The Influence of Hand Posture on Corticospinal Excitability during Motor Imagery: A Transcranial Magnetic Stimulation Study

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In order to study the interaction between proprioceptive information and motor imagery, we herein investigate how compatible and incompatible postural signals influence corticospinal excitability during the mental simulation of hand movements. Subjects were asked to imagine themselves joining the tips of the thumb and the little finger while they maintained one of the two following hand postures: posture A (PA, compatible), little finger, index and thumb extended, the remaining fingers flexed; or posture B (PB, incompatible), index and thumb extended, other fingers flexed. All subjects rated the imagined finger opposition movements as easier to perform when the hand was kept in PA than in PB ($P < 0.01$) and the correlation between the duration of motor imagery and movement execution was also higher for PA than PB ($P < 0.01$). For each posture, motor evoked potentials (MEPs) elicited by focal transcranial magnetic stimulation (TMS) of the left motor cortex were recorded from the right *opponens pollicis* muscle during both motor imagery (MI) and rest (R) conditions. MEP area varied according to the hand posture: PA induced a higher increase in corticospinal excitability, when compared with PB. These results indicate that the actual limb posture affects the process of motor imagery. The source of this postural modulation effect is discussed.

Keywords: mental simulation, motor control, proprioception, TMS

Introduction

Motor imagery consists of a dynamic process in which a subject feels him or herself executing a movement. As such, it implies that a motor plan of the given action is brought forth and that the subject actively monitors its unfolding. It has been proposed that the mental simulation of an action relies on the same mechanisms as its actual execution, except for the absence of overt motor behavior (Jeannerod, 1994). Contemporary behavioral and neuroimaging research has confirmed that there is a striking parallelism between simulated and executed actions. For instance, the time course of a mentally simulated movement is positively correlated to its actual execution (Decety and Michel, 1989; Jeannerod, 1994; Parsons, 1994; Sirigu *et al.*, 1995, 1996; Johnson, 2000a) and autonomic responses are modulated likewise during both motor imagery and motor performance (Decety *et al.*, 1991). Similarly, mental rehearsal of a motor task has been shown to produce changes in force strengths (Yue and Cole, 1992). Moreover, there is an overlap of brain networks activated during imagery and execution of a movement (Roland *et al.*, 1980; Decety *et al.*, 1994; Lotze *et al.*, 1999; Gerardin *et al.*, 2000; Stippich *et al.*, 2002).

How does the mental simulation of a hand movement interact with the biomechanical constraints induced by body posture? Earlier behavioral studies showed that the time spent for mentally rotating one's limb in order to judge its handedness is shorter when the hand is kept in a 'canonical' posture than when it is maintained in a more awkward posture (Parsons, 1994). Parsons (1994) suggested that the longer response time obtained in the latter condition results from an additional mental step needed to bring the hand from the awkward position to the more canonical one. More recently, Sirigu and Duhamel (2001) asked subjects to imagine their hand in a given spatial orientation and to respond to queries about the location of a single finger of the imagined hand. While solving the task subjects kept their hands resting either on the lap (compatible condition) or behind the back (incompatible condition). Shorter response times were observed for the compatible condition, suggesting that maintaining the hands in a ready-for-action position automatically triggers motor imagery processes. Response times for the incompatible condition were three times longer as compared to the compatible one. According to the authors, this delay, produced by an incompatibility between the mental representation of the imagined movement and the actual hand posture, would reflect a suppression or blockage of motor imagery processes (Sirigu and Duhamel, 2001).

The transcranial magnetic stimulation (TMS) technique has become a valuable tool to map primary motor cortex (M1) excitability during motor imagery tasks (Yahagi *et al.*, 1996; Kasai *et al.*, 1997; Kiers *et al.*, 1997; Yahagi and Kasai, 1998; Abbruzzese *et al.*, 1999; Fadiga *et al.*, 1999; Hashimoto and Rothwell, 1999; Ridding and Rothwell, 1999; Rossini *et al.*, 1999). These authors have consistently shown that the corticospinal excitability, as estimated from the amplitude of motor evoked potentials (MEP), is enhanced during the mental simulation of a movement. Moreover, this facilitation has proven to be effector-specific (Yahagi and Kasai, 1998; Fadiga *et al.*, 1999). We herein investigate, by means of the TMS, how compatible and incompatible postural signals influence the corticospinal excitability during motor imagery. In agreement with our hypothesis of an interaction between proprioceptive information and motor imagery processes, TMS induced motor evoked potentials (MEP) are expected to vary according to the adopted hand posture, namely, a compatible hand posture should enhance the MEP response while an incompatible one should produce a reverse effect.

