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Motor imagery beyond the joint limits: A transcranial magnetic stimulation study

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ABSTRACT

The processes and neural bases used for motor imagery are also used for the actual execution of correspondent movements. Humans, however, can imagine movements they cannot perform. Here we explored whether plausibility of movements is mapped on the corticospinal motor system and whether the process is influenced by visuomotor vs. kinesthetic-motor first person imagery strategy. Healthy subjects imagined performing possible or biomechanically impossible right index finger movements during single pulse TMS of the left motor cortex. We found an increase of corticospinal excitability during motor imagery which was higher for impossible than possible movements and specific for the muscle involved in the actual execution of the imagined movement. We expand our previous action observation studies, suggesting that the plausibility of a movement is computed in regions upstream the primary motor cortex, and that motor imagery is a higher-order process not fully constrained by the rules that govern motor execution.

1. Introduction

Studies converge to indicate a substantial similarity of the rules and mechanisms underlying execution, observation, and imagery of actions. These three processes rely upon largely overlapping neural substrates (Buccino et al., 2001; Calvo-Merino et al., 2005; Decety et al., 1991, 1994; Gerardin et al., 2000; Jeannerod, 1994; Kiers et al., 1997; Lotze et al., 1999; Stippich et al., 2002; Roland et al., 1980). Moreover, motor images may share the same characteristics (e.g., kinematic properties) of correspondent movements performed in daily life (Jeannerod, 1994). The time for mentally grasping an object, for example, increases with the amount of change in anatomical configuration, which would occur during actual execution of the very same action (Decety and Michel, 1989). In a similar vein, the time course of an imagined movement is correlated to the time course of its actual execution (Decety and Michel, 1989; Jeannerod, 1994; Johnson, 2000; Parsons et al., 1995; Sirigu et al., 1995, 1996), and autonomic responses are similarly modulated during motor imagery and motor performance (Decety et al., 1991). Transcranial magnetic stimulation (TMS) studies report that motor imagery generates an increase of excitability in motor representations of muscles that are activated during actual execution of the imagined movement (Kasai et al., 1997; Kiers et al., 1997; Rossini et al., 1999; Yahagi and Kasai, 1998). Importantly, the facilitation of motor evoked potentials during imagination of actions has been demonstrated to be muscle-specific (Facchini et al., 2002; Fadiga et al., 1999; Fourkas et al., 2006a,b; Hashimoto and Rothwell, 1999), suggesting an extremely tight link between motor imagery and execution. People can, however, try and imagine movements that they are not able to perform, either because they have not learned the movement or because they physically cannot execute it (due to injury or biological impossibility). Moreover, the perception of impossible movements can be induced by manipulating proprioceptive afferents even in healthy subjects (Craske, 1977), or by internally generated mechanisms in amputees (Moseley and Brugger, 2009). Exploring the link between motor imagery, action observation and motor execution may help to explain such a counterintuitive, illusory experience. However, the issue whether impossible movements can – or cannot – be mapped onto the cortex and share common neural representations with possible movements has only recently been addressed, and only in the domain of action observation (Avenanti et al., 2007; Buccino et al., 2004; Costantini et al., 2005; Romani et al., 2005; Stevens et al., 2000). In two TMS studies we asked subjects to observe biomechanically possible and impossible (i.e., cannot be performed due to anatomical muscle, joint, and skeletal constraints) index- or little finger movements. We found that observation of the two

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types of movements induces equivalent levels of muscle-specific corticospinal facilitation in response to stimulation of the primary motor cortex (Avenanti et al., 2007; Romani et al., 2005). Also, while observation of possible and impossible hands movements triggered similar hemodynamic responses in the frontal node of the action observation network (AON), higher response to impossible than possible human biological movements was found in the AON parietal node (Costantini et al., 2005). Additionally, virtual lesions of ventral premotor cortex (vPMc) suppressed mirror motor facilitation contingent upon observation of possible movements, while virtual lesion of primary somatosensory cortex (S1) suppressed mirror motor facilitation contingent upon observation of impossible ones (Avenanti et al., 2007).

