (2001) used a modified paradigm asking participants to imagine a hand in a specific spatial orientation and to report the location of a single finger on the imagined hand. In addition, the participants' hand position was varied (hands on the lap vs. hands behind the back), and they had to solve the discrimination task either with a first- or a third-person image. The authors found a remarkable interaction between imagery perspective and hand position. In the first-person perspective, reaction times were about three times longer for hands behind the back than for hands on the lap (for an extension of this finding, see Ionta et al., 2007); the opposite was the case for the third-person perspective. Hence, motor constraints seem to interfere primarily with the first-person perspective when using a motor imagery strategy. Results from the third-person perspective imply a more visual and object-centered rotation strategy. Further evidence for this conclusion comes from two patients: one with an impairment of motor imagery; the other, an impairment of visual imagery (Sirigu and Duhamel, 2001). In the patient with a parietal lesion leading to motor imagery impairment, results for the third-person perspective (and probably a visual strategy) resembled those in healthy controls. More importantly, the advantage for the first-person perspective (implying a motor imagery strategy for hands on the lap) disappeared. The opposite was found in the second patient with visual imagery deficits resulting from inferior-temporal damage: first-person results mirrored those of controls, whereas no advantage of a third-person perspective was found for hands behind the back. This and other studies reveal a strong influence of motor constraints on reaction times in mental rotation tasks. This indirect proof of an involvement of motor processes in motor imagery is further supported by brain imaging studies reported below.

Early PET studies revealed that mental rotation tasks lead to an activation of premotor areas and subcortical areas in the cerebellum and the basal ganglia (Bonda et al., 1995; Parsons and Fox, 1998; Parsons et al., 1995). However, some studies also show activation of the primary motor cortex (M1) (Kosslyn et al., 1998). Although there has been a major discussion about M1 involvement in motor imagery in general (Lotze and Halsband, 2006; and see below), evidence for M1 activation during mental rotation of hands and feet comes from a TMS study conducted by Ganis et al. (2000). Single magnet pulses placed above the hand area of M1 influenced times for completing the mental rotation task, especially for mentally rotating hands.

Because the mental rotation of innate objects does not activate premotor areas in all but only in some participants (Cohen et al., 1996), Kosslyn et al. (2001) tested whether activation of motor areas depends on the strategies participants use on such tasks. Before mental rotation, participants saw either a hand rotating the cubes or a motor-driven rotation of the objects. They were instructed to rotate the figures mentally as seen before. In this study, M1 activation was found in the hand-rotating but not in the motor-driven condition. This demonstrates that the involvement of premotor areas and eventually M1 in motor imagery depends on the strategy a participant applies to manipulate objects or body parts mentally. This view has been corroborated by a recent meta-analysis integrating imaging studies of mental rotation tasks (Zacks, 2008). This author reports that activation in the precentral sulcus is greatest when a motor simulation strategy is adopted, and that this particularly involves medial superior parts of the precentral sulcus (see, also, Michelon et al., 2006).

The mental rotation paradigm serves as a fundamental extension to our understanding of the mental durations of movements. Instead of assessing the accuracy of mental durations directly, it relies on implicit measures that are less prone to strategic alternatives like those discussed above for mental walking times. Accepting that mental rotation tasks require mental simulation, reaction times can be taken as a valid indicator for analogous processes of motor imagery and motor execution. In the present context, results on the mental

rotation of body parts or the whole body support the premise that motor execution and motor imagery share a common representational basis.

3. Neural correlates of motor imagery: brain imaging studies

One central issue, as noted above, is the activation of cortical and subcortical areas during motor imagery. Motor areas of the cerebral cortex are subdivided into primary motor cortex (M1) and several premotor areas, including the supplementary motor area (SMA), presupplementary motor area (pre-SMA), and ventral and dorsal parts of the premotor cortex (PMC). These cortical motor areas are linked closely to the cerebellum and the basal ganglia, thereby creating feedback loops (Krakauer and Ghez, 2000). Traditionally, the cerebellum has been associated to a greater or lesser extent with coordination, sensorimotor integration, movement correction, and feedback control (Ohyama et al., 2003). Brain research has shown that the motor cortex receives afferent information through the cerebello-thalamo-cortical loop, and it is assumed that this loop enables cerebellar signals to modulate the motor cortex and its functions (Krakauer and Ghez, 2000; Ramnani, 2006; Rouiller et al., 1994). Other areas that are relevant for motor execution and possibly for motor imagery are the primary somatosensory cortex (S1) and parts of the parietal lobe, particularly the superior and inferior parietal cortex.

Although there is now general consensus that SMA plays a major role in motor imagery, some studies report that the locations of SMA activity for motor imagery and motor execution overlap only partially (Deiber et al., 1996; Stephan et al., 1995). This suggests that at least some parts of the SMA play a specific role in motor imagery alone. A very recent study by Kasess et al. (2008) using dynamic causal modeling suggests that some SMA neurons inhibit M1 activity and thereby prevent motor execution. Overlapping activity in motor imagery and motor execution was also found in the dorsal part of the PMC, but there are some inconsistencies concerning the more ventral parts of PMC (PMCv). Gerardin et al. (2000) reported the PMCv to be activated more robustly in motor imagery than in motor execution. Considering that this area has been well studied in other S states such as action observation, the dissociation between motor imagery and motor execution appears dubious at first glance, because area PMCv is considered to be part of the mirror neuron system (Rizzolatti and Craighero, 2004) that responds to both motor execution and action observation. These inconsistencies might be due to the use of different movements and stimuli in research. In direct measures, only goal- and object-oriented movements elicited signals in mirror neurons, whereas intransitive movements left the mirror neurons silent (Rizzolatti and Craighero, 2004). In conclusion, both motor imagery and motor execution recruit PMC and SMA neurons, but the overlap is not complete. Which factors exactly drive activity in these areas still needs to be clarified. Other motor-related cortical areas covered in motor imagery literature are the inferior and superior parietal lobe. Both have been found to be activated in motor imagery, with increasing activity related to increased spatial task demands (Wolbers et al., 2003).

Whereas the activation of premotor areas during motor imagery is a common finding in brain imaging studies, activation of M1 during motor imagery is considered to be more controversial. It has often been argued that M1 is the gateway for motor commands to the periphery, and that this stage has to be suppressed to avoid overt behavior. However, early PET studies (Decety et al., 1988; Roland et al., 1980) and a multiplicity of studies to date have failed to reveal M1 activation consistently. Nonetheless, this has now been challenged by a great number of studies revealing significant M1 activation (Table 1). It has been found for different tasks, with different brain imaging methods (fMRI, MEG, EEG, PET, NIRS), and in different populations. Nonetheless, M1 activation in motor imagery is typically smaller compared with that in execution (see, for an exception, Caldara et al., 2004), and it cannot always be seen in all participants.

All studies demonstrating M1 activity used motor imagery. Unfortunately, however, these studies often failed to report the exact imagery instructions. Solodkin et al. (2004) examined different modalities within the same study. When comparing neural activation for motor imagery and visual imagery of movement explicitly, they found M1 activation only for motor imagery. Typical effects of M1 for motor execution, such as lateralization and somatotopic organization (see, for the latter, Stippich et al., 2002) have also been reported for motor imagery. Lateralization was often found to be weaker compared with motor execution (Gemignani et al., 2004; Lotze et al., 1999). Additionally, activation of M1 during motor imagery was used for neurofeedback (Neuper et al., 1999). These findings have been extended more recently by deCharms et al. (2004) using real-time fMRI. Participants in this study learned to regulate neural activity in motor and sensorimotor areas in the absence of muscle activity. Although results are not decisive, they support mental simulation theory by partly bridging the gap between the activation patterns of motor execution and motor imagery. Table 1 provides an overview of brain imaging studies revealing M1 activation during motor imagery.

Alongside this interpretation, there is an alternative view that M1 also supports more cognitive functions (Sanes and Donoghue, 2000) rather than just being an area for core movement production. M1 reveals anticipatory activity for movement sequences (Bremmer, 2005; Lu and Ashe, 2005); it receives input from the muscle spindles (Naito et al., 2002); and its posterior part 4p is modulated by attentional processes, whereas its anterior part 4a is not (Binkofski et al., 2002; see also Geyer et al., 1996; Johansen-Berg and Matthews, 2002). It seems difficult to determine the contribution of different cognitive subprocesses of motor imagery to an activation of M1. Nevertheless, it has been argued that it is particularly preparation for motor imagery that impacts significantly on M1 activation (Johnson et al., 2002; Zang et al., 2003).

M1 involvement during motor imagery is also reported in studies with amputees and patients with spinal cord injury (SCI). Some of the studies reported in Table 2 reveal similar M1 activation during motor imagery of movements with the impaired limb to that during motor execution with the unimpaired limb or to that in healthy controls during motor execution of the same movement. This has been found for amputees (Ersland et al., 1996) and persons with SCI (Alkadhi et al., 2005). Amputees often report a very vivid feeling of a

Table 2 – Studies revealing M1 activity during motor imagery in amputees and patients with spinal cord injury			
Authors	Task	Method	Specific results
Amputees			
Ersland et al., 1996	Alternative tapping of unimpaired and amputated hand	fMRI	Similar M1 activation for both movements
Campos da Paz et al., 2000	Dorsal and plantar flexion movements of existing and prosthetic foot	fMRI	Activity in BA 4 in 9/9 patients
Lotze et al., 2001	Hand movements	fMRI	11/14 amputees revealed contralateral M1 activity
Roux et al., 2001	Movements with missing limbs	fMRI	Contralateral activation of sensorimotor areas for both patients with arm amputation; bilateral activation of sensorimotor areas for a patient with leg amputation
Roux et al., 2003	Virtual movements with impaired and normal movements with unimpaired limb	fMRI/PET	Contralateral M1 activity for virtual movements (fMRI and PET)
Spinal cord injury			
Luft et al., 1998	Sequential finger-to-thumb opposition	fMRI	Intention: 8/9 M1 activation imagery: 6/9 M1 activation
Sabbah et al., 2002	Intention to move and motor imagery	fMRI	M1 activity with movement preparation
Cramer et al., 2005	Attempted and imagined plantarflexion of right foot	fMRI	Reduced activation of precentral gyrus for attempted (8%) and imagined (4%) movements compared to controls; contralateral activation of M1
Cramer et al., 2007	Attempted right foot movement	fMRI	More medial activation of primary sensorimotor cortex in SCI patients
Hotz-Boendermaker et al., 2008	Intention to move and motor imagery of foot movements	fMRI	Intention: 9/9 M1 activations in patients; Imagery: 7/9 M1 activations in patients (but only 3/10 M1 activations in healthy controls)
Lesion in the peripheral nervous system			
Foltys et al., 2000	Finger tapping	fMRI	Activation of contralateral sensorimotor cortex for imagining movements in patient with a unilateral traumatic brachial plexus avulsion

moving phantom limb when asked to imagine movements. The resulting M1 activation has been reported to depend on the vividness of the moving phantom limb (Lotze et al., 2001). A similar correlation between M1 activity and vividness of motor imagery has been reported for SCI patients (Alkadhi et al., 2005). The M1 activation seems even higher in patients than in healthy controls (Lotze et al., 2001; see, also, Lacourse et al., 1999, for similar results on motor imagery in SCI patients; for contradictory results, Cramer et al., 2005, showing significant but reduced activity in the precentral gyrus for attempted and imagined movements in SCI patients). It has been argued that the high level of activation during motor imagery in the disconnected limb is due to plastic changes resulting from the chronic lack of somatosensory feedback (Alkadhi et al., 2005). However, it cannot be ruled out that amputees or SCI patients use a different strategy compared with healthy participants when generating motor imagery. Because these patients do not need to inhibit the motor outcome, their strategy might be to attempt a movement and not to imagine it.

Stating that an inhibition of the efferent command is a prerequisite for motor imagery does not necessarily imply a complete suppression of the motor outflow—specifically in healthy participants. It has been shown repeatedly, using different methods, that motor imagery may influence spinal excitability (Kiers et al., 1997; Li et al., 2004a; for very small changes in H reflex, see, also, Gandevia et al., 1997). During motor imagery, a significant but subthreshold signal may be generated by M1 that produces changes of excitability at the spinal level. This makes it possible to conclude that a suprathreshold signal has to be suppressed, but that sub-threshold signals may leave M1 and cause a change in excitability at the spinal level.