Materials and Methods

This study involved a behavioral and TMS investigation and was approved by the local ethical committee.

Subjects

Behavioral data were collected from 11 right-handed volunteers (seven males, ages 19–30 years) of whom six of them were tested with TMS. Subjects were informed on the general purpose of the study and signed a formal consent. A brief list of questions confirmed their willingness to participate in the TMS testing (Rossini *et al.*, 1994).

Behavioral Testing

The task consisted in imaging or executing joining the tips of the thumb and little finger while keeping each of the following postures (Fig. 1): posture A (PA, considered as 'compatible' with the movement to be imagined), the little finger, the index finger and the thumb were kept extended, while the remaining fingers flexed; and posture B (PB, considered as 'incompatible' with the movement to be imagined), the index finger and the thumb were extended and the other fingers remained flexed. Response times for motor imagery and execution while keeping each of the above described postures were recorded by means of a stopwatch. Subjects were instructed to close their eyes and imagine and then execute the movement from one to five times at random. Posture order was randomized between subjects. They were then asked to evaluate, on a scale from 1 to 5, the degree of comfort and the easiness to imagine the movement while maintaining each posture. Pearson's test was used to estimate the degree of correlation between imagination and execution.

Transcranial Magnetic Stimulation Procedure

Subjects sat comfortably in an armchair with the elbow flexed and the hand relaxed. They wore a tight swimming cap with a grid of predefined stimulation points that were used to guide coil positioning on the scalp. The grid consisted of a set of 10×10 points, each point placed 10 mm apart, covering an area of 10 cm lateral from the vertex and extending 6 cm anterior and 4 cm posterior from the line connecting the vertex to the preauricolar points (tragus). TMS was applied over the left primary motor cortex (M1) by means of a Magstim 200® stimulator with a 70 mm figure-of-eight coil. The coil was held manually with the handle pointing backwards and kept tangential to the subject's scalp. Motor potentials evoked by TMS stimulation were recorded by means of Ag–AgCl surface electrodes positioned on the *opponens pollicis* (OP) according to a tendon–belly arrangement. Prior to the experimental session, motor threshold (MT) was assessed by identifying the scalp region where the minimal intensity of TMS stimulation elicited MEPs larger than 50 μV in 50 % of the trials (Rossini *et al.*, 1994). OP cortical representation was assessed at 120% of MT by moving the coil at 1 cm steps around MT site until no discernible MEPs were evoked. The excitability of the whole OP map (~30 points per subject) was then explored to obtain information relative to task-dependent modulation of both MEP amplitude and OP map spatial modulation. The experiment consisted of two imaging and two control tasks, randomized across subjects. During motor imagery tasks (MI), subjects were asked to close their eyes and imagine joining the tips of the thumb and little finger while maintaining either PA or PB.
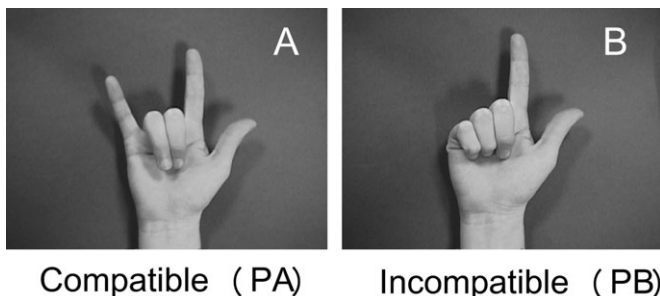

Figure 1. The task (joining the tips of the thumb and the little finger) was performed while keeping either posture A (PA, compatible) or posture B (PB, incompatible).

The imagined movement was triggered by an auditory go signal. During the rest control condition (R) subjects were instructed to keep the same hand posture as during the imaging trials but think of nothing in particular.