Here we sought to determine whether imagining to self-perform – instead of simply observe (Avenanti et al., 2007; Costantini et al., 2005; Romani et al., 2005) – biomechanical possible vs. impossible actions would trigger differential activity in the corticospinal motor system. Based on the notion that observation and imagination of possible hand movements produce similar patterns of corticospinal facilitation (Clark et al., 2004), we attempted to make comparable our previous action observation research and the current one by asking participants to imagine the same hand movements viewed by the subjects in our previous study (Avenanti et al., 2007). Motor evoked potentials (MEPs) were recorded from two hand muscles during single pulse transcranial magnetic stimulation (TMS). In one condition subjects were requested to imagine abduction–adduction movements of the index finger with angular displacements easily reached during actual movements (possible condition, PC; Fig. 1). In another condition subjects imagined the same type of index finger movement but within a range of angular displacement well beyond the maximal angular displacement allowed by the metacarpo-phalangeal joint (impossible condition, IC; Fig. 1); thus, this type of movement cannot actually be performed because of biomechanical joint constraints. In the third condition subjects imagined their hand in a static position (static condition, SC). The plausibility of the different movements, however, might give rise to the automatic adoption of different visual or kinesthetic imagery strategies across conditions, e.g., kinesthetic in PC and visual in IC. Therefore, since different imagery strategies can affect the corticospinal excitability (Fourkas et al., 2006b; Stinear et al., 2006), participants performed each imagery condition twice, once using a visual and once using a kinesthetic strategy.

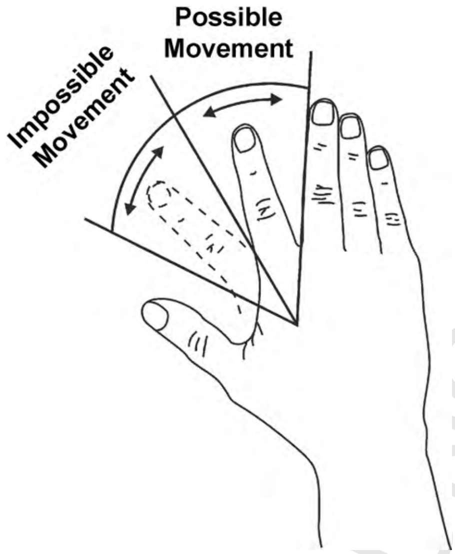

Fig. 1. Angular displacements for the possible and impossible conditions. Participants were asked to imagine performing abduction–adduction of the right index finger in a range of angular displacement in which the action is biomechanically possible (0–35°: Possible Condition (PC)) or in a range of angular displacement in which the action is biomechanically impossible (60–95°; Impossible Condition (IC)). Thus, in both PC and IC the range of angular displacement depicted was comparable (35°) but the action occurred in independent workspaces.

The subjective quality of the imagery was captured by asking the participants to answer on a Likert-type scale a series of statements measuring different aspects of the adopted strategy (e.g., vividness of visual or kinesthetic components; difficulty in adopting a specific strategy) and imagined movement (e.g., how much the movements were imagined in a first person perspective, how easy was controlling imagery or limit it to a specific finger). We explored whether the perceived quality of the imagery changed according to the type of strategy or the plausibility of the imagined movement (or both) using non-parametric statistics as well as polychoric correlations. The latter method was adopted to estimate if the same trait definitions underlie possible and impossible movements when imagined under different strategies.

2. Methods and materials

2.1. Participants

Fifteen right-handed (Oldfield, 1971) healthy subjects (8 men) ranging in age from 19 to 31 (mean = 23.5) years participated in the study. Two subjects were replacements in the data set (see Section 2.7) yielding $N = 13$. None had neurological, psychiatric, or other medical problems, nor had any contraindication to TMS (Wassermann, 1998). All procedures were approved by the local ethics committee of the Santa Lucia Foundation and were in accordance with the ethical standards of the 1964 Declaration of Helsinki. Written informed consent was obtained for each participant. Participants were paid for their participation in the study.