Because motor imagery is functionally equivalent to motor preparation, it is thought to imply a strong tendency toward movement execution. This makes it conceivable for small movements during motor imagery to cause M1 activity within this condition. Some studies have controlled movement artifacts visually, although this would not seem to be very accurate. A more effective method is to control muscle discharges during motor imagery. Therefore, some research-ers have used EMG monitoring to control movement artifacts. These studies have shown that muscle activity during motor imagery in training sessions is much smaller than that found during motor execution of the same movement (Lafleur et al., 2002; Lotze et al., 1999). More recently, fMRI studies have succeeded in controlling EMG activity within the scanning session (Bakker et al., 2008; deCharms et al., 2004). This is a more direct control of artifacts than EMG monitoring during training sessions. Nevertheless, movement artifacts continue to be a potentially critical aspect when interpreting M1 activity during motor imagery. It has to be noted that, up to now, few studies have used a control of movement artifacts within a training session, and even fewer have examined muscle discharges during the core experimental session during fMRI. One promising approach to controlling this artifact comes from studies using a glove during fMRI. This could well prove to be a good way to analyze very small movements more effectively (Sharma et al., 2008).

A fundamental experimental paradigm for examining M1 activation is transcranial magnetic stimulation (TMS). Corti-cospinal excitability of M1 can be analyzed by studying

electromyographic responses using external stimulation of M1 by magnetic fields (Kobayashi and Pascual-Leone, 2003). It has been demonstrated frequently that motor imagery enhances excitability as shown by motor evoked potentials (MEPs). Table 3 provides a summary of studies demonstrating this effect. Most provided evidence that motor imagery facilitates effector-specific MEPs in muscles normally active during the movements to be imagined, whereas MEPs for

Table 3 – Studies revealing enhancement of corticospinal excitability of M1 during motor imagery		
Authors	Task	Specific results
Izumi et al., 1995	Thumb abduction	Stronger MEPs compared with rest, but weaker MEPs compared with active movement
Abbruzzese et al., 1996	(1) Repetitive thumb-to-index opposition (2) Sequential finger movements	Facilitation of MEPs for sequential finger movements, but not for repetitive movements
Yahagi et al., 1996	Wrist flexion	Facilitation of flexor carpi radialis
Kasai et al., 1997	Wrist flexion	Facilitation of MEPs in flexor, but also in the antagonist muscle; no change in H-reflex
Kiers et al., 1997	Thumb abduction	First-person perspective and thinking about the movement facilitated MEPs
Rossi et al., 1998	Wrist flexion and extension	Facilitation of MEPs in the agonist muscle for all participants, and in the antagonist muscle for 2/7 participants
Yahagi and Kasai, 1998	Flexion, abduction, and extension of index finger	Muscle-specific activation during different images with the same limb
Abbruzzese et al., 1999	Sequential finger movement	Paired-pulse TMS changed cortico–cortico inhibition similarly for both motor imagery and active movements
Fadiga et al., 1999	(1) Flexion/extension of limbs (2) Opening or closing left and right hand	Stimulation of left M1 revealed a facilitation of MEPs on the contralateral side; stimulation of left M1 facilitated contralateral and lateral MEPs
Hashimoto and Rothwell, 1999	Repetitive flexion and extension of wrist	Facilitation of flexor muscles during imagined flexion and of extensor muscles during imagined extension; H-reflex of flexor in 4/9 participants
Rossini et al., 1999	Little and index finger abduction	Effector-specific MEPs
Tremblay et al., 2001	Leg extension	Facilitation of MEPs in quadriceps, but not in biceps femoris
Facchini et al., 2002	Imagery of contralateral and ipsilateral thumb abduction	Increased MEPs for contralateral, but not for ipsilateral movements
Hiraoka, 2002	Imaging to stumble while staying	Decreasing MEPs in the soleus, but no changes in the tibialis anterior
Stinear and Byblow, 2003	Isometric muscle contraction of a digit	Temporally modulated increase of MEPs for intrinsic muscle
Levin et al., 2004	Cyclical unimanual and bimanual wrist flexion–extension	Increased reciprocal excitability changes for symmetrical in-phase movements compared with antiphase and unimanual movements
Li et al., 2004b	Finger force production by the index finger or by four fingers simultaneously	Increase of MEPs for both imagery conditions compared with rest; no differences between imagery conditions
Vargas et al., 2004	Joining thumb and little finger	Excitability depended on actual hand position; stronger excitability for compatible hand positions
Quartarone et al., 2005	Abduction of index finger	Smaller increase in MEPs for patients with writer's cramp than in controls; bilateral facilitation in patients, but not in controls
Fourkas et al., 2006a	Index finger abduction	Stronger facilitation of MEPs during third-person compared with first-person imagery
Fourkas et al., 2006b	Thumb-palm opposition	Facilitation of MEPs in opponens pollicis, but not in a control muscle; facilitation dependent on hand position
Stinear et al., 2006a	Phasic thumb movement	Stronger facilitation of MEPs during kinesthetic than during visual imagery of movement
Stinear et al., 2006b	Unimanual and bimanual thumb movements	Facilitation of dominant M1 for left- and right-handed, as well as bimanual movements
Léonard and Tremblay, 2007	Hand movements	Facilitation of M1 in younger and older adults; reduced selectivity for specific muscles in older adults
Liang et al., 2007	Index finger abduction	MEPs in an agonist and synergist muscle were measured depending on hand posture
Marconi et al., 2007	Thumb-little finger opposition	Similar facilitation of M1 for MI and observation of movements
Stinear et al., 2007	Phasic thumb movement	Facilitation of left M1 during right-hand imagery in right-handers, no facilitation of right M1 during left-hand imagery
Fourkas et al., 2008	Tennis forehand, table tennis forehand, golf drive	Tennis experts exhibited stronger facilitation for MI of tennis strokes compared with table tennis strokes and golf drives; this effect did not occur in novices
Kumru et al., 2008	Simple reaction time task (squeeze)	Larger MEPs for MI at 50 ms before movement onset
Liang et al., 2008	Index finger abduction	MI of left index finger modulated MEPs in left and right index finger
Mercier et al., 2008	Joining thumb and little finger	Excitability depended on actual hand position; stronger excitability for compatible hand positions in controls

muscles inactive during these movements show no signs of increase. With one exception, most studies used arm and finger movements. The exception is Tremblay et al. (2001) who examined MEPs in leg movements and found effects comparable to those in finger or hand movements. A recent study has also analyzed motor imagery for complex sports behavior (Fourkas et al., 2008).

Recent studies have demonstrated that the actual hand position during TMS influences MEPs. When Vargas et al. (2004) asked participants to position their hand either compatibly or incompatibly to the imagined movement, they found a significant interaction between imagery condition and hand position: excitability for compatible hand positions was higher than for incompatible hand positions during motor imagery (see, also, similar results for healthy controls in Mercier et al., 2008). Data from a deafferented participant suffering from polyneuropathy showed differences only in a condition with compatible hand position and eyes open (Mercier et al., 2008). It can therefore be argued that afferent feedback may be responsible for the facilitation of congruent hand positions. These findings are underlined by the fact that immobilization of a limb results in decreased excitability during motor imagery (Kaneko et al., 2003). Fourkas et al. (2006b) extended these findings by showing that they also depend on imagery modality. During visual imagery of one's own movements, they found almost zero decrement for incompatible position. In comparison, they demonstrated a dramatic decrement when actual hand position was incompatible. Recent research has also examined specific effects of imagery modalities and perspectives. Whereas Fourkas et al. (2006b) found no general difference between imagery modalities but an interaction with hand position, Stinear et al. (2006a) found stronger excitability for kinesthetic compared with visual movement imagery. Another study (Fourkas et al., 2006a) examined different visual perspectives and found a stronger effect for a third- compared with a first-person perspective. The authors interpreted this effect against the background that the third-person visual perspective is similar to movement observation, and that movement observation of other persons has also been seen to enhance motor cortex excitability (Hari et al., 1998).

Both fMRI and TMS studies have revealed M1 activation in motor imagery. It can be shown that this M1 activation is not a result of mere inhibitory processes preventing the efferences from producing motor execution. However, it can also be shown that motor imagery is not a total off-line process because of its sensitivity to afferent processes like the congruency of actual and mental hand positions.

4. Motor imagery in patients with lesions

4.1. Motor imagery in stroke patients

Due to the overlap of the neural circuitries involved in motor imagery and motor execution, lesions of these areas and loops should lead to a deficit in both processes. Indeed, comparisons between healthy participants and stroke patients indicate such a relationship, and several studies have demonstrated an impairment of motor imagery after a stroke incident. For

example, one repeated observation has been a parallel slowing of real and imagined movement after stroke (González et al., 2005; Malouin et al., 2004a,b; Sabaté et al., 2007).

Several studies have used fMRI to investigate neural activation loci during motor imagery and motor execution. One finding is increased ipsilateral activation in M1 and SMA in stroke patients while performing motor imagery with the impaired limb compared with a contralateral activation in M1, S1, SMA, and pre-SMA regions in healthy controls (Kimberley et al., 2006). In stroke patients, ipsilateral neural activation has also been demonstrated for motor execution of simple tasks (Carey et al., 2002; Strens et al., 2003). This led to the premise that ipsilateral human motor structures might compensate functionally for contralateral motor cortex dysfunction, especially in very early stages of rehabilitation (Calautti et al., 2001; Lacourse et al., 2004). One TMS study presented contradictory results showing that the imagery-induced excitability was higher in the affected than in the unaffected hemisphere due to a different excitatory state of the motor cortex in the former (Cicinelli et al., 2006). However, Stinear et al. (2007) recently demonstrated that the side of the stroke affects the lateralization of motor facilitation during motor imagery. In patients with a left-hemisphere stroke, only the right (i.e., contralesional) M1 demonstrated facilitation during motor imagery of hand movements. In patients with a right-hemisphere stroke, facilitation was found neither in the right nor the left M1 during motor imagery. Thus, the heterogeneity of samples regarding the lateralization of the stroke might have contributed to the inconsistent results. For example, Cicinelli et al. (2006) investigated 17 patients—10 with an ischemic lesion in the left and 7 in the right hemisphere. Other studies (e.g., Kimberley et al., 2006; Carey et al., 2002) do not specifically report stroke localization, and the results of Stinear et al. (2007) indicate that such patient subgroups are not comparable in terms of their task-related behavior or the associated neural basis.

A consideration of cellular processes might help to resolve the observed inconsistencies. Animals with a focal infarct exhibit a down-regulation of $GABA_A$ receptors as well as an up-regulation of NMDA receptors. NMDA and GABA receptors are involved in the regulation of excitatory and inhibitory processes, and both play a critical role in reorganization following cortical injury. Additionally, reorganization takes place in both the impaired and the unimpaired hemisphere (Nudo, 1999; Nudo and Duncan, 2004). Taking into consideration that both hemispheres underlie these receptor-related reorganizational processes, the inconsistent findings on ipsi- or contralateral hyperactivation might be explained by a time-dependent sequential restructuring of both hemispheres. Thus, the time lag between the lesion event and data acquisition might be a critical variable for short-term plasticity, influencing excitability and activation of the examined cortical structures described in the studies mentioned above.

Clinical studies with stroke patients provide further information on the relation between subcortical structures and functional outcome. For example, Li (2000) instructed patients exhibiting a putamen lesion due to a hemorrhagic or an ischemic infarct to engage in motor imagery and visual imagery. Data revealed a deficit for motor imagery but not for visual imagery. These results provide evidence that the basal

ganglia as well as cortical structures belong to a network involved in motor imagery. After a cerebellar stroke, a reduced excitability of motor areas can be observed, depending on the disruption of the cerebello-thalamo-cortical loop. Consequences are a decrease in motor-evoked potentials during motor imagery as well as a parallel slowing down for motor execution and motor imagery (Battaglia et al., 2006; Gonzáles et al., 2005).

Generally, the reported results show that a complex cortico-subcortical network contributes to motor-related processes such as motor imagery. These multiple representations along with the brain's neuroplasticity processes help to generate the system's best possible motor output. For example, it can be argued that hyperexcitability of brain regions after a lesion is part of a compensation strategy implemented in the motor system.

4.2.   Motor imagery in patients with Parkinson's disease

Because motor imagery is defined as a state in which a movement plan is generated without execution, it can be assumed that motor imagery will also be impaired in movement disorders exhibiting a disturbed movement initiation like that often observed in Parkinson's disease (PD). PD is a disorder resulting from the degeneration of the dopaminergic nigrostriatal pathways (Kish et al., 1988; Turner et al., 2003; Yu et al., 2007). It has been claimed that the impaired movement initiation is due to the incorrect generation of internal states, which also includes motor imagery tasks (Dominey et al., 1995). Indeed, a couple of studies provide evidence for a reduced capacity to simulate body movements in PD patients. For example, they showed more deficits during the mental rotation of body parts compared with the mental rotation of letters or 3D objects (Amick et al., 2006; Dominey et al., 1995).