Definition of TMS Time Course Pulse Application

In order to define a time window for the TMS pulse application, the interval between an auditory go signal and the end of movement execution was measured in five subjects. OP electromyographic (EMG) activity was collected and stored for off-line analysis. Each subject performed a total of 50 trials per posture, divided in blocks of 25 trials each. Posture order was randomized between subjects. For posture A, the time interval between the beep signal and the end of movement execution was 688.21 ms (SD = 187.22), while for posture B, it attained 756.64 ms (SD = 147.71), these values being statistically different (paired *t*-test, $P < 0.001$). Based on these results, TMS pulse was delivered at 500 ms after the go signal. In two out of six subjects, MEPs evoked by TMS delivered 800 ms after the go signal were also acquired.

Signal Analysis

EMG signals were amplified and band pass filtered (20–1000 Hz, Neurolog instruments; Digitimer Ltd). The signal was then digitized at a sampling rate of 2000 Hz (CED 1401 interface; CED Ltd, Cambridge, UK) and stored on an IBM PC computer for off-line analysis. Trials with high background EMG activity were rejected 'on-line'. Trial rejection was further performed 'off-line' with a baseline criterion set at 50 μV.

TMS Data Analysis

MEP amplitude and area were measured from rectified EMG recordings. These measurements were then used to calculate a facilitation index defined as follows: {motor imagery – rest/motor imagery + rest * 100} for each stimulated point gathered per condition. This index was also calculated from rectified basal EMG activity, collected during the 200 ms immediately before the TMS pulse.

Software made with Matlab® (Mathworks, Natick, MA) was employed to interpolate MEP area values in space. By these means, an OP map per condition was built for each subject. The same procedure was applied for facilitation index values. Statistical significance was assessed by means of two- and three-way analysis of variance (ANOVA) for repeated measures as well as by paired *t*-test for dependent samples. Analysis was performed by means of the software statistics with the significance threshold set at $P < 0,05$.

Results

TMS Results

Mean area MEP values obtained for each condition are represented in Figure 2A. A two-way ANOVA was performed using compatibility and imagery as main factors. Results revealed an effect of imagery [$F(1,231) = 50.20$, $P < 0.0001$, MSe = 16.84]. Furthermore, an interaction was found between factors [$F(1,231) = 5.88$, $P < 0.02$, MSe = 16.84] indicating that motor imagery is significantly modulated by hand posture compatibility. Comparison of the facilitation index calculated from MEP area for each posture (Fig. 2B) revealed a significant facilitation for posture A (60.44, SE = 5.61) with respect to posture B (30.82, SE = 6.86; paired *t*-test, $P < 0.001$), demonstrating that corticospinal excitability is higher when the actual hand posture and the imagined movement are compatible. To verify whether background EMG activity was similar in both compatible and incompatible conditions we compared the facilitation index obtained from activity collected during the 200 ms before the TMS pulse. Results revealed no statistical difference between postures (PA = 51.72, SE = 15.10; PB = 50.31, SE = 44.22; paired *t*-test, $P = 0.976$).
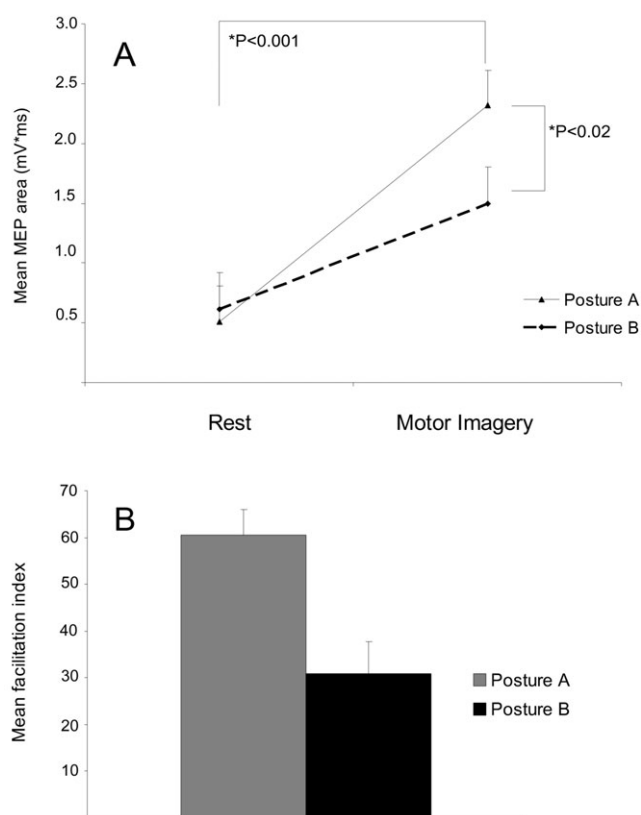
Figure 2. (*A*) Comparison of mean (and SE) motor evoked potential (MEP) area obtained for each posture during rest and motor imagery. (*B*) Mean (and SE) of the facilitation index computed from motor evoked potentials (MEP) for postures A and B.