2.2. Electromyography (EMG)

Surface EMG recording was performed using Ag–AgCl cup electrodes (1 cm diameter) placed in a belly-tendon montage over the motor point of the right first dorsal interosseous (FDI) and abductor digiti minimi (ADM) muscles. Activity was recorded and amplified with a Viking IV D electromyograph (Nicolet Biomedical, USA), band pass filtered (10 Hz to 3 kHz), and sampled at 10 kHz. Signals were displayed in two channels set at high sensitivity (50 μV) to ensure the absence of unwanted muscular contraction prior to TMS pulses. During the electrophysiological preparation, EMG signals were sent to loudspeakers allowing subjects to use auditory feedback to practice avoiding background muscle activity.

2.3. Transcranial magnetic stimulation (TMS)

The focal TMS methodology was largely identical to that which we have previously described (Fourkas et al., 2006b, 2008). The following details are specific to the current study. The figure-of-eight coil was attached to a Magstim SuperRapid® (Magstim, Whitland, Dyfed, UK). The optimal scalp position (OSP) over the left primary motor cortex for eliciting right hand motor evoked potentials (MEPs) in FDI was selected so that it was also possible to record stable MEPs in the control muscle (ADM) of all subjects. Resting motor threshold (rMT) was defined using the control muscle to ensure that any failure to find modulation of corticospinal excitability in ADM was not due to inadequate stimulation intensity (stimulation intensity throughout data collection = 120% of rMT). To double check for any muscle contraction due to lack of relaxation, EMG signal was monitored through online visual inspection during the experiment and through auditory signal prior to the recording session.

2.4. Imagery instructions

Three video clips were used to illustrate to subjects what they should imagine. The videos (3 s in length) have previously been described in Avenanti et al. (2007), where the clips can be viewed in the online supplemental materials. In brief, one video shows the dorsal view of a right hand resting on a tabletop [Static Condition (SC)]. A second video shows the right index finger of the hand performing abduction–adduction three times in a range of angular displacement (0–35°; Fig. 1) in which the action is biomechanically possible [Possible Condition (PC)]. A third video shows the right index finger of the hand performing abduction–adduction three times in a range of angular displacement (60–95°; Fig. 1) in which the action, due to physiological limitations of the metacarpo-phalangeal joint, is biomechanically impossible [Impossible Condition (IC)]. Thus, in both PC and IC the range of angular displacement depicted was comparable (35°) but the action occurred in independent workspaces; in both videos, the abduction–adduction movement was displayed at a frequency of ∼1 Hz.

The subjects received verbal instructions in addition to viewing the videos. Subjects were told to imagine the action they had viewed using a first person perspective

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with egocentric coding in all conditions. The verbally delivered instructions for SC were to imagine, throughout each trial, the unmoving hand; they were explicitly told to avoid imagining any kind of movement at all. The PC instructions were to imagine, throughout each trial, the right index finger performing repetitive and continuous abduction–adduction in the range of displacement seen on the video. The instructions in the IC were to imagine, throughout each trial, the right index finger performing repetitive and continuous abduction–adduction in the range of angular displacement biomechanically impossible to reach, as shown on the movie. For both PC and IC they were told to adopt a constant movement frequency that matched that one observed in the video clips. Since possible and impossible movements were involved, video instructions were used to make subjects unambiguously aware of the type of movements they had to imagine. It is worth noting that, subjects tend to rely primarily on visuomotor imagery especially when they are inexperienced with the task. To reduce such priming of the visual over the kinesthetic modality, before the kinesthetic session we also asked the participants to perform the possible movements. Moreover, we asked participants to try and move the index finger beyond joint constraints, so as to try and simulate the sensations associated with the impossible movements. Moreover, we asked participants to use the left hand to try to stretch the right index finger beyond the actual limit of finger excursion.

In each of the three imagery conditions, six of the subjects first imagined the actions using a kinesthetic imagery strategy (i.e., "try to imagine how it 'feels' – the sensations related to the movement or static posture of the hand, and avoid visually representing it"), and then performed the same tasks using a visuomotor imagery strategy (i.e., "try to imagine how it 'looks' – try to 'see' the moving or static hand, and avoid feeling the sensation related to that movement or posture"). The other seven subjects started with visuomotor imagery, and then used kinesthetic imagery strategy.