PD patients regularly show a reduction in central metabolic and electrophysiological activity while performing motor imagery tasks (Cunnington et al., 1997, 1999, 2001; Dominey et al., 1995; Samuel et al., 1997; Thobois et al., 2000). For example, in a TMS study, Filippi et al. (2001) found that hemiparkinsonian patients showed a decreased excitability of motor areas in the affected hemisphere during motor imagery. Reduced neural activation in PD has also been shown with $H_2^{15}O$ PET. Here, a significant underactivation in the dorsolateral prefrontal cortex and regions of the mesial frontal cortex was found in patients during motor execution and motor imagery of a simple movement task, showing that these structures are involved in loops that subserve imagery and motor programming processes (Samuel et al., 2001). Thus, one interpretation is that the frontostriatal system is involved in the control of internal states and movement simulation, which is known to be defective in these patients (e.g., Kish et al., 1988; Turner et al., 2003; Yu et al., 2007).

A couple of PD studies have assessed the activation of the SMA during motor imagery and motor execution. An underactivation of SMA was observed in PD patients performing simple motor tasks (Jenkins et al., 1992; Playford et al., 1992). This was thought to reflect a deficit in the basal ganglia-thalamo-cortical-motor loop. Due to the relative overlap of activated structures during motor imagery and motor execution, a similar SMA underactivation was expected for motor imagery tasks in PD patients (Cunnington et al., 2001; Thobois et al., 2000, 2002). However, these studies failed to demonstrate an activation deficit, but revealed a preserved SMA function in motor imagery. For example, Cunnington et al. (2001) conducted a PET study asking PD patients and controls to imagine a sequential finger-opposition task, known as a robust method to activate SMA. They found no activation impairment of SMA in PD patients compared with healthy controls. They explained these results in terms of the anatomic as well as functional differences in the SMA itself. In this context, Sabatini et al. (2000) used a complex sequential finger-tapping task to demonstrate that PD patients exhibited decreased activation in the rostral part of the SMA as well as in the dorsolateral prefrontal cortex. Concomitantly, PD patients showed a significant increase in neural activation of the caudal part of the SMA (SMA proper). Recent high-resolution imaging studies have refined the concept of SMA functional organization and described a heterogeneity between rostral and caudal parts of the SMA that are correspondent to the pre-SMA and the SMA proper (Akkal et al., 2007). Both parts are integrated with different basal ganglia-cortical loops. SMA proper is involved in a core motor loop, whereas pre-SMA receives its input from different pallidal neurons bound to associative tasks as well as from connections to the prefrontal areas. Functionally, the pre-SMA is thought to play a crucial role in activities prior to execution, whereas the SMA proper is more important for motor execution itself (Picard and Strick, 1996). It has been argued that the phenomenon of under- and over-activation in pre-SMA and SMA proper observed in PD patients illustrates the capacity of the adult human brain for functional plasticity. The mechanism might serve to compensate for a failing motor circuit by recruiting another one involved in motor imagery.

PD has been characterized predominantly by motor impairments. But recent research highlights that sensory processing is also affected (Maschke et al., 2003). As shown by de Lange et al. (2006), motor imagery as well as movement-planning-related processes depends on the input of proprioceptive information. In this context, it has to be considered that PD patients exhibit a lack of sensory feedback. Helmich et al. (2007) found an impaired processing of mental rotations of the hand accompanied by an increased activity in the right extrastriate body area (EBA) and the occipitoparietal cortex (OPC) in PD patients, and argued that their reduced kinesthetic feedback caused an over-activation of regions involved in visual processing such as the EBA and the OPC. These findings characterize the neuronal representation of the increased dependence on visual information processing during the generation of motor plans in PD patients and offer a further interesting link between on- and off-line movement processes.

In sum, patient studies on motor imagery clearly show the complexity of the neural network that contributes to motor planning and motor imagery. They also suggest that different structures within the network might be involved in potential compensation mechanisms for severe impairments. Furthermore, motor imagery studies demonstrate that the severe motor problems exhibited by PD and stroke patients are also due to a loss of adequate motor-planning processes. This aspect reveals the possibility of applying these techniques in therapeutic settings.

5. Application of motor imagery in sports and therapeutic settings

5.1. Applications of mental training for learning motor skills in sports

Mental practice of motor behavior such as the systematic and repetitive use of imagery is regarded as a powerful tool to enhance skill learning in sports. Several meta-analyses have revealed a systematic, but moderate effect of mental training on motor learning (Driskell et al., 1994; Feltz and Landers, 1983; Feltz et al., 1988; Hinshaw, 1991/92; Richardson, 1967a, 1967b). Different mediators have been identified that influence the mental training/performance relationship. Skill level, task characteristics, imagery abilities, and the distinction between an internal versus external perspective are considered to be important within this context. By focusing on the behavioral consequences of mental training, this research has placed less emphasis on the study of the basic processes underlying motor imagery and, therefore, mental training.

The main focus of mental training research in sports has been on the visual imagery of movement and not on motor imagery as emphasized in the neurosciences (cf. Weinberg, 2008). Additionally, mental training has been used as a label for a variety of techniques relying on visual imagery, motor imagery, and self-instructions, as well as ones containing relaxation processes. Although this makes it difficult to interpret meta-analyses like that of Feltz and Landers (1983), their general effect size of .48 indicates a positive effect of mental training compared with control groups, and stronger learning and performance effects for groups with physical practice compared with mental practice. As it is difficult to conduct experiments with top athletes for a variety of reasons, studies investigating imagery use by elite athletes are seen as helpful. These reveal that elite athletes use imagery more extensively and systematically and that they exhibit better imagery skills than less successful athletes (Calmels et al., 2003).

Imagery perspective is one of the key points connecting motor imagery in the sports domain with neuroscientific studies. For the latter, motor imagery unfolds its specific effects especially when a person generates an image of a motor act that gives him or her the feeling as if he or she is actually performing it. Whereas a first-person perspective can be used in this context, this is not necessarily the case in sports. It has to be mentioned here that assessment criteria are based on performance measures. For example, one study found learning and retention effects for kinesthetic feedback for a rock-climbing task (Hardy and Callow, 1999). But it has also to be noted that kinesthetic imagery can be associated with different visual perspectives (Hardy and Callow, 1999; White and Hardy, 1995).

Mental training in sports has also been used to enhance transfer effects of a peak power training to sprint performance (Van Gyn et al., 1990). After a 6-week training period, groups that had received either power training or a combination of power and mental training did better on the power training task than controls and participants with only mental training. When sprint performance was tested, only the group with a combination of physical and mental training showed significant enhancement, but not the power training group.

Mental training has also been used for the rehabilitation of sport injuries. Positive effects were demonstrated for muscle endurance after ankle sprain (Christakou et al., 2007) and in terms of significantly greater knee strength after anterior cruciate ligament reconstruction (Cupal and Brewer, 2001). Obviously, these effects of mental training in injury rehabilitation are based on an enhancement of force production. This might also have been the reason for superior postural stability in older women after mental training (Fansler et al., 1985; Linden et al., 1989).

Furthermore, effects of mental training on performance are also reported for other skill domains like surgery (Immenroth et al., 2007) and piano playing (Meister et al., 2004). It has to be considered that these complex activities require mental training programs that include not only motor imagery but also more cognitive routines and processes like those discussed for the sports domain.

Applied cognitive psychology has misrepresented motor imagery as a mere cognitive process and has long neglected neurophysiological results. However, we believe that psychology should acknowledge the neurophysiological basis of its tasks and procedures. Likewise, neurophysiology needs to gain a detailed understanding of the sensitivity and malleability of cognitive processes.

5.2. Motor imagery as a promising therapeutic tool

Motor imagery techniques might well be powerful enough to serve as a therapeutic tool in neurological rehabilitation and in prevention programs for the elderly (cf. Fansler et al., 1985; Linden et al., 1989; Lotze and Cohen, 2006; Mulder, 2007). The physiological basis might be associated with the phenomenon that cortical representations of the adult brain are not fixed but highly dynamic (Buonomano and Merzenich, 1998; Spitzer, 1999). Thus, cortical connections and responses are being reorganized continuously as a result of peripheral and central alterations of input. This ability to reorganize is an important component of motor learning and recovery after neural injury. The question is whether motor imagery alone is able to produce representational changes and changes in neural plasticity comparable to those observed after motor practice (Jackson et al., 2003; Pascual-Leone et al., 1995). Pascual-Leone et al. (1995), for example, used a musical performance training to demonstrate that a period of 5 days of physical training and motor imagery training combined with physical training resulted in an increase of the contralateral primary motor cortex map size of the long finger flexors and extensors as assessed with TMS. Most interestingly, the motor imagery group demonstrated the same training effect after one additional physical training as the physical-only group, pointing to the importance of combining motor imagery and physical training.

Focusing on the impact of motor imagery in patient groups with lesions, it must be stated that one significant predictor for motor outcome of the hand function after a lesion of the brain is the activation in the contralateral primary motor hand area. Lotze and Cohen (2006) tested an fMRI-based feedback training of M1 activation using imagery techniques. They found that

activation in M1 without ME could be accomplished easily together with BOLD-feedback. This underpins the notion that imagery techniques can be used to either train the concept of a movement and regain access to new assemblies of M1 in cases of cortical lesions and motor impairment.

Several therapy outcome studies have investigated the potential of motor imagery in the context of neurological rehabilitation, and shown that it seems to offer considerable advantages in the therapeutic context. First, it provides an opportunity to add additional training effects. It involves little cost, needs no institutional context, and exposes patients to no safety risks. Additionally, it seems possible to start the intervention at an earlier stage of rehabilitation when little or no movement is possible (Lotze and Cohen, 2006; Page et al., 2001; Tamir et al., 2007). The essence of motor imagery in the rehabilitation context lies in teaching patients strategies that facilitate the reorganization of the affected areas and loops by recruiting intact neurons and strengthening activity in other neuronal loops. This compensation mechanism is promoted by using cognitive strategies to trigger and initiate motor acts (Lotze and Cohen, 2006; Tamir et al., 2007). Recent studies have revealed a strong effect of feedback with real-time fMRI on the plasticity of cortical areas (deCharms et al. 2004; Weiskopf et al., 2004; see, for an overview, deCharms, 2008). This method may well deliver an additional tool for motor rehabilitation in the near future.

Arguments for the application of motor imagery as a rehabilitative strategy for motor recovery after brain damage have been offered by several studies revealing its positive impact on therapy outcomes (Crosbie et al., 2004; Dunsky et al., 2006; Gagglio et al., 2006; Johnson-Frey, 2004; Malouin et al., 2004a,b; Yoo et al., 2001). Page et al. (2001, 2007) conducted two randomized, controlled therapy outcome studies with stroke patients. Both showed that motor imagery is a clinically feasible intervention. One of these studies compared conventional motor therapy with a therapy form combining mental and physical practice, and it will be described in more detail here. After the pretest, each participant was randomly assigned to the R+PP (relaxation and physical practice) or MI+PP (motor imagery and physical practice) group. Therapy outcome was evaluated by measuring upper- and lower-extremity motor function. The observed changes between pre- and posttest indicated a positive impact of the MI+PP combination in the experimental group but not in the control group. These results underpin the usefulness of an integration of motor imagery in physical rehabilitation programs. Results on everyday movements including reaching, wrist extension, pronation, and supination of the wrist (Stevens and Stoykov, 2003) demonstrate that the performance of the paretic limb improves after an imagery intervention, as indicated by an increase in functionality and a decrease in movement time. Alongside increased competence on the trained task, other studies observed transfer effects to untrained tasks (Gentili et al., 2006; Liu et al., 2004). Both effects might be important for a successful rehabilitation process.

Recent research has stressed the potential of motor imagery in PD rehabilitation programs. PD patients, similar to stroke patients, benefit more strongly from the application of motor imagery combined with physical practice than from physical practice alone. Findings document an advantage of the combination of physical therapy with motor imagery, probably due to the application of a cognitive strategy for facilitating an upcoming motor act (Tamir et al., 2007). Lim et al. (2006) proposed a neurophysiological explanation for the beneficial outcomes of motor imagery in PD rehabilitation. They investigated late contingent negative variation (CNV), a slow negative movement- and sensory-related potential that can be divided into two parts: early and late. Late CNV is generated by the basal-ganglia-thalamo-cortical loop and serves as an indicator for the activation in these structures (Ikeda et al., 1994, Lim et al., 2006). It was found that motor imagery can alter the movement-related potentials in PD patients by increasing the amplitude of the late CNV. No such changes in amplitude were recorded after visual imagery of movement. However, when it comes to relatively difficult motor tasks, PD patients do not show any improvement through either physical or mental training (Yágüez et al., 1999). The authors thought that problems with an attentional focus in PD patients might have been responsible for this result.