The spatial distribution of the effect of postural modulation over motor imagery was assessed through a map of MEP area computed for each experimental condition at the region of representation of the OP muscle in M1, as exemplified in Figure 3*A*–*D*. For posture A, compatible with the imagined movement, MEPs were much larger throughout the stimulated area during the motor imagery condition (MI; Fig. 3*B*) comparatively to those obtained in the rest condition (R; Fig. 3*A*). The inverse pattern was found for posture B, incompatible with the imagined movement. For this condition, MEP area frequently attained higher values during R (Fig. 3*C*) than MI (Fig. 3*D*). Comparison of the maps computed for postures A and B during R (Fig. 3*A*,*C*) further suggested a lesser excitatory drive in M1 required by posture A with respect to posture B.

The strength of the postural modulation effect was also made evident when the facilitation index score computed per stimulated point for postures A and B was plotted (Fig. 3*E*,*F*). A spread of facilitation was found for posture A (Fig. 3 *E*) whereas a clear reduction of facilitation was observed for posture B (Fig. 3*F*).

MEP area values gathered at time intervals of 500 and 800 ms after the go signal obtained in two subjects (CC and CB) were analyzed through a three-way ANOVA, using compatibility, time interval and imagery as main factors. Results showed a facilitation effect for motor imagery [$F(1,106)$ = 17.13, P < 0.001, MSe = 0.65], the compatibility factor having approached statistical significance [$F(1,106)$ = 3.46, P = 0.06, MSe = 0.65] with respect to the time interval. Although very preliminary, these results give support for a long-lasting postural modulation effect by motor imagery.

Behavioral Results

Subjects were asked to evaluate the degree of comfort in keeping each of the postures by using a 1–5 point scale. As shown in Figure 4*A*, all subjects rated posture B (3.83, SD = 0.75) as easier to keep than posture A (2.33, SD = 0.51; paired *t*-test, P < 0.001). Thus, posture A was considered as more awkward to keep with respect to posture B. However, when they had to judge with which posture it was easier to perform the imagined finger opposition movement (Fig. 4*B*), subjects rated posture A (4.33, SD = 0.81) as easier to imagine than posture B (2.83, SD = 1.60; paired *t*- test, P < 0.01).

As shown in Figure 5, a significantly higher degree of correlation was found between motor imagery and movement execution for posture A than for posture B (PA, r^2 = 0.97; PB, r^2 = 0.78, P < 0.01), thus confirming that the task is more easily achieved when there is a compatibility between motor imagery and actual hand posture.

Discussion

Motor Imagery Modulation of Cortical Excitability

In agreement with previous reports (Yahagi *et al.*, 1996; Kasai *et al.*, 1997; Kiers *et al.*, 1997; Yahagi and Kasai, 1998; Abbruzzese *et al.*, 1999; Fadiga *et al.*, 1999; Hashimoto and Rothwell, 1999; Ridding and Rothwell, 1999; Rossini *et al.*, 1999), in the present study we describe a facilitation of the MEPs during a motor imagery task. How does motor imagery modulate M1 excitability? By means of a paired pulse paradigm, Abbruzzese *et al.* (1999) have shown that the cortico-cortical inhibition is significantly reduced in the region of representation of the relaxed OP muscle during motor imagery, in a manner that reproduces a mild voluntary contraction of this muscle (but see Ridding and Rothwell, 1999). Similarly, Hashimoto and Rothwell (1999) cautiously evaluated background EMG activities and H-reflex changes during motor imagery of a sequential task and concluded that the motor imagery processes have dynamic effects over the motor cortex excitability similar to those observed during motor performance. Both studies suggested that the modulation of inhibition occurring during motor imagery has a cortical origin (Abbruzzese *et al.*, 1999; Hashimoto and Rothwell, 1999).