2.5. Procedure

Subjects sat in front of a table with the right hand and the forearm resting on a pillow to avoid any unwanted contraction. At the start of each block, subjects watched the appropriate video to obtain a clear idea of what action to imagine and received the verbal instructions. The video was displayed on a 19″ monitor located 80 cm away. The video was turned off prior to data collection and therefore the subjects were never simultaneously observing and imagining action while MEPs were being recorded. Within each imagery strategy (kinesthetic, visuomotor), a pseudo-Latin square design was used to determine the order of the imagery conditions (SC, PC, IC). Each imagery condition was presented in a separate block, with 18 MEPs collected in each block. The order of the blocks in the first imagery strategy was reversed for the second strategy.

Subject's eyes were closed during imagery. Each trial started with a beep tone, which signaled to the subjects that they should begin their imagery. The TMS pulse was delivered 3–5 s after the beep at a randomly selected interval (steps of 400 ms). The minimum of 3 s was allowed in order to provide subjects with sufficient time to generate their imagery, while the random interval was used to minimize priming effects related to the pulse. Based on Chen et al. (1997), an inter-trial interval of ~10 s was used (cf. Fourkas et al., 2006a,b). In PC and IC, subjects were required to report the direction of the imagined finger movement ('toward' or 'away' from themselves, i.e., abduction or adduction) after each magnetic pulse to facilitate the maintenance of attention (cf. Fourkas et al., 2006a).

2.6. Post-experimental manipulation check

Participants provided written descriptions of their imagery for each block of PC and IC. A series of statements were also rated on Likert-type scales for both imagery strategies. Several of these statements (or close variations) have been reported in the post-experimental manipulation checks of our previous motor imagery studies (cf. Fourkas et al., 2006a,b, 2008). The statement related to first person perspective imagery controlled for first–third person perspective switching and that the spatial coding was internal (egocentric) rather than external of self (item 1). Subjects rated the amount of control they had over the imagined movement (including frequency/pacing; item 2), and that the action occurred in the area specified for that condition (item 3). Other statements assessed the difficulty of imagining the action using the specified strategy (kinesthetic – item 4; visuomotor – item 8), aspects of imagery quality (clarity and vividness of visuomotor imagery – item 10; imagined muscle tension; imagined stretch, items 5 and 6), and whether kinesthetic imagery was concomitant with visuomotor imagery (items 7 and 9). A final statement allowed subjects to state whether they found the action pleasant or unpleasant to imagine ("if yes, please describe"), or neither (i.e., had no opinion one way or the other). This last statement was included in light of the high ratings of aversion reported in the action observation studies of Romani et al. (2005) and Avenanti et al. (2007).

2.7. Data handling

MEPs were analyzed off-line (cf. Fourkas et al., 2006a, 2008). To ensure the absence of background EMG activity confounding the MEP analysis, visual inspection of the data was performed. Trials were removed if there was activity within 100 ms of the pulse, the MEP amplitude could not be distinguished from the background, or if overt movements were observed. These criteria lead to the replacement of two subjects who displayed extensive background activity on nearly all trials in the IC kinesthetic block, possibly inflating their MEP amplitudes through a reduction of motor threshold. Next, outliers (±2 SD) were identified for each muscle in each block and the data removed for both muscles. In total, 8–34 trials were rejected per subject (for each block of each subject retained trials ≥ 10). Peak-to-peak millivolt (mV) amplitudes were calculated using the Viking system and the data were normalized (natural log + 1) to address non-normality resulting from positive skew.

Due to the reduced influence of the TMS pulse on ADM excitability when FDI is the OSP (Fourkas et al., 2006a) and the probable inter-individual morphological differences in the distance between the cortical representations of the two muscles (Krings et al., 1998), we decided to maximize the chances of detecting effects in ADM using separate repeated measures analyses of variance (ANOVAs) for each muscle. Peak-to-peak MEP amplitudes from each muscle were analyzed with Strategy (visual, kinesthetic) and Conditions (SC, PC, IC) as the main factors. Newman–Keuls post hoc comparisons were performed where appropriate, with effect sizes calculated using a modified Cohen d' to eliminate the bias introduced by the correlation between items (Dunlap et al., 1996).