However, when discussing more practical arguments for the implementation of motor imagery in rehabilitation, Butler and Page (2006) reasoned that motor imagery can be employed when and where the trainee wants to use it and as often as he or she wants. Additionally, the patient can imagine the movements in whatever context he or she considers to be relevant.

However, due to these findings, it is still not possible to draw a final conclusion on the usefulness of mental training in rehabilitation processes (Mulder, 2007). For example, it is worth noting that there is a weak but significant shift from motor to visual-guided motor imagery as a function of increasing age. Furthermore, a small relationship has been reported between physical status and the imagination of self-performed movements (Mulder et al., 2007), so that a change within the imagery capacity across age might significantly affect the outcome of mental training. This requires particular consideration in light of the many aged persons in clinical settings. In this context, it should be noted that motor imagery is also a cognitively challenging task that requires working memory capacity while internally simulating the movement. Mental rehearsal requires the manipulation of visual and kinesthetic information in working memory. Therefore deficits in working memory, as observed for example in PD, may affect the ability to use imagery techniques successfully in the rehabilitation process (see, for a review, Dubois and Pillon, 1997). Results of a study conducted by Malouin et al. (2004a,b) emphasize the role of cognitive factors in the outcomes of mental training in the rehabilitation process (see, also, Stinear et al., 2007, for a discussion on this aspect). These facts should be taken into account when selecting an adequate therapeutic program.

Results reporting impaired motor imagery capabilities in stroke and PD patients also reveal the limitations of motor imagery as a therapeutic tool. If patients are unable to generate proper motor images, it is hardly likely that motor imagery protocols will be effective. In particular, lesions to the parietal lobes seem to cut back motor imagery abilities and therefore reduce the impact of mental rehearsal in these patients (Jackson et al., 2001; Lotze and Halsband, 2006; Mulder, 2007).

5.3. Strength increases following mental training

Mental training has been applied in the context of both sports and rehabilitation to overcome strength losses or to produce strength gains. The reaction to motor imagery seems to be similar in both fields. A pioneering study by Yue and Cole (1992) demonstrated effects of motor imagery on training isometric force for finger abduction with the little finger. A strength increase for mental training was found not only for the trained digit but also for the contralateral untrained little finger (see, for an assessment of contralateral transfer, Carroll et al., 2006). Mental training increased maximal isometric force in the trained finger by about 22% and in the untrained contralateral finger by about 10%. The effects were smaller than those of physical training. Similar results on the isometric forces of fingers were replicated by Ranganathan et al. (2004). This study also revealed a correlation between strength increases and movement-related cortical potentials. Effects of mental training on force production are also reported for elbow flexion (Ranganathan et al., 2004; but see Herbert et al., 1998) and upper leg muscles (Sidaway, 2005; Zijdewind et al., 2003).

Mental procedures have also been used to examine strength losses after immobilization of limbs. Newsom et al. (2003) reported no significant loss of grip strength for a mental training group after 10 days of forearm immobilization, but a significant decrease in strength for a control group. Clark et al. (2006) found no significant effect of mental training in reducing strength loss. In contrast, Yue et al. (1996) even found strength gains for a mental training group after a 10-week immobilization of the little finger, whereas a control group revealed no significant changes in force production.

A recent study has demonstrated that motor imagery and observation of movements produce similar effects in force production tasks (Porro et al., 2007). This effect in an observation condition is particularly surprising. In an isometric force production task, both physical activity and observation resulted in significant gains. Interestingly, these gains were similar for the trained and the untrained contralateral hand in the observation condition but stronger for the trained hand in the active condition. In an isotonic force production task, no effect was found for the contralateral, untrained hand. But effects for physical activity and observation were now significant, with no relevant difference between conditions. An additional TMS experiment, including physical, imagery, and observation conditions, showed a larger increase in MEPs for active compared with mental, and a larger increase for mental compared with observational conditions. Nevertheless, observational conditions also showed a significant difference between pre- and posttest. These results corroborate the prediction in mental simulation theory of similar outcomes for motor imagery and action observation. This was the first study to validate this for force production tasks.

Permanent strength increase does not just depend on changes in muscle mass and muscle composition but also on neural adaptations. At least three arguments support this assumption: (a) early strength increase following training within the first weeks precedes a significant change in muscle mass; (b) training of one limb also produces strength increase in the contralateral but untrained limb; and (c) training of a specific muscle does not transfer to all motor tasks that integrate the trained muscle (Enoka, 1997). Positive effects of motor imagery provide strong arguments in favor of centrally modulated processes for motor imagery. As discussed in the sections on fMRI and TMS results, motor imagery activates motor programming processes, as predicted by mental simulation theory. These processes also alter the recruitment and firing frequency of motoneurons, which is one way to obtain strength increases. While the present experiments exclude other options like muscle hypertrophy because of their short duration, they can be taken as confirmation for the effects of repeated motor programming during motor imagery.

6. Conclusion

Neuroscientific studies confirm a profound and reproducible effect of motor imagery on the neural activation of motor areas and, in the context of power training, on behavioral learning. Effects of motor imagery on motor learning are not restricted to laboratory tasks but are also found for applications in physical therapy. In particular, training regimes with applications of mental training for stroke patients have demonstrated a reasonable degree of effectiveness (Page et al., 2001). Moreover, neural activation during motor imagery may serve as a control device for brain-machine interfaces (deCharms, 2007; Lebedev and Nicolelis, 2006; Weiskopf et al., 2004). In this case, brain activation during imagery may serve as control signal to support communication and the motor control of a prosthetic device.

Whereas the activation of M1 can be confirmed in a large number of studies (see Table 1), the status of primary sensory areas during motor imagery remains unclear. For example, Munzert et al. (2008) have found activation in S1 and in the insula during motor imagery (see, also, Lotze et al., 1999; Sacco et al., 2006; Solodkin et al., 2004). Searching for further evidence of activation of sensory areas seems to be a promising direction for future research. Studying such activation as a consequence of motor imagery might help to build up a theoretical link between mental simulation theory (Jeannerod, 1994, 2001) and forward model concepts (Miall, 2003; Miall and Wolpert, 1996). Forward models contain an expectation about sensory consequences (Miall, 2003). They afford an activation of the motor network to create an image of future action consequences. Therefore, it seems plausible to predict activation in primary and secondary sensory areas during motor imagery. Nonetheless, this is a problem that is still under discussion.

Applications of mental training in sports show that athletes can switch between imagery modalities quite easily, although individual preferences do remain. The feasibility of doing this depends on individual experience and the instructional setting. Neuroscientific studies have particularly failed to stress the latter point. This is astonishing when considering the significant differences found for neural activation associated with motor imagery versus visual imagery. For example, stronger effects on M1 activation (Solodkin et al., 2004) and M1 excitability (Fourkas et al., 2006b; Stinear et al., 2006a) have been reported repeatedly. A closer look at the experimental

conditions in these experiments reveals that imagery conditions differ only in terms of initial instructions but not in terms of stimuli or tasks. Mental durations can be taken as an indirect measure for the control of imagery processes (Munzert et al., 2008). Nonetheless, no direct compliance check is available (see, also, Sharma et al., 2006, 2008).

Taking these methodological constraints into consideration, one might ask how differences between instructions can trigger significant changes in the neural activation of cortical and subcortical areas. It can be argued that imagery instructions change the attentional focus on different aspects of motor control in participants. Visual imagery focuses on external aspects with special reference to the relation of body and environment, whereas motor imagery focuses on internal states of movement dynamics and force production. These differences can explain why motor imagery specifically activates motor areas. Attention is drawn to own movements and therefore to the agency of actions. This causes activation of cortical motor areas and subcortical areas that are integrated in cerebello-thalamo-cortical loops. Taking these arguments as a central prerequisite of imagery research, future research needs to analyze the contents of imagery instructions in a more subtle way.

REFERENCES

Abbruzzese, G., Trompetto, C., Schieppati, M., 1996. The excitability of the human motor cortex increases during execution and mental imagination of sequential but not repetitive finger movements. Exp. Brain Res. 111, 465–472.

Abbruzzese, G., Assini, A., Buccolieri, A., Marchese, R., Trompetto, C., 1999. Changes of intracortical inhibition during motor imagery in human subjects. Neurosci. Lett. 263, 113–116.

Akkal, D., Dum, R.P., Strick, P.L., 2007. Supplementary motor area and presupplementary motor area: targets of basal ganglia and cerebellar output. J. Neurosci. 27, 10659–10673.

Alkadhi, H., Brugger, P., Boendermaker, S.H., Crelier, G., Curt, A., Hepp-Reymond, M.-C., Kollias, S.S., 2005. What disconnection tells about motor imagery: evidence from paraplegic patients. Cereb. Cortex 15, 131–140.

Amick, M.M., Schendan, H.E., Ganis, G., Cronin-Golomb, A., 2006. Frontostriatal circuits are necessary for visuomotor transformation: mental rotation in Parkinson's disease. Neuropsychologia 44, 339–349.

Annett, J., 1995. Motor imagery: perception or action? Neuropsychologia 33, 1395–1417.

Bakker, M., de Lange, F.P., Stevens, J.A., Toni, I., Bloem, B.R., 2007. Motor imagery of gait: a quantitative approach. Exp. Brain Res. 179, 497–504.

Bakker, M., de Lange, F., Helmich, R.C., Scheeringa, R., Bloem, B.R., Toni, I., 2008. Cerebral correlates of motor imagery of normal and precision gait. NeuroImage 41, 998–1010.

Battaglia, F., Quartarone, A., Ghilardi, M.F., Dattola, R., Bagnato, S., Rizzo, V., Morgante, L., Girlanda, P., 2006. Unilateral cerebellar stroke disrupts movement preparation and motor imagery. Clin. Neurophysiol. 117, 1009–1016.

Beisteiner, R., Höllinger, P., Lindinger, G., Lang, W., Berthoz, A., 1995. Mental representations of movements. Brain potentials associated with imagination of hand movements. Electroencephalogr. Clin. Neurophysiol. 96, 183–193.

Binkofski, F., Fink, G.R., Geyer, S., Buccino, G., Gruber, O., Shah, N.J., Taylor, J.G., Seitz, R.J., Zilles, K., 2002. Neural activity in human primary motor cortex areas 4a and 4p is modulated differentially by attention to action. J. Neurophysiol. 88, 514–519.

Boecker, H., Ceballos-Baumann, A.O., Bartenstein, P., Dagher, A., Forster, K., Haslinger, B., Brooks, D.J., Schwaiger, M., Conrad, B., 2002. A H(2)(15)O positron emission tomography study on mental imagery of movement sequences: the effect of modulating sequence length and direction. NeuroImage 17, 999–1009.

Bonda, E., Petrides, M., Frey, S., Evans, A., 1995. Neural correlates of mental transformations of the body-in-space. Proc. Natl. Acad. Sci. U. S. A. 92, 11180–11184.

Bremmer, F., 2005. What's next? Sequential movement encoding in primary motor cortex. Neuron 45, 819–821.

Buonomano, D.V., Merzenich, M.M., 1998. Cortical plasticity: from synapses to maps. Annu. Rev. Neurosci. 21, 149–186.

Butler, A.J., Page, S.J., 2006. Mental practice with motor imagery: evidence for motor recovery and cortical reorganization after stroke. Arch. Phys. Med. Rehabil. 87 (Suppl 2), 2–11.

Calautti, C., Leroy, F., Guincestre, J.Y., Marié, R.M., Baron, J.C., 2001. Sequential activation brain mapping after subcortical stroke: changes in hemispheric balance and recovery. NeuroReport 21, 3883–3886.

Caldara, R., Deiber, M.P., Andrey, C., Michel, C., Thut, G., Hauert, C.A., 2004. Actual and mental motor preparation and execution: a spatiotemporal ERP study. Exp. Brain Res. 159, 389–399.

Calmels, C., Fournier, J.F., 2001. Duration of physical and mental execution of gymnastic routines. Sport Psychol. 15, 142–150.

Calmels, C., d'Arripe-Longueville, F., Fournier, J.F., Soulard, A., 2003. Competitive strategies among elite female gymnasts: an exploration of the relative influence of psychological skills training and natural learning experiences. Int. J. Sport Exerc. Psychol. 1, 327–352.

Calmels, C., Lopez, E., Holes, P., Naman, V., 2006. Chronometric comparison of actual and imagined complex movement patterns. J. Mot. Behav. 38, 339–348.