Postural Modulation over M1 Excitability

In the present study, we showed that the M1 facilitation effect was very robust when the hand posture was consistent with the imagined movement, being however, significantly weaker when the hand was kept in an incompatible position. The postural modulation was also evident by mapping the distribution of MEP area at the region of representation of the *opponens pollicis* in M1. Taken together, these results consistently show that corticospinal excitability is enhanced when the compatibility between the actual hand posture and the imagined movement is maximized. Behavioral results, as shown by the correlation analysis, further confirm that the task is more easily achieved when there is a compatibility between motor imagery and actual hand posture even when the subjects consider the latter as more awkward than the former. Thus, it seems that both the facilitation effect for the compatible hand posture and its reduction for the incompatible one, as quantified with the TMS technique, are mirrored at the behavioral level.
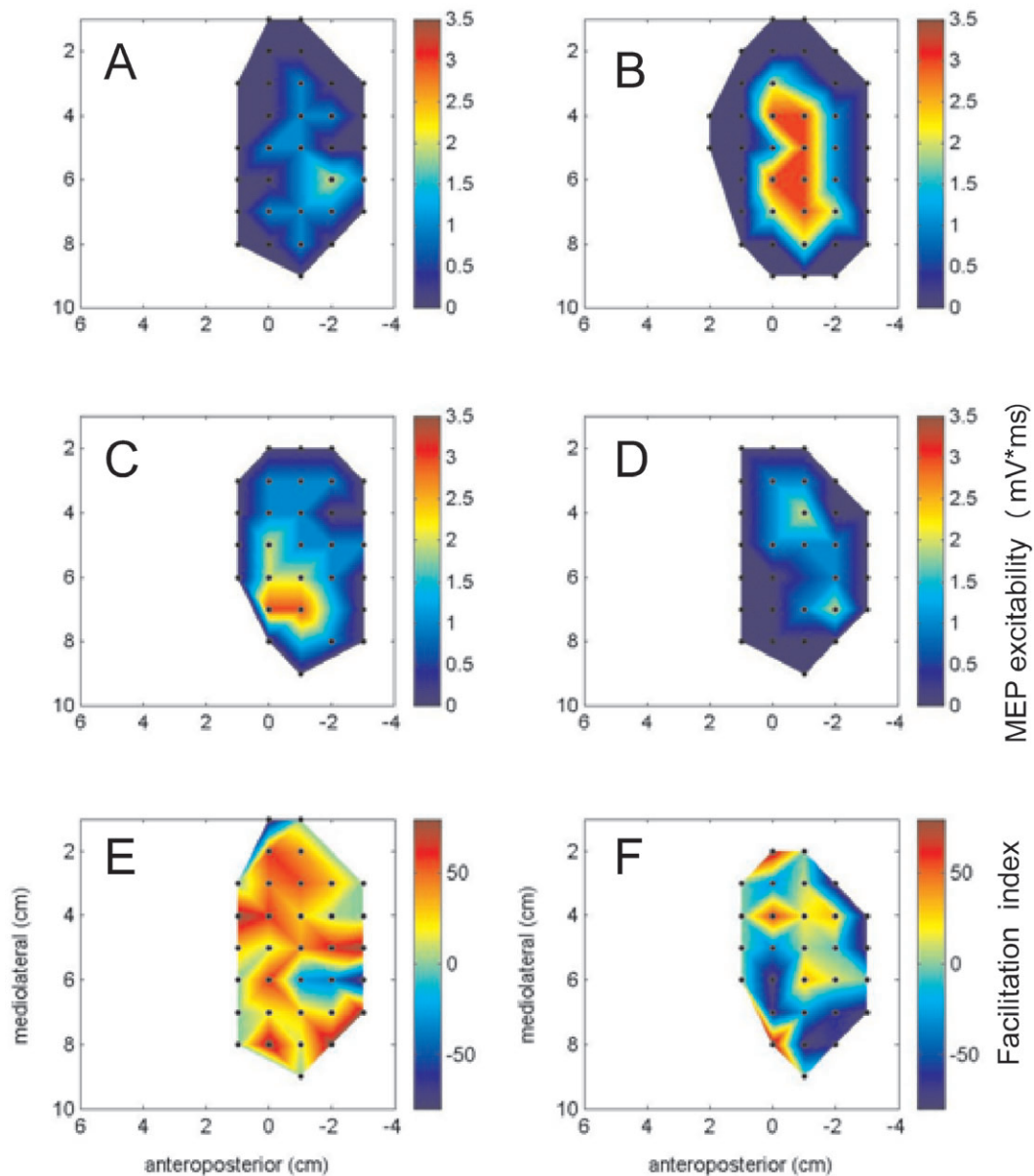
Figure 3. MEP excitability maps obtained during rest (*A, C*) and motor imagery (*B, D*) in one subject (BS). (*A, B*) Posture A (compatible). (*C, D*) Posture B (incompatible). Facilitation index values were also plotted for postures A (*E*) and B (*F*).