We applied two statistical approaches to explore the subject's subjective experience in the four imagined movement blocks. In the first, responses on the subjective reports were converted to numeric values and analyzed with non-parametric Friedman ANOVA and Wilcoxon matched-pairs tests (cf. Fourkas et al., 2006b, 2008). In the second, the polychoric correlation coefficient between responses to each statement on the manipulation check for each block (IC kinesthetic, PC kinesthetic, IC visual, PC visual), and between tasks and strategy (PC–IC kinesthetic, PC–IC visual), was calculated in PRELIS (Scientific Software International). The polychoric correlation is used when analyzing items on self-report instruments (e.g., personality tests, surveys, and questionnaires assessing opinions or attitudes) that typically use Likert-type ratings and provide ordinal variables. Opinions, however, cannot be directly observed or measured and thus the response to the probe question is an indirect measurement of something unobservable. Thus, since imagery is a covert mental process, the use of the polychoric correlation coefficient provided a way to link the subjective ratings for each task to the imagery being performed. For each of our Likert-type questions, ordinal variable X (i.e., the response to a question) represents the unobserved continuous variable X^* (i.e., the imagery experienced). The correlation between 2 ordinal variables is known as the polychoric correlation coefficient, and it is an estimate of the relationship between the 2 variables (Gilley and Uhlig, 1993). In more practical terms, the correlation coefficient between two questionnaire items is an expression of rater agreement on the trait definition and its specific categories over different rating sessions. For example, a low number of correlated items between PC-k and IC-k conditions (or within PC-k but not within IC-k items) would suggest that the two imagined movements were produced differently with that imagery strategy. In other words, if items are highly correlated across one but not the other condition, the suggestion is made that the two conditions differ from each other.

The polychoric correlation has the assumption of bivariate normality which in PRELIS is tested with a Chi Square Likelihood Ratio (Test of Model) and the Root Mean Square Error of Approximation (RMSEA; Test of Close Fit). The correlation coefficients reported below all meet the assumption of bivariate normality and have $r \geq 0.60$. Given that ordinal variables have no inherent unit of measure and hence no mean or variance, there is no accepted method of calculating a polychoric correlation p value. The level $r \geq 0.60$ was selected as a reasonable level of correlation as its size corresponds to that which would be significant using more common types of correlation.

3. Results

3.1. MEP data

Fig. 2 (FDI in panel A, ADM in panel B) illustrates the means and standard errors of peak-to-peak MEP amplitudes of each Condition by imagery Strategy. Analysis of MEP amplitudes recorded from the target muscle (FDI) revealed no interaction ($F(2,24) = 0.019$; $p = .98$). There was a main effect of Condition ($F(2,24) = 18.223$; $p < .000$). All conditions differed from one another: SC < PC ($p = .043$; $d' = 0.28$), SC < IC ($p = .0008$; $d' = 0.55$), and PC < IC ($p = .044$; $d' = 0.28$).

There was also a clear main effect of Strategy ($F(1,12) = 8.786$; $p = .01$), with higher amplitudes recorded during visuomotor than kinesthetic imagery (Fig. 3).

Differences in MEP amplitudes recorded from the control muscle (ADM) revealed no interaction ($F(2,24) = 2.026$; $p = .15$) or main effect of Strategy ($F(1,12) = 0.688$; $p = .42$). There was an effect of Condition ($F(2,24) = 5.156$; $p = .014$) but post hoc analysis detected