Campos da Paz, A., Braga, L.W., Downs, J.H., 2000. A preliminary functional brain study on amputees. Appl. Neuropsychol. 7, 121–125.

Carey, J.R., Kimberley, T.J., Lewis, S.M., Auerbach, E.J., Dorsey, L., Rundquist, P., Ugurbil, K., 2002. Analysis of fMRI and finger tracking in subjects with chronic stroke. Brain 125, 773–788.

Carrillo-de-la-Peña, M.T., Lastra-Barreira, C., Galdo-Álvarez, S., 2006. Limb (hand vs. foot) and response conflict have similar effects on event-related potentials (ERPs) recorded during motor imagery and overt execution. Eur. J. Neurosci. 24, 635–643.

Carroll, T.J., Herbert, R.D., Munn, J., Lee, M., Gandevia, S.C., 2006. Contralateral effects of unilateral strength training: evidence and possible mechanisms. J. Appl. Physiol. 101, 1514–1522.

Cerritelli, B., Maruff, P., Wilson, P., Currie, J., 2000. The effect of an external load on the force and timing components of mentally represented actions. Behav. Brain Res. 108, 91–96.

Christakou, A., Zervas, Y., Lavallee, D., 2007. The adjunctive role of imagery on the functional rehabilitation of a grade II ankle sprain. Hum. Mov. Sci. 26, 141–154.

Cicinelli, P., Marconi, B., Zaccagnini, M., Pasqualetti, P., Filippi, M.M., Rossini, P.M., 2006. Imagery-induced cortical excitability changes in stroke: a transcranial magnetic stimulation study. Cereb. Cortex 16, 247–253.

Clark, B.C., Maninin, T.M., Bolanowski, S.J., Ploutz-Snyder, L.L., 2006. Adaptations in human neuromuscular function following prolonged unweighting: II. Neurological properties and motor imagery efficacy. J. Appl. Physiol. 101, 264–272.

Cohen, M.S., Kosslyn, S.M., Breiter, H.C., DiGirolamo, G.J., Thompson, W.L., Anderson, A.K., Bookheimer, S.Y., Rosen, B.R., Belliveau, J.W., 1996. Changes in cortical activity during mental rotation: a mapping study using functional MRI. Brain 119, 89–100.

Cooper, L.A., Shepard, R.N., 1975. Mental transformations in the identification of left and right hands. J. Exp. Psychol. 104, 48–56.

Courtine, G., Papaxanthis, C., Gentili, R., Pozzo, T., 2004. Gait-dependent motor memory facilitation in covert movement execution. Cogn. Brain Res. 22, 67–75.

Cramer, S.C., Lastra, L., Lacourse, M., Cohen, M.J., 2005. Brain motor system function after chronic, complete spinal cord injury. Brain 128, 2941–2950.

Cramer, S.C., Orr, E.L., Cohen, M.J., Lacourse, M.G., 2007. Effects of motor imagery training after chronic, complete spinal cord injury. Exp. Brain Res. 177, 233–242.

Crammond, D.J., 1997. Motor imagery: never in your wildest dream. Trends Neurosci. 20, 54–57.

Crosbie, J.H., McDonough, S.M., Gilmore, D.H., Wiggam, M.I., 2004. The adjunctive role of mental practice in the rehabilitation of the upper limb after hemiplegic stroke: a pilot study. Clin. Rehabil. 18, 60–68.

Cunnington, R., Iansek, R., Johnson, K.A., Bradshaw, J.L., 1997. Movement-related potentials in Parkinson's disease: motor imagery and movement preparation. Brain 120, 1339–1353.

Cunnington, R., Iansek, R., Bradshaw, J.L., 1999. Movement-related potentials in Parkinson's disease: external cues and attentional strategies. Mov. Disord. 14, 63–68.

Cunnington, R., Egan, G.F., O'Sullivan, J.D., Hughes, A.J., Bradshaw, J.L., Colebatch, J.G., 2001. Motor imagery in Parkinson's disease: a PET study. Mov. Disord. 16, 849–857.

Cupal, D.D., Brewer, B.W., 2001. Effects of relaxation and guided imagery on knee strength, reinjury anxiety, and pain following anterior cruciate ligament reconstruction. Rehabil. Psychol. 46, 28–43.

Decety, J., 1996a. Do imagined and executed actions share the same neural substrate? Cogn. Brain Res. 3, 87–93.

Decety, J., 1996b. The neurophysiological basis of motor imagery. Behav. Brain Res. 77, 45–52.

Decety, J., Jeannerod, M., 1996. Mentally simulated movements in virtual reality: does Fitts' law hold in motor imagery? Behav. Brain Res. 72, 127–134.

Decety, J., Michel, F., 1989. Comparative analysis of actual and mental movement times in two graphic tasks. Brain Cogn. 11, 87–97.

Decety, J., Philippon, B., Ingvar, D.H., 1988. RCBF landscapes during motor-performance and motor ideation of a graphic gesture. Eur. Arch. Psychiatry Clin. Neurosci. 238, 33–38.

Decety, J., Jeannerod, M., Prablanc, C., 1989. The timing of mentally represented actions. Behav. Brain Res. 34, 35–42.

Decety, J., Jeannerod, M., Durozard, D., Baverel, G., 1993. Central activation of autonomic effectors during mental simulation of motor actions in man. J. Physiol. 461, 549–563.

deCharms, R.C., 2007. Reading and controlling human brain activation using real-time functional magnetic resonance imaging. Trends Cogn. Sci. 11, 473–481.

deCharms, R.C., 2008. Applications of real-time fMRI. Nat. Rev. Neurosci. 9, 720–729.

deCharms, R.C., Christoff, K., Glover, G.H., Pauly, J.M., Whitfield, S., Gabrieli, J.D.E., 2004. Learned regulation of spatially localized brain activation using real-time fMRI. NeuroImage 21, 436–443.

Dechent, P., Merboldt, K.-D., Frahm, J., 2004. Is the human primary motor cortex involved in motor imagery? Cogn. Brain Res. 19, 138–144.

Deiber, M.P., Ibanez, V., Sadato, N., Hallett, M., 1996. Cerebral structures participating in motor preparation in humans: a positron emission tomography study. J. Neurophysiol. 75, 233–247.

de Lange, F.P., Helmich, R.C., Toni, I., 2006. Posture influences motor imagery: an fMRI study. NeuroImage 33, 609–617.

de Lange, F.P., Roelofs, K., Toni, I., 2008. Motor imagery: a window into the mechanisms and alterations of the motor system. Cortex 44, 494–506.

Dominey, P., Decety, J., Broussole, E., Chazot, G., Jeannerod, M., 1995. Motor imagery of a lateralized sequential task is asymmetrically slowed in hemi-Parkinson's patients. Neuropsychologia 33, 727–741.

Driskell, J.E., Copper, C., Moran, A., 1994. Does mental practice enhance performance? J. Appl. Psychol. 79, 481–492.

Dubois, B., Pillon, B., 1997. Cognitive deficits in Parkinson's disease. J. Neurol. 244, 2–8.

Dunsky, A., Dickstein, R., Ariav, C., Deutsch, J., Marcovitz, E., 2006. Motor imagery practice in gait rehabilitation of chronic post-stroke hemiparesis: four case studies. Int. J. Rehabil. Res. 29, 351–356.

Enoka, R.M., 1997. Neural adaptations with chronic physical activity. J. Biomech. 30, 447–455.

Ersland, L., Rosen, G., Lundervold, A., Smievoll, A.I., Tillung, T., Sundberg, H., Hugdahl, K., 1996. Phantom limb imaginary fingertapping causes primary motor cortex activation: an fMRI study. NeuroReport 8, 207–210.

Facchini, S., Muellbacher, W., Battaglia, F., Boroojerdi, B., Hallet, M., 2002. Focal enhancement of motor cortex excitability during motor imagery: a transcranial magnetic stimulation study. Acta Neurol. Scand. 105, 146–151.

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 27, 147–158.

Fansler, C.L., Poff, C.L., Shepard, K.F., 1985. Effects of mental practice on balance in elderly women. Phys. Ther. 65, 1332–1338.

Farah, M.J., 1984. The neurological basis of mental imagery: a componential analysis. Cognition 18, 245–272.

Feltz, D.L., Landers, D.M., 1983. The effects of mental practice on motor skill learning and performance: a meta-analysis. J. Sport Psychol. 5, 25–57.

Feltz, D.L., Landers, D.M., Becker, B.J., 1988. Improving motor skills. In: Druckman, D., Swets, J.A. (Eds.), Enhancing Human Performance: Issues, Theories, and Techniques. National Academy Press, Washington, DC, pp. 61–102.

Filippi, M.M., Oliveri, M., Pasqualetti, P., Cicinelli, P., Traversa, R., Vernieri, F., Palmieri, M.G., Rossini, P.M., 2001. Effects of motor imagery on motor cortical output topography in Parkinson's disease. Neurology 57, 55–61.

Fiorio, M., Tinazzi, M., Ionta, S., Fiaschi, A., Moretto, G., Edwards, M.J., Bhatia, K.P., Aglioti, S.M., 2007. Mental rotation of body parts and non-corporeal objects in patients with idiopathic cervical dystonia. Neuropsychologia 45, 2346–2354.

Foltys, H., Kemeny, S., Krings, T., Boroojerdi, B., Sparing, R., Thron, A., Töpper, R., 2000. The representation of the plegic hand in the motor cortex: a combined fMRI and TMS study. NeuroReport 11, 147–150.

Fourkas, A.D., Avenanti, A., Urgesi, C., Aglioti, S.M., 2006a. Corticospinal facilitation during first and third person imagery. Exp. Brain Res. 168, 143–151.

Fourkas, A.D., Ionta, S., Aglioti, S.M., 2006b. Influence of imagined posture and imagery modality on corticospinal excitability. Behav. Brain Res. 168, 190–196.

Fourkas, A.D., Bonavolontà, V., Avenanti, A., Aglioti, S.M., 2008. Kinesthetic imagery and tool-specific modulation of corticospinal representations in expert tennis players. Cereb. Cortex 18, 2382–2390.

Frak, V., Paulignan, Y., Jeannerod, M., 2001. Orientation of the opposition axis in mentally simulated grasping. Exp. Brain Res. 136, 120–127.

Gagglio, A., Meneghini, A., Morganti, F., Alcaniz, M., Riva, G., 2006. A strategy for computer-assisted mental practice in stroke rehabilitation. Neurorehabilitation Neural Repair 20, 503–507.

Galdo-Álvarez, S., Carrillo de la Peña, M.T., 2004. ERP evidence of MI activation without motor response execution. NeuroReport 15, 2067–2070.

Gandevia, S.C., Wilson, L.R., Inglis, J.T., Burke, D., 1997. Mental rehearsal of motor tasks recruits α-motoneurones but fails to recruit human fusiform neurones selectively. J. Physiol. 505, 259–266.

Ganis, G., Keenan, J.P., Kosslyn, S.M., Pascual-Leone, A., 2000. Transcranial magnetic stimulation of primary motor cortex affects mental rotation. Cereb. Cortex 10, 175–180.

Gemignani, A., Di Stefano, M., Sebatiani, L., Ghelarducci, B., Jeannerod, M., Guazelli, M., Massarelli, R., 2004. Influence of mental motor imagery on the execution of a finger-to-thumb opposition task. Arch. Ital. Biol. 142, 1–9.

Gentili, R., Cahouet, V., Ballay, Y., Papaxanthis, C., 2004. Inertial properties of the arm are accurately predicted during motor imagery. Behav. Brain Res. 155, 231–239.

Gentili, R., Papaxanthis, C., Pozzo, T., 2006. Improvement and generalization of arm motor performance through motor imagery practice. Neuroscience 137, 761–772.

Gerardin, E., Sirigu, A., Lehericy, S., Poline, J.B., Gaymard, B., Marsault, C., Agid, Y., Le Bihan, D., 2000. Partially overlapping neural networks for real and imagined hand movements. Cereb. Cortex 10, 1093–1104.

Geyer, S., Ledberg, A., Schleicher, A., Kinomura, S., Schormann, T., Burgel, U., Klingberg, T., Larsson, J., Zilles, K., Roland, P.E., 1996. Two different areas within the primary motor cortex of man. Nature 382, 805–807.

Gonzáles, B., Rodríguez, M., Ramirez, C., Sabaté, M., 2005. Disturbance of motor imagery after cerebellar stroke. Behav. Neurosci. 119, 622–626.

Guillot, A., Collet, C., 2005. Contribution from neurophysiological and psychological methods to the study of motor imagery. Brain Res. Rev. 50, 387–397.