Our results are in agreement with previous findings, which demonstrated that incompatible postural signals affect motor imagery (Parsons, 1994; Sirigu and Duhamel, 2001). What mechanism underlies this behavior? Is this a central or a purely peripheral effect? Let us first consider the role of hand posture in modulating the MEPs. In a recent study, Wassermann *et al.* (1998) have shown that TMS applied over the hand representation in M1 induced an abduction of the index finger when the hand was kept in a relaxed posture. Interestingly, TMS induced a flexion of the same finger when the hand was kept in a pincer configuration. This postural modulation effect was obtained irrespectively of the stimulated scalp position over M1, leading the authors to suggest that a bias imposed on the motor output system by sub-threshold activity related to the hand posture would swamp any variation in response to changes in the site of stimulation (Wassermann *et al.*, 1998). By the same token,

Shimura and Kasai (2002) have shown that the MEPs recorded from upper extensor muscles are modulated by the limb position: keeping an arm posture that facilitates its extension produced MEPs of higher amplitude and shorter latency in the muscles *triceps brachii* and *brachioradialis*, comparatively to a neutral position. The authors proposed that a facilitatory limb position would enhance the cortical and spinal excitability due to the higher amount of sensory input coming from the periphery (Shimura and Kasai, 2002). Ridding and Rothwell (1999), using a paired pulse TMS paradigm, have further demonstrated that electrical peripheral nerve stimulation reduces the degree of intracortical inhibition in M1. Electrophysiological recordings performed in the monkey M1 confirm that the gain of neurons is strongly influenced by limb posture (Caminiti *et al.*, 1990; Scott and Kalaska, 1997; Kakei *et al.*, 1999; Ajemian *et al.*, 2001). Taken together, these results, in
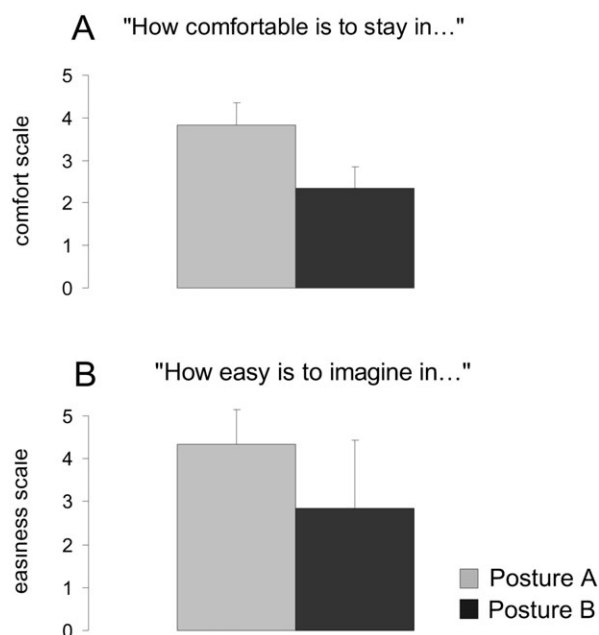
Figure 4. (*A*) Subjective evaluation of the degree of comfort while keeping each posture in a scale from 1 to 5. (*B*) Subjective evaluation of the easiness to imagine the movement while keeping each posture in a 1–5 scale.

conjunction with our findings, corroborate the hypothesis that actual limb position influences the pattern of excitability in M1, regardless of the origin of the postural modulation.