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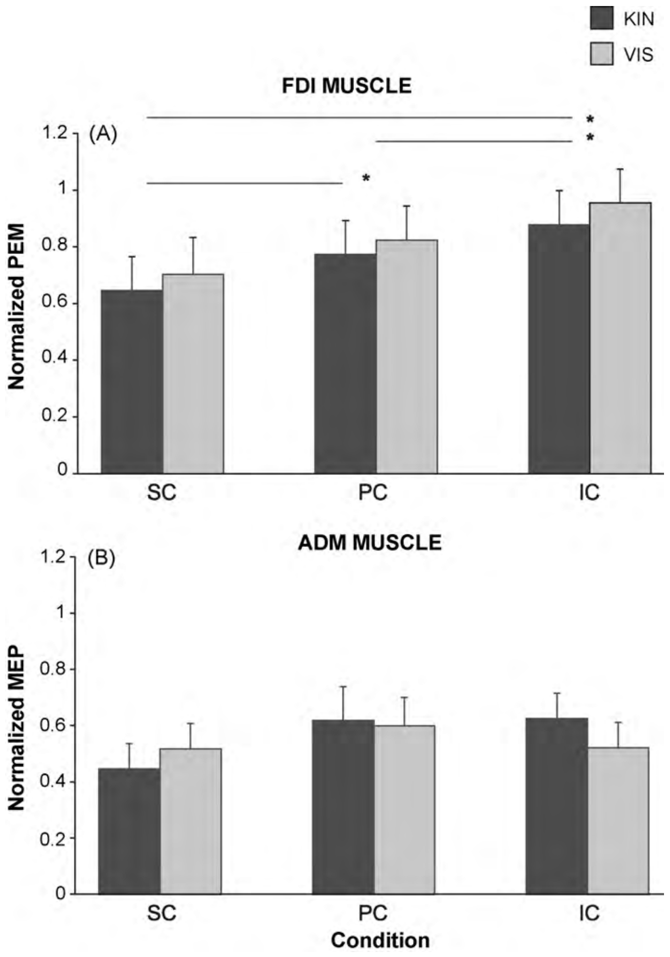

Fig. 2. MEP amplitudes by Condition and imagery Strategy. Panel (A) depicts data from the target muscle FDI. Post hoc analysis for factor Condition revealed that MEPs in the Static Condition were significantly smaller than in the Possible and Impossible Conditions; MEPs in the Possible Condition were smaller than in the Impossible Condition. Panel (B) depicts data for the control muscle ADM. Error bars are standard error of the mean. Vis = Visuomotor Strategy; Kin = Kinesthetic Strategy. SC = Static Condition; PC = Possible Condition; IC = Impossible Condition. $^{*}p < .05$.

no differences among conditions (all $p > .092$). Hence, although sufficient stimulation intensity (120% rMT of ADM) was applied at a coil position from which stable MEPs could be recorded, analysis of amplitudes suggests no significant effect on excitability in this muscle.

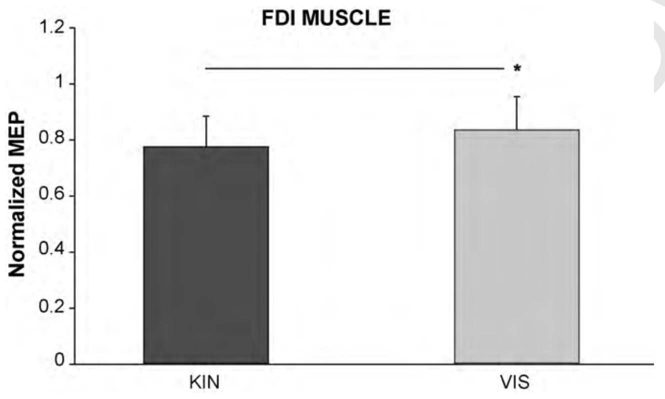

Fig. 3. Effect of imagery Strategy on MEP amplitude. Analysis of factor Strategy for the target muscle FDI revealed amplitudes in the Visuomotor strategy were larger than the kinesthetic strategy. Error bars are standard error of the mean. Vis = Visuomotor Strategy; Kin = Kinesthetic Strategy. $^{*}p = .01$.