Guillot, A., Haguenauer, M., Dittmar, A., Collet, C., 2005. Effect of a fatiguing protocol on motor imagery accuracy. Eur. J. Appl. Physiol. 95, 186–190.

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.

Hall, C.R., Martin, K.E., 1997. Measuring movement imagery abilities: a revision of the Movement Imagery Questionnaire. J. Ment. Imag. 21, 143–154.

Hardy, L., Callow, N., 1999. Efficacy of external and internal visual imagery perspectives for the enhancement of performance on tasks in which form is important. J. Sport Exerc. Psychol. 21, 95–112.

Hari, R., Forss, N., Avikainen, S., Kirveskari, E., Salenius, S., Rizzolatti, G., 1998. Activation of human primary motor cortex during action observation: a neuromagnetic study. Proc. Natl. Acad. Sci. U. S. A. 95, 15061–15065.

Hashimoto, R., Rothwell, J.C., 1999. Dynamic changes in corticospinal excitability during motor imagery. Exp. Brain Res. 125, 75–81.

Helmich, R.C., Lange, F.P., de Bloem, B.R., Toni, I., 2007. Cerebral compensation during motor imagery in Parkinson's disease. Neuropsychologia 45, 2201–2215.

Herbert, R.D., Dean, C., Gandevia, S.C., 1998. Effects of real and imagined training on voluntary muscle activation during maximal isometric contractions. Acta Physiol. Scand. 163, 361–368.

Hinshaw, K.E., 1991–1992. The effects of mental practice on motor skill performance: critical evaluation and meta-analysis. Imagin. Cogn. Pers. 11, 3–35.

Hiraoka, K., 2002. Imagining stumbling inhibits motor-evoked potentials in the soleus muscle. Int. J. Neurosci. 112, 613–622.

Hotz-Boendermaker, S., Funk, M., Summers, P., Brugger, P., Hepp-Reymond, M.C., Curt, A., Kollias, S.S., 2008. Preservation of motor programs in paraplegics as demonstrated by attempted and imagined foot movements. NeuroImage 39, 383–394.

Ikeda, A., Shibasaki, H., Nagamine, T., Terada, K., Kaji, R., Fukuyama, H., 1994. Dissociation between contingent negative variation and Bereitschaftspotential in a patient with cerebellar efferent lesion. Electroencephalogr. Clin. Neurophysiol. 90, 359–364.

Immenroth, M., Bürger, T., Brenner, J., Nagelschmidt, M., Eberspächer, H., Troidl, H., 2007. Mental training in surgical education: a randomized controlled trial. Ann. Surg. 245, 385–391.

Ionta, S., Fourkas, A.D., Fiorio, M., Aglioti, S.S., 2007. The influence of hands posture on mental rotation of hands and feet. Exp. Brain Res. 183, 1–7.

Izumi, S., Findley, T.W., Ikai, T., Andrews, J., Daum, M., Chino, N., 1995. Facilitatory effect of thinking about movement on motor-evoked potentials to transcranial magnetic stimulation of the brain. Am. J. Phys. Med. Rehabil. 74, 207–213.

Jackson, P.L., LaFleur, M.F., Malouin, F., Richards, C., 2001. Potential role of mental practice using motor imagery in neurologic rehabilitation. Arch. Phys. Med. Rehabil. 82, 1133–1141.

Jackson, P.L., Lafleur, M.F., Malouin, F., Richards, C.L., Doyon, J., 2003. Functional cerebral reorganization following motor sequence learning through mental practice with motor imagery. NeuroImage 20, 1171–1180.

Jeannerod, M., 1994. The representing brain: neural correlates of motor intention and imagery. Behav. Brain Sci. 17, 187–245.

Jeannerod, M., 2001. Neural simulation of action: a unifying mechanism for motor cognition. NeuroImage 14, 103–109.

Jenkins, I.H., Fernandez, W., Playford, E.D., Lees, A.J., Frackowiak, R.S., Passingham, R.E., Brooks, D.J., 1992. Impaired activation of the supplementary motor area in Parkinson's disease is reversed when akinesia is treated with apomorphine. Ann. Neurol. 32, 749–757.

Johansen-Berg, H., Matthews, P.M., 2002. Attention to movement modulates activity in sensori-motor areas, including primary motor cortex. Exp. Brain Res. 142, 13–24.

Johnson-Frey, S.H., 2004. Stimulation through simulation? Motor imagery and functional reorganization in hemiplegic stroke patients. Brain Cogn. 55, 328–331.

Johnson, S.H., 2000. Imagining the impossible: intact motor representations in hemiplegics. NeuroReport 11, 729–732.

Johnson, S.H., Rotte, M., Grafton, S.T., Hinrichs, H., Gazzaniga, M.S., Heinze, H.J., 2002. Selective activation of a parietofrontal circuit during implicitly imagined prehension. NeuroImage 17, 1693–1704.

Jola, C., Mast, F.W., 2005. Mental object rotation and egocentric body transformation: two dissociable processes? Spat. Cogn. Comput. 5, 217–237.

Kaneko, F., Murakami, T., Onari, K., Kurumadani, H., Kawaguchi, K., 2003. Decreased cortical excitability during motor imagery after disuse of an upper limb in humans. Clin. Neurophysiol. 114, 2397–2403.

Kasai, T., Kawai, S., Kawanishi, M., Yahagi, S., 1997. Evidence for facilitation of motor evoked potentials (MEPs) induced by motor imagery. Brain Res. 744, 147–150.

Kasess, C.H., Windischberger, C., Cunnington, R., Lanzenberger, R., Pezawas, L., Moser, E., 2008. The suppressive influence of SMA on M1 in motor imagery revealed by fMRI and dynamic causal modeling. NeuroImage 40, 828–837.

Kiers, L., Fernando, B., Tomkins, D., 1997. Facilitatory effect of thinking about movement on magnetic motor-evoked potentials. Electroencephalogr. Clin. Neurophysiol. 105, 262–268.

Kimberley, T.J., Khandekar, G., Skraba, L.L., Spencer, J.A., van Gorp, E.A., Walker, S.R., 2006. Neural substrates for motor imagery in severe hemiparesis. Neurorehabilitation Neural Repair 20, 268–277.

Kish, S.J., Shannak, K., Hornykiewicz, O., 1988. Uneven pattern of dopamine loss in the striatum of patients with idiopathic Parkinson's disease. Pathophysiologic and clinical implications. N. Engl. J. Med. 318, 876–880.

Kobayashi, M., Pascual-Leone, A., 2003. Transcranial magnetic stimulation in neurology. Lancet Neurol. 2, 145–156.

Kosslyn, S.M., 1987. Seeing and imagining in the cerebral hemispheres: a computational approach. Psychol. Rev. 94, 148–175.

Kosslyn, S.M., 1994. Image and Brain: The Resolution of the Imagery Debate. MIT Press, Cambridge, MA.

Kosslyn, S.M., DiGirolamo, G.J., Thompson, W.L., Alpert, N.M., 1998. Mental rotation of objects versus hands: neural mechanisms revealed by positron emission tomography. Psychophysiology 35, 151–161.

Kosslyn, S.M., Ganis, G., Thompson, W.L., 2001. Neural foundations of imagery. Nat. Rev. Neurosci. 2, 635–642.

Krakauer, J., Ghez, C., 2000. Voluntary movement. In: Kandel, E.R., Schwarz, J.H., Jesell, T.M. (Eds.), Principles of Neural Science. McGraw-Hill, New York, pp. 756–781.

Krams, M., Rushworth, M.F.S., Deiber, M.-P., Frackowiak, R.S.J., Passingham, R.E., 1998. The preparation, execution and suppression of copied movements in the human brain. Exp. Brain Res. 120, 386–398.

Kuhtz-Buschbeck, J.P., Mahnkopf, C., Holzknecht, C., Siebner, H., Ulmer, S., Jansen, O., 2003. Effector-independent representations of simple and complex imagined finger movements: a combined fMRI and TMS study. Eur. J. Neurosci. 18, 3375–3387.

Kumru, H., Soto, O., Casanova, J., Valls-Sole, J., 2008. Motor cortex excitability changes during imagery of simple reaction time. Exp. Brain Res. 189, 373–378.

Lacourse, M.G., Cohen, M.J., Lawrence, K.E., Romero, D.H., 1999. Cortical potentials during imagined movements in individuals with chronic spinal cord injuries. Behav. Brain Res. 104, 73–88.

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. J. Rehabil. Res. Dev. 41, 505–524.

Lafleur, M.F., Jackson, P.L., Malouin, F., Richards, C.L., Evans, A.C., Doyon, J., 2002. Motor learning produces parallel dynamic functional changes during the execution and imagination of sequential foot movements. NeuroImage 16, 142–157.

Lang, W., Cheyne, D., Höllinger, P., Gerschlager, W., Lindinger, G., 1996. Electric and magnetic fields of the brain accompanying internal simulation of movement. Cogn. Brain Res. 3, 125–129.

Lebedev, M.A., Nicolelis, M.A.L., 2006. Brain–machine interfaces: past, present and future. Trends Neurosci. 29, 536–546.

Léonard, G., Tremblay, F., 2007. Corticomotor facilitation associated with observation, imagery and imitation of hand actions: a comparative study in young and old adults. Exp. Brain Res. 177, 167–175.

Leonardo, M., Fieldman, J., Sadato, N., Campbell, G., Ibanez, V., Cohen, L., Deiber, M.-P., Jezzard, P., Pons, T., Turner, R., Le Bihan, D., Hallett, M., 1995. A functional magnetic resonance imaging study of cortical regions associated with motor task execution and motor ideation in humans. Hum. Brain Mapp. 3, 83–92.

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. Neurosci. Lett. 359, 185–189.

Li, C.R., 2000. Impairment of motor imagery in putamen lesions in humans. Neurosci. Lett. 287, 13–16.

Li, S., Kamper, D.G., Stevens, J.A., Rymer, W.Z., 2004a. The effect of motor imagery on spinal segmental excitability. J. Neurosci. 24, 9674–9680.

Li, S., Latash, M.L., Zatsiorsky, V.M., 2004b. Effects of motor imagery on finger force responses to transcranial magnetic stimulation. Cogn. Brain Res. 20, 273–280.

Liang, N., Ni, Z., Takahashi, M., Murakami, T., Yahagi, S., Funase, K., Kato, T., Kasai, T., 2007. Effects of motor imagery are dependent on motor strategies. Neuroreport 18, 1241–1245.

Liang, N., Murakami, T., Funase, K., Narita, T., Kasai, T., 2008. Further evidence for excitability changes in human primary motor cortex during ipsilateral voluntary contractions. Neurosci. Lett. 433, 135–140.

Lim, V.K., Polych, M.A., Holländer, A., Byblow, W.D., Kirk, I.J., Hamm, J.P., 2006. Kinesthetic but not visual imagery assists in normalizing the CNV in Parkinson's disease. Clin. Neurophysiol. 117, 2308–2314.

Linden, C.A., Uhley, J.E., Smith, D., Bush, M.A., 1989. The effects of mental practice on walking balance in an elderly population. Occup. Ther. J. Res. 9, 155–169.

Liu, K.P., Chan, C.C., Lee, T.M., Hui-Chan, C.W., 2004. Mental imagery for promoting relearning for people after stroke: a randomized controlled trial. Arch. Phys. Med. Rehabil. 85, 1403–1408.

Lotze, M., Cohen, L.G., 2006. Volition and imagery in neurorehabilitation. Cogn. Behav. Neurol. 19, 135–140.

Lotze, M., Halsband, U., 2006. Motor imagery. J. Physiol. 99, 386–395.

Lotze, M., Montoya, P., Erb, M., Hülsmann, E., Flor, H., Klose, U., Birbaumer, N., Grodd, W., 1999. Activation of cortical and cerebellar motor areas during executed and imagined hand movements: an fMRI study. J. Cogn. Neurosci. 11, 491–501.

Lotze, M., Flor, H., Grodd, W., Larbig, W., Birbaumer, N., 2001. Phantom movements and pain. An fMRI study in upper limb amputees. Brain 124, 2268–2277.

Lotze, M., Scheler, G., Tan, H.R., Braun, C., Birbaumer, N., 2003. The musician's brain: functional imaging of amateurs and professionals during performance and imagery. NeuroImage 20, 1817–1829.

Luft, A.R., Skalej, M., Stefanou, A., Klose, U., Voigt, K., 1998. Comparing motion- and imagery-related activation in the human cerebellum: a functional MRI study. Hum. Brain Mapp. 6, 105–113.

Lu, X.F., Ashe, J., 2005. Anticipatory activity in primary motor cortex codes memorized movement sequences. Neuron 45, 967–973.