Interaction between Motor Imagery and Posture in M1

Data gathered in the present study have shown that the degree of compatibility of hand posture actively interferes with mental simulation of a hand movement. For posture A, compatible with the imagined movement, MEPs per stimulated grid point had larger area and were obtained from a more extended cortical region during motor imagery (MI) comparatively to the rest condition (R). The inverse pattern was found for posture B, incompatible with the imagined movement. In this case, MEP area recorded per stimulated grid point frequently attained higher values during R than MI. The index score analysis confirmed a spread of facilitation for posture A and a much more restricted spatial distribution of excitability for posture B. Thus, it seems plausible to suppose that the postural effect over motor imagery shown in the present study is put forth by a mechanism of modulation of inhibitory circuits in M1.

The validity of a M1 excitability map depends, however, on the consistency of MEPs across sessions. It has been previously shown that MEP amplitude variability correlates with both the relative muscle location (proximal muscles are associated with more variable MEP responses in comparison to distal ones) and the distance of the TMS pulse from the scalp position defined as optimal to activate the muscle under investigation (Brasil-Neto *et al.*, 1992). In the present study, even though each MEP response was found to vary from trial to trial (data not shown), when MEP values obtained in M1 and R conditions for each stimulated point were paired and used to compute the facilitation index, this variability effect was overcome and the postural facilitation effect emerged as a significant result. The effect of posture upon motor imagery was absent from back-
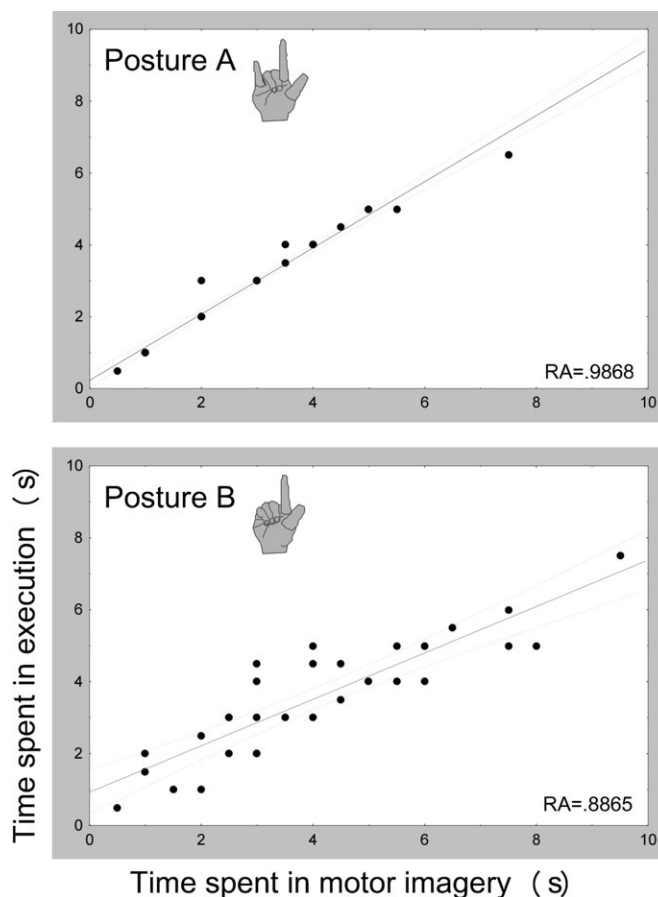

Figure 5. Correlation between time spent during motor imagery and movement execution for each posture. Correlation indexes (rA and rB) are statistically different ($P < 0.01$).

ground EMG recordings collected during the 200 ms that preceded the TMS pulse, suggesting that the modulation obtained during the task originated at the cortical level. The maps plotted for each experimental condition as shown in Figure 3 can thus be viewed as updates of how cortical excitability is spatially distributed in M1.

Postural Modulation of Motor Imagery Measured at Two Time Intervals

In the present study we measured movement execution time for each posture in order to define the time course of TMS pulse application. Based on the behavioral results, the postural effect over motor imagery was tested at both 500 and 800 ms after the go signal. Preliminary results obtained in two subjects showed a facilitation effect for motor imagery, irrespective of the tested time interval. The effect of compatibility approached statistical significance, thus suggestive of a long lasting effect of posture over motor imagery processes occurring at M1. Although preliminary, our results suggest that M1 is recruited both in early and late phases of the motor simulation process and the postural modulation effect upon motor imagery occurs throughout the task completion.