3.2. Subjective data

The written descriptions indicated that subjects performed the imagery tasks assigned, and most subjects (8–10 per block) explicitly stated they imagined their own hand. For each strategy of PC and IC, 11 and 12 subjects marked that they “agree” or “completely agree” that they used first person imagery, suggesting the imagery was of their own hand. One subject had considerable difficulty using a kinesthetic strategy for the impossible imagery condition (rating = “very hard”), rated the imagined muscle tension and joint stretch as “very weak”, and “completely disagreed” that the imagined action was always in the specified area. The ratings of the other 12 subjects, however, indicated that they could kinesthetically imagine the impossible action. On the question about whether the imagined action was pleasant or unpleasant to imagine (“if yes, please describe”), all subjects marked “neither” for PC visual, while 12 marked “neither” and 1 “pleasant” for PC kinesthetic. For IC using a kinesthetic strategy, 6 marked “neither”, 6 described it as “unpleasant”, and 1 said it was “funny”; for the visual strategy, 8 marked “neither”, 2 described it as “unpleasant”, 1 as “strange/unusual”, and 2 as “funny”. This suggests that, in contrast to action observation studies using highly similar (Costantini et al., 2005; Romani et al., 2005) or identical (Avenanti et al., 2007) stimuli, the imagination of biomechanically impossible action did not induce high levels of physical aversion across subjects. Rather it suggests that subjects understood the instructional focus to be on sensations of kinesthesia and joint position sense (i.e., conscious proprioception).

Non-parametric analyses indicated that the perceived quality of the imagery consciously manipulated was similar during PC and IC, regardless of strategy. Median responses are reported in Table 1. There were no differences in responses for egocentric first person imagery (item 1: χ^2 (3) = 1.983; $p = .602$), the amount of control participants had over the imagined movement (item 2: χ^2 (3) = 5.560; $p = .134$), or if the action occurred in the area specified for that condition (item 3: χ^2 (3) = 1.737; $p = .824$).

No differences were also found when comparing IC and PC conditions in items describing specific aspects of the two imagery strategies. When considering the kinesthetic strategy (items 4–7), there was no difference between IC and PC in the difficulty to imagine the physical sensation (item 4: $Z = 1.602$; $p = .109$), in the amount of muscular tension or joint stretch there was in the imagery (item 5: $Z = 0.356$, $p = .828$; item 6: $Z = 1.081$, $p = .320$), or in the amount of concomitant visual imagery experienced (item 7: $Z = 0.816$; $p = .750$). When a visual imagery strategy was used (items 8–10), there were no differences between IC and PC in the difficulty to imagine seeing the movement (item 8: $Z = 1.761$; $p = .104$), in the amount of concomitant kinesthetic imagery experienced (item 9: $Z = 1.667$; $p = .188$), or in the clarity and vividness of the visual imagery (item 10: $Z = 0.272$; $p = 1.000$).

The correlative approach was used to explore if subject’s subjective experience showed underlying latent traits (rater’s agreement) within items of PC and IC separately for the visuomotor and kinesthetic strategies, or between items of PC and IC within the same imagery strategy. With regard to the PC kinesthetic feedback (for intuitive clarity, all correlation r values are reported as positive), only one correlation was found between the items: the less difficulty with kinesthetic imagery (item 4), the stronger the ratings of imagined joint stretch (item 6) ($r = 0.670$). By contrast, a number of correlations were found among items when the feedback was for IC kinesthetic. Less difficulty with kinesthetic imagery correlated with stronger ratings of imagined muscle tension (item 5) ($r = 0.765$) and imagined joint stretch ($r = 0.730$), and more agreement that the action occurred in the specified location (item 3) ($r = 0.728$). Stronger ratings of imagined muscle tension correlated with stronger ratings of imagined joint stretch ($r = 0.871$). And,

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Table 1
Subjective feedback.