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. Hum. Brain Mapp. 19, 47–62.

Malouin, F., Richards, C.L., Desrosiers, J., Doyon, J., 2004a. Bilateral slowing of mentally simulated actions after stroke. NeuroReport 15, 1349–1359.

Malouin, F., Richards, C.L., Doyon, J., Desrosiers, J., Belleville, S., 2004b. Training mobility tasks after stroke with combined mental and physical practice: a feasibility study. Neurorehabilitation Neural Repair 18, 66–75.

Marconi, B., Pecchioli, C., Koch, C., Caltagirone, C., 2007. Functional overlap between hand and forearm motor cortical representations during motor cognitive tasks. Clin. Neurophysiol. 118, 1767–1775.

Maschke, M., Gomez, C.M., Tuite, P.J., Konczak, J., 2003. Dysfunction of the basal ganglia, but not the cerebellum, impairs kinaesthesia. Brain 126, 2312–2322.

Meister, I.G., Krings, T., Foltys, H., Boroojerdi, B., Muller, M., Topper, R., Thron, A., 2004. Playing piano in the mind: an fMRI study on music imagery and performance in pianists. Cogn. Brain Res. 19, 219–228.

Mercier, C., Aballea, A., Vargas, C.D., Paillard, J., Sirigu, A., 2008. Vision without proprioception modulates cortico-spinal excitability during hand motor imagery. Cereb. Cortex 18, 272–277.

Miall, R.C., 2003. Connecting mirror neurons and forward models. NeuroReport 14, 2135–2137.

Miall, R.C., Wolpert, D.M., 1996. Forward models for physiological motor control. Neural Netw. 9, 1265–1279.

Michelon, P., Vettel, J.M., Zacks, J.M., 2006. Lateral somatotopic organization during imagined and prepared movements. J. Neurophysiol. 95, 811–822.

Miyai, I., Tanabe, H.C., Sase, I., Eda, H., Oda, I., Konishi, I., Tsunazawa, Y., Suzuki, T., Yanagida, T., Kubota, K., 2001.

Cortical mapping of gait in humans: a near-infrared spectoscopic topography study. NeuroImage 14, 1186–1192.

Moseley, G.L., 2004. Why do people with complex regional pain syndrome take longer to recognize their affected hand? Neurology 62, 2182–2186.

Mulder, T., 2007. Motor imagery and action observation: cognitive tools for rehabilitation. J. Neural Transm. 114, 1265–1278.

Mulder, T., Hochstenbach, J.B.H., van Heuvelen, M.J.G., den Otter, A.R., 2007. Motor imagery: the relation between age and imagery capacity. Hum. Mov. Sci. 26, 203–211.

Munzert, J., 2002. Temporal accuracy of mentally simulated transport movements. Percept. Mot. Skills 94, 307–318.

Munzert, J., 2008. Does level of expertise influence imagined durations in open skills? Played versus imagined durations of badminton sequences. Int. J. Sport Exerc. Psychol. 6, 24–38.

Munzert, J., Zentgraf, K., Stark, R., Vaitl, D., 2008. Neural activation in cognitive motor processes: comparing motor imagery and observation of gymnastic movements. Exp. Brain Res. 188, 437–444.

Mutsaarts, M., Steenbergen, B., Bekkering, H., 2007. Impaired motor imagery in right hemiparetic cerebral palsy. Neuropsychologia 45, 853–859.

Nair, D.G., Purcott, K.L., Fuchs, A., Steinberg, F., Kelso, J.A.S., 2003. Cortical and cerebellar activity of the human brain during imagined and executed unimanual and bimanual action sequences: a functional MRI study. Cogn. Brain Res. 15, 250–260.

Naito, E., Kochiyama, T., Kitada, R., Nakamura, S., Matsumura, M., Yonekura, Y., Sadato, N., 2002. Internally simulated movement sensations during motor imagery activate cortical motor areas and the cerebellum. J. Neurosci. 22, 3683–3691.

Neuper, C., Schlogl, A., Pfurtscheller, G., 1999. Enhancement of left–right sensorimotor EEG differences during feedback-regulated motor imagery. J. Clin. Neurophysiol. 16, 373–382.

Neuper, C., Scherer, R., Reiner, M., Pfurtscheller, G., 2005. Imagery of motor actions: differential effects of kinesthetic and visual-motor mode of imagery in single-trial EEG. Cogn. Brain Res. 25, 668–677.

Newsom, J., Knight, P., Balnave, R., 2003. Use of mental imagery to limit strength loss after immobilization. J. Sport Rehabil. 12, 249–258.

Nico, D., Daprati, E., Rigal, F., Parsons, L., Sirigu, A., 2004. Left and right hand recognition in upper limb amputees. Brain 127, 120–132.

Nudo, R.J., 1999. Recovery after damage to motor cortical areas. Curr. Opin. Neurobiol. 9, 740–747.

Nudo, R.J., Duncan, P.W., 2004. Recovery and rehabilitation in stroke: introduction. Stroke 35, 2690.

Nyberg, L., Petersson, K.M., Nilsson, L.G., Sandblom, J., Aberg, C., Ingvar, M., 2001. Reactivation of motor brain areas during explicit memory for actions. NeuroImage 14, 521–528.

Ohyama, T., Nores, W.L., Murphy, M., Mauk, M.D., 2003. What the cerebellum computes. Trends Neurosci. 26, 222–227.

Orliaguet, J.P., Coello, Y., 1998. Differences between actual and imagined putting movements in golf: a chronometric analysis. Int. J. Sport Psychol. 29, 157–169.

Orr, E.L.R., Lacourse, M.G., Cohen, M.J., Cramer, S.C., 2008. Cortical activation during executed, imagined, and observed foot movements. NeuroReport 19, 625–630.

Osman, A., Muller, K.M., Syre, P., Russ, B., 2005. Paradoxical lateralization of brain potentials during imagined foot movements. Cogn. Brain Res. 24, 727–731.

Ozel, S., Larue, J., Dosseville, F., 2004. Effect of arousal on internal clock speed in real action and mental imagery. Can. J. Exp. Psychol. 58, 196–205.

Page, S.J., Levine, P., Sisto, S., Johnston, M.V., 2001. A randomized efficacy and feasibility study of imagery in acute stroke. Clin. Rehabil. 15, 233–240.

Page, S.J., Levine, P., Leonard, A., 2007. Mental practice in chronic stroke: results of a randomized, placebo-controlled trial. Stroke 38, 1293–1297.

Papaxanthis, C., Pozzo, T., Skoura, X., Schieppati, M., 2002a. Does order and timing in performance of imagined and actual movements affect the motor imagery process? The duration of walking and writing task. Behav. Brain Res. 134, 209–215.

Papaxanthis, C., Schieppati, M., Gentili, R., Pozzo, T., 2002b. Imagined and actual arm movements have similar durations when performed under different conditions of direction and mass. Exp. Brain Res. 143, 447–452.

Papaxanthis, C., Pozzo, T., Kasprinski, R., Berthoz, A., 2003. Comparison of actual and imagined execution of whole-body movements after a long exposure to microgravity. Neurosci. Lett. 339, 41–44.

Parsons, L.M., 1987. Imagined spatial transformation of one's body. J. Exp. Psychol 116, 172–191.

Parsons, L.M., 1994. Temporal and kinematic properties of motor behavior reflected in mentally simulated action. J. Exp. Psychol. 20, 709–730.

Parsons, L.M., Fox, P.T., 1998. The neural basis of implicit movements used in recognising hand shape. Cogn. Neuropsychol. 15, 583–615.

Parsons, L.M., Fox, P.T., Downs, J.H., Glass, T., Hirsch, T.B., Martin, C.C., Jerabek, P.A., Lancaster, J.L., 1995. Use of implicit motor imagery for visual shape-discrimination as revealed by PET. Nature 375, 54–58.

Pascual-Leone, A., Nguyet, D., Cohen, L.G., Brasil-Neto, J.P., Cammarota, A., Hallet, M., 1995. Modulation of muscle responses evoked by transcranial magnetic stimulation during the acquisition of new fine motor skills. J. Neurophysiol. 74, 1037–1045.

Petit, L.S., Harris, I.M., 2005. Anatomical limitations in mental transformations of body parts. Vis. Cogn. 12, 737–758.

Petit, L.S., Pegna, A.J., Mayer, E., Hauert, C.A., 2003. Representation of anatomical constraints in motor imagery: mental rotation of a body segment. Brain Cogn. 51, 95–101.

Pfurtscheller, G., Neuper, C., 1997. Motor imagery activates primary sensorimotor area in humans. Neurosci. Lett. 239, 65–68.

Pfurtscheller, G., Neuper, C., Ramoser, H., Müller-Gerking, J., 1999. Visually guided motor imagery activates sensorimotor areas in humans. Neurosci. Lett. 269, 153–156.

Picard, N., Strick, P.L., 1996. Motor areas of the medial wall: a review of their location and functional activation. Cereb. Cortex 6, 342–353.

Playford, E.D., Jenkins, I.H., Passingham, R.E., Nutt, J., Frackowiak, R.S., Brooks, D.J., 1992. Impaired mesial frontal and putamen activation in Parkinson's disease: a positron emission tomography study. Ann. Neurol. 32, 151–161.

Porro, C.A., Francescato, M.P., Cettolo, V., Diamond, M.E., Baraldi, P., Zuiani, C., Bazzocchi, M., di Prampero, P.E., 1996. Primary motor and sensory cortex activation during motor performance and motor imagery: a functional magnetic resonance imaging study. J. Neurosci. 16, 7688–7698.

Porro, C.A., Cettolo, V., Francescato, M.P., Baraldi, P., 2000. Ipsilateral involvement of primary motor cortex during motor imagery. Eur. J. Neurosci. 12, 3059–3063.

Porro, C.A., Facchin, P., Fusi, S., Dri, G., Fadiga, L., 2007. Enhancement of force after action observation. Behavioural and neurophysiological studies. Neuropsychologia 45, 3114–3121.

Quartarone, A., Bagnato, S., Rizzo, V., Morgante, F., Sant'Angelo, A., Crupi, D., Romano, M., Mesina, C., Berardelli, A., Girlanda, P., 2005. Corticospinal excitability during motor imagery of a simple tonic finger movement in patients with writer's cramp. Mov. Disord. 20, 1488–1495.

Ramnani, N., 2006. The primate cortico-cerebellar system: anatomy and function. Nat. Rev. Neurosci. 7, 511–522.

Ranganathan, W.K., Siemionow, V., Liu, J.Z., Sahgal, V., Yue, G.H., 2004. From mental power to muscle power — gaining strength by using the mind. Neuropsychologia 42, 944–956.

Reed, C.L., 2002. Chronometric comparisons of imagery to action: visualizing versus physically performing springboard dives. Mem. & Cogn. 30, 1169–1178.

Richardson, A., 1967a. Mental practice: review and discussion 1. Research Quarterly 38, 95–107.

Richardson, A., 1967b. Mental practice: review and discussion 2. Research Quarterly 38, 263–273.

Rizzolatti, G., Craighero, L., 2004. The mirror-neuron system. Annu. Rev. Neurosci. 27, 169–192.

Rodriguez, M., Muniz, R., Gonzalez, B., Sabate, M., 2004. Hand movement distribution in the motor cortex: the influence of a concurrent task and motor imagery. NeuroImage 22, 1480–1491.

Roland, P.E., Larsen, B., Lassen, N.A., Skinhoj, E., 1980. Supplementary motor area and other cortical areas in organization of voluntary movements in man. J. Neurophysiol. 43, 118–136.

Rossini, P.M., Rossi, S., Pasqualetti, P., Tecchio, F., 1999. Corticospinal excitability modulation to hand muscles during movement imagery. Cereb. Cortex 9, 161–167.

Rossi, S., Pasqualetti, P., Tecchio, F., Pauri, F., Rossini, P.M., 1998. Corticospinal excitability modulation during mental simulation of wrist movements in human subjects. Neurosci. Lett. 243, 147–151.

Roth, M., Decety, J., Raybaudi, M., Massarelli, R., Delon-Martin, C., Segebarth, C., Morand, S., Gemignani, A., Decorps, M., Jeannerod, M., 1996. Possible involvement of primary motor cortex in mentally simulated movement: a functional magnetic resonance imaging study. NeuroReport 7, 1280–1284.

Rouiller, E.M., Liang, F., Babalian, A., Moret, V., Wiesendanger, M., 1994. Cerebellothalamocortical and pallidothalamocortical projections to the primary and supplementary motor cortical areas: a multiple tracing study in macaque monkeys. J. Comp. Neurol. 345, 185–213.