Sites of Interaction between Motor Imagery and Postural Information

Although the possibility of a peripheral modulation of the hand posture upon the process of mental simulation taking place

mostly at M1 level can not be ruled out, an alternative explanation to account for the lack of facilitation observed during the incompatible condition is that this is a purely central effect. In other words, the actual hand posture would yield a discrepant signal with respect to the posture predicted by the motor imagery process.

One location for this interaction to occur is the parietal cortex. Brain lesions that include the left inferior parietal lobe (Brodmann's area 40) often lead to a deficit in a high-level representation of body posture which seems to alter specifically the capacity to process target postures (Goldenberg, 2001), without, however, affecting other movement parameters such as speed of execution (Sunderland and Sluman, 2000). Similarly, bilateral lesions in monkey parietal areas 5, 7B and MIP produce a strong disruption of the relation between hand position and limb postural configuration, without affecting the range or velocity of joint movements (Rushworth et al., 1998). These results were duly interpreted as evidence that these parietal areas should play a role in comparing intended and actual postures.

Patients with left parietal cortex lesions loose their ability to perform motor imagery tasks (Sirigu et al., 1996; review in Crammond, 1997), whereas a lesion in M1 does not disrupt the ability to generate imagined movements (Sirigu et al., 1996; Johnson, 2000b). Brain imaging studies have revealed prominent left parietal cortex activation during a hand movement simulation (Gerardin et al., 2000; Johnson et al., 2002; Hanakawa et al., 2003). During motor imagery, the parietal cortex is thought to generate a forward model that predicts the sensory outcome of the mentally simulated action (Sirigu et al., 1996; Blakemore and Sirigu, 2003; for a review, see Wolpert and Flanagan, 2001). Within the parieto-frontal circuit involved in computing the action-specific motor representations, Johnson and co-workers (Johnson, 2000a; Johnson et al., 2002) proposed that the superior parietal lobe would be responsible for generating representations that are used to evaluate the response options in advance of movement selection, leading to an estimate of their biomechanical awkwardness. We herein hypothesize that the parietal cortex may also be important in computing the discrepancy between on line hand posture and the mental simulation of a hand movement.

This effect of postural compatibility would seem to occur mostly for a first person, motor imagery condition. Sirigu and Duhamel (2001) have recently compared the effect of a simple change in the phrasing of the imagery instructions (first- or third-person imagery) during a hand mental rotation task. According to these authors, under instructions of first person imagery, subjects would use primarily motor resources while under instructions of third person imagery, they would solve the task using visual resources. In their experiment, when the hands were held in a compatible posture, normal subjects were faster in the first- compared to the third-person imagery mode, whereas a parietal damaged subject employed the same amount of time to perform the task irrespectively of task instructions. When the hands where held in an incompatible hand position, the performance of the parietal subject was similar to that of normal subjects. Thus, a parietal cortex lesion seems to affect specifically the capacity to take one's own body representation into account during motor imagery, preserving, however, performance guided by visual imagery (Sirigu and Duhamel, 2001).

Let us suppose that the postural modulation upon motor imagery takes place in the parietal cortex when the motor command is issued. In this scenario, if a copy of the motor command is used by the CNS to predict movement unfolding and build an internal model of movement, it may be possible that the degree of compatibility is already taken into account by the internal model. In the compatible condition, the parietal cortex could thus drive the facilitation effect found in M1, through the parietal-premotor loop, whereas an inhibition of the internal model unfolding would occur at this brain region during the incompatible condition. As pointed out by Sirigu and Duhamel (2001), a cognitive task such as mental rotation of imagined hands can be accomplished by calling upon different subsets of processing resources, which, at a functional level, correspond to different routes toward a single solution. In the context of the present study, one could suppose that the lack of activation of the parietal cortex during the incompatible hand posture could induce the use of a visual strategy to solve the task, leading to a reduced facilitation of corticospinal excitability.

In conclusion, our results show that corticospinal excitability is enhanced when the compatibility between the actual hand posture and the imagined movement is maximized. This postural effect has been shown to exert a modulatory influence upon the TMS-induced MEPs in M1, pending its compatibility with the imagined movement. This modulation seems to result from the interaction between the facilitatory effects driven by mental simulation and the hand shaping effects driven by proprioceptive information.

Notes

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