Roux, F.E., Ibarrola, D., Lazorthes, Y., Berry, I., 2001. Virtual movements activate primary sensorimotor areas in amputees: report of three cases. Neurosurgery 49, 736–741.

Roux, F.E., Lotterie, J.A., Cassol, E., Lazorthes, Y., Sol, J.C., Berry, I., 2003. Cortical areas involved in virtual movement of phantom limbs: comparison with normal subjects. Neurosurgery 53, 1342–1352.

Ruby, P., Decety, J., 2001. Effect of subjective perspective taking during simulation of action: a PET investigation of agency. Nat. Neurosci. 4, 546–550.

Sabaté, M., González, B., Rodríguez, M., 2007. Adapting movement planning to motor impairments: the motor-scanning system. Neuropsychologia 45, 378–386.

Sabatini, U., Boulanouar, K., Fabre, N., Martin, F., Carel, C., Colonnese, C., Bozzao, L., Berry, I., Montastruc, J.L., Rascol, O., 2000. Cortical motor reorganization in akinetic patients with Parkinson's disease: a functional MRI study. Brain 2, 394–403.

Sabbah, P., De Schonen, S., Leveque, C., Gay, S., Pfefer, F., Nioche, C., Sarrazin, J.-L., Barouti, H., Tadie, M., Cordoliani, Y.-S., 2002. Sensorimotor cortical activity in patients with complete spinal cord injury: a functional magnetic resonance imaging study. J. Neurotrauma. 19, 53–60.

Sacco, K., Cauda, F., Cerliani, L., Mate, D., Duca, S., Geminiani, G.C., 2006. Motor imagery of walking following training in locomotor attention. The effect of "the tango lesson". NeuroImage 32, 1441–1449.

Samuel, M., Ceballos-Baumann, A.O., Blin, J., Uema, T., Boecker, H., Passingham, R.E., Brooks, D.J., 1997. Evidence for lateral premotor and parietal overactivity in Parkinson's disease during sequential and bimanual movements: a PET study. Brain 120, 963–976.

Samuel, M., Ceballos-Baumann, A.O., Boecker, H., Brooks, D.J., 2001. Motor imagery in normal subjects and Parkinson's disease patients: an $H_2^{15}O$ PET study. NeuroReport 12, 821–828.

Sanes, J.N., Donoghue, J.P., 2000. Plasticity and primary motor cortex. Annu. Rev. Neurosci. 23, 393–415.

Sauner, D., Bestmann, S., Siebner, H.R., Rothwell, J.C., 2006. No evidence for substantial involvement of primary motor hand area in handedness judgements: a transcranial magnetic stimulation study. Eur. J. Neurosci. 23, 2215–2224.

Schnitzler, A., Salenius, S., Salmelin, R., Jousmäki, V., Hari, R., 1997. Involvement of primary motor cortex in motor imagery: a neuromagnetic study. NeuroImage 6, 201–208.

Schott, N., Munzert, J., 2007. Temporal accuracy of motor imagery in older women. Int. J. Sport Psychol. 38, 304–320.

Schwoebel, J., Friedman, R., Duda, N., Coslett, H.B., 2001. Pain and the body schema: evidence for peripheral effects on mental representations of movement. Brain 124, 2098–2104.

Sharma, N., Pomeroy, V.M., Baron, J.C., 2006. Motor imagery: a backdoor to the motor system after stroke? Stroke 37, 1941–1952.

Sharma, N., Jones, P.S., Carpenter, T.A., Baron, J.C., 2008. Mapping the involvement of BA 4a and 4p during motor imagery. NeuroImage 41, 92–99.

Shepard, R.N., Metzler, J., 1971. Mental rotation of three-dimensional objects. Science 171, 701–703.

Sidaway, B., 2005. Can mental practice increase ankle dorsiflexor torque? Phys. Ther. 85, 1053–1060.

Sirigu, A., Duhamel, J.R., 2001. Motor and visual imagery as two complementary but neurally dissociable mental processes. J. Cogn. Neurosci. 13, 910–919.

Sirigu, A., Cohen, L., Duhamel, J.R., Pillon, B., Dubois, B., Agid, Y., Pierrot-Deseilligny, C., 1995. Congruent unilateral impairments for real and imagined hand movements. NeuroReport 6, 997–1001.

Sirigu, A., Duhamel, J.R., Cohen, L., Pillon, B., Dubois, B., Agid, Y., 1996. The mental representation of hand movements after parietal cortex damage. Science 273, 1564–1568.

Skoura, X., Papaxanthis, C., Vinter, A., Pozzo, T., 2005. Mentally represented motor actions in normal aging I. Age effects on the temporal features of overt and covert execution of actions. Behav. Brain Res. 165, 229–239.

Solodkin, A., Hlustik, P., Chen, E.E., Small, S.L., 2004. Fine modulation in network activation during motor execution and motor imagery. Cereb. Cortex 14, 1246–1255.

Spitzer, M., 1999. The Mind Within the Net: Models of Learning, Thinking, and Acting. MIT Press, Cambridge, MA.

Steenbergen, B., van Nimwegen, M., Crajé, C., 2007. Solving a mental rotation task in congenital hemiparesis: motor imagery versus visual imagery. Neuropsychologia 45, 3324–3328.

Stephan, K.M., Fink, G.R., Passingham, R.E., Silbersweig, D., Ceballos Baumann, A.O., Frith, C.D., Frackowiak, R.S., 1995. Functional anatomy of the mental representation of upper extremity movements in healthy subjects. J. Neurophysiol. 73, 373–386.

Stevens, J.A., Stoykov, M.E.P., 2003. Using motor imagery in the rehabilitation of hemiparesis. Arch. Phys. Med. Rehabil. 84, 1090–1092.

Stinear, C.M., Byblow, W.D., 2003. Motor imagery of phasic thumb abduction temporally and spatially modulates corticospinal excitability. Clin. Neurophysiol. 114, 909–914.

Stinear, C.M., Byblow, W.D., Styvers, M., Levin, O., Swinnen, S.P., 2006a. Kinesthetic, but not visual, motor imagery modulates corticomotor excitability. Exp. Brain Res. 168, 157–164.

Stinear, C.M., Fleming, M., Byblow, W.D., 2006b. Lateralization of unimanual and bimanual motor imagery. Exp. Brain Res. 1095, 139–147.

Stinear, C.M., Fleming, M., Barber, P.A., Byblow, W.D., 2007. Lateralization of motor imagery following stroke. Clin. Neurophysiol. 118, 1794–1801.

Stippich, C., Ochmann, H., Sartor, K., 2002. Somatotopic mapping of the human primary sensorimotor cortex during motor imagery and motor execution by functional magnetic resonance imaging. Neurosci. Lett. 331, 50–54.

Strens, L.H., Fogelson, N., Shanahan, P., Rothwell, J.C., Brown, P., 2003. The ipsilateral human motor cortex can functionally compensate for acute contralateral motor cortex dysfunction. Curr. Biol. 13, 1201–1205.

Szameitat, A.J., Shen, S., Sterr, A., 2007. Motor imagery of complex everyday movements. An fMRI study. NeuroImage 34, 702–713.

Tamir, R., Dickstein, R., Huberman, M., 2007. Integration of motor imagery and physical practice in group treatment applied to subjects with Parkinson's disease. Neurorehabil. Neural Repair 21, 68–75.

Thobois, S., Dominey, P.F., Decety, J., Pollak, P., Gregoire, M.C., Le Bars, D., Broussole, E., 2000. Motor imagery in normal subjects and in asymmetrical Parkinson's disease: a PET study. Neurology 55, 996–1002.

Thobois, S., Dominey, P., Fraix, V., Mertens, P., Guenot, M., Zimmer, L., Pollack, P., Benabid, A.L., Broussolle, E., 2002. Effects of subthalamic nucleus stimulation on actual and imagined movement in Parkinson's disease: a PET study. J. Neurol. 249, 1689–1698.

Tremblay, F., Tremblay, L.E., Colcer, D.E., 2001. Modulation of corticospinal excitability during imagined knee movements. J. Rehabil. Med. 33, 230–234.

Turner, R.S., Grafton, S.T., McIntosh, A.R., DeLong, M.R., Hoffman, J.M., 2003. The functional anatomy of parkinsonian bradykinesia. NeuroImage 19, 163–179.

Van Gyn, G.H., Wenger, H.A., Gaul, C.A., 1990. Imagery as a method of enhancing transfer from training to performance. J. Sport Exerc. Psychol. 12, 366–375.

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. Cereb. Cortex 14, 1200–1206.

Weinberg, R., 2008. Does imagery work? Effects of performance and mental skills. J. Ment. Imag. 3, 1–21.

Weiskopf, N., Mathiak, K., Bock, S.W., Scharnowski, F., Veit, R., Grodd, W., Goebel, R., Birbaumer, N., 2004. Principles of a brain–computer interface (BCI) based on real-time functional magnetic resonance imaging (fMRI). IEEE Trans. Biomed. Eng. 51, 966–970.

White, A., Hardy, L., 1995. Use of different imagery perspectives on the learning and performance of different motor skills. Br. J. Psychol. 86, 169–180.

Wilson, P.H., Maruff, P., Ives, S., Currie, J., 2001. Abnormalities of motor and praxis imagery in children with DCD. Hum. Mov. Sci. 20, 135–159.

Wolbers, T., Weiller, C., Büchel, C., 2003. Contralateral coding of imagined body parts in the superior parietal lobe. Cereb. Cortex 13, 392–399.

Wriessnegger, S.C., Kurzmann, J., Neuper, C., 2008. Spatio-temporal differences in brain oxygenation between movement execution and imagery: a multichannel near-infrared spectroscopy study. Int. J. Psychophysiol. 67, 54–63.

Wuyam, B., Moosavi, S.H., Decety, J., Adams, L., Lansing, R.W., Guz, A., 1995. Imagination of dynamic exercise produced ventilatory responses which were more apparent in competitive sportsmen. J. Physiol. 482, 713–724.

Yáguez, L., Canavan, A.G.M., Lange, H.W., Hömberg, V., 1999. Motor learning by imagery is differentially affected in Parkinson's and Huntington's diseases. Behav. Brain Res. 102, 115–127.

Yahagi, S., Kasai, T., 1998. Facilitation of motor evoked potentials (MEPs) in first dorsal interosseous (FDI) muscle is dependent on different motor images. Electromyogr. Motor Control-Electroencephalogr. Clin. Neurophysiol. 109, 409–417.

Yahagi, S., Shimura, K., Kasai, T., 1996. An increase in cortical excitability with no change in spinal excitability during motor imagery. Percept. Mot. Skills 83, 288–290.

Yoo, E., Park, E., Chung, B., 2001. Mental practice effect on line-tracing accuracy in persons with hemiparetic stroke: a preliminary study. Arch. Phys. Med. Rehabil. 82, 1213–1218.

Yoo, S.-S., Lee, J.-H., O'Leary, H., Panych, L.P., Jolesz, F.A., 2008. Neurofeedback fMRI-mediated learning and consolidation of regional brain activation during motor imagery. Int. J. Imaging Syst. Technol. 18, 69–78.

Yue, G., Cole, K.J., 1992. Strength increases from the motor program: comparison of training with maximal voluntary and imagined muscle contractions. J. Neurophysiol. 67, 1114–1123.

Yue, G.H., Wilson, S.L., Cole, K.J., Darling, W.G., Yuh, W.T.C., 1996. Imagined muscle contraction training increases voluntary neural drive to muscle. J. Psychophysiol. 10, 198–208.

Yu, H., Sternad, D., Corcos, D.M., Vaillantcourt, D.E., 2007. Role of hyperactive cerebellum and motor cortex in Parkinson's disease. NeuroImage 35, 222–233.

Zacks, J.M., 2008. Neuroimaging studies of mental rotation: a meta-analysis and review. J. Cogn. Neurosci. 20, 1–19.

Zang, Y., Jia, F., Weng, X., Li, E., Cui, S., Wang, Y., Hazeltine, E., Ivry, R., 2003. Functional organization of the primary motor cortex characterized by event-related fMRI during movement preparation and execution. Neurosci. Lett. 337, 69–72.

Zentgraf, K., Stark, R., Reiser, M., Künzell, S., Schienle, A., Kirsch, P., Walter, B., Vaitl, D., Munzert, J., 2005. Differential activation of pre-SMA and SMA proper during action observation: effects of instructions. NeuroImage 26, 662–672.

Zijdewind, I., Toering, S.T., Bessem, B., Laan van der, O., Diercks, R.L., 2003. Effects of imagery motor training on torque production of ankle plantar flexor muscle. Muscle Nerve 28, 168–173.