	Possible		Impossible	
	Kinesthetic	Visual	Kinesthetic	Visual
1. First person				
Median	4.00	4.00	4.00	4.00
Mean	3.15	3.46	3.46	3.69
SD	1.46	0.66	0.97	0.63
2. Control				
Median	3.00	3.00	2.00	3.00
Mean	3.08	3.15	2.15	2.77
SD	0.95	0.69	1.21	1.09
3. Localization				
Median	4.00	4.00	4.00	4.00
Mean	3.69	3.77	3.54	3.62
SD	0.48	0.44	1.13	0.65
4. Kin difficulty				
Median	2.00	–	3.00	–
Mean	2.00	–	3.00	–
SD	1.53	–	1.68	–
5. Tension				
Median	3.00	–	3.00	–
Mean	2.92	–	3.00	–
SD	1.19	–	1.63	–
6. Stretch				
Median	3.00	–	4.00	–
Mean	3.00	–	3.62	–
SD	1.15	–	1.76	–
7. Vis during kin				
Median	3.00	–	3.00	–
Mean	2.69	–	2.85	–
SD	1.18	–	0.90	–
8. Vis difficulty				
Median	–	1.00	–	2.00
Mean	–	1.54	–	2.38
SD	–	1.45	–	1.71
9. Kin during vis				
Median	–	1.00	–	1.00
Mean	–	1.15	–	0.77
SD	–	1.07	–	0.83
10. Vivid/clear				
Median	–	4.00	–	4.00
Mean	–	4.00	–	3.92
SD	–	1.29	–	0.95

Numbers represent median, mean and standard deviation values. Five statements (items 1–3, 7, 9) were rated along a 5-point scale (*completely agree* (4), *agree* (3), *not sure* (2), *disagree* (1), *completely disagree* (0)): a 'first person' perspective was always used; the imagined action could be 'controlled' (including movement frequency); the 'localization' of the action was always in the specified area (0–35°, 60–95°); that there was concomitant 'visual imagery during kinesthetic imagery'; that there was concomitant 'kinesthetic imagery during visual imagery'. The remaining statements used 7-point scales. Items 4 and 8, the difficulty or ease in which the visual and kinesthetic imagery aspects of the mental practice were formed, were rated *very easy* (1), *easy* (2), *fairly easy* (3), *not easy or hard* (4), *fairly hard* (5), *hard* (6), *very hard* (7); items 5 and 6, the level of imagined muscle tension and joint stretch, were rated *very weak* (1), *weak* (2), *fairly weak* (3), *not weak or strong* (4), *fairly strong* (5), *strong* (6), *very strong* (7); item 10, the clarity and vividness of the visual imagery component, was rated *no image seen* (1), *hazy* (2), *fairly hazy* (3), *not hazy or clear* (4), *fairly clear* (5), *clear* (6), *like real vision* (7).

stronger ratings of imagined joint stretch were correlated with more agreement that the action occurred in the specified location ($r = 0.629$).

When subjects performed PC with a visuomotor strategy, more agreement that the action occurred in the specified location correlated with more agreement that the imagined action could be controlled ($r = 0.636$), less difficulty in performing visual imagery (item 8) ($r = 0.913$), clearer and more vivid images (item 10) ($r = 0.659$), and more disagreement that there was concomitant kinesthetic imagery (item 9) ($r = 0.659$). More agreement the action could be controlled also correlated with less difficulty in performing visual imagery ($r = 0.967$). In IC visual, greater agreement the action occurred in the specified location correlated with less difficulty in performing visual imagery ($r = 0.611$), and with clearer and more vivid images ($r = 0.674$).

Considering that non-parametric analyses showed that subjective scores did not differ between IC and PC conditions within the two kinesthetic and visuomotor strategies, we would expect a high amount of correlated items between IC and PC conditions under the different strategies. However, this was true only for visuomotor strategy. Indeed, comparing the two kinesthetic conditions directly, PC and IC subjective scores correlated only for the amount of concomitant visual component (item 7) ($r = 0.933$). Hence, the polychoric correlations suggest only one instance of rater agreement (of 7 possible) on the feedback items. This, in turn, suggests that the subjects experienced the task of kinesthetic PC quite differently from kinesthetic IC.

In stark contrast, for the two visual conditions, five (of six) items were correlated. The more subjects agreed to the imagined action could be controlled in PC, the more they agreed in IC (0.949). Claims of less difficulty with visual imagery in PC coincided with the ratings of less difficulty in IC (0.626). More agreement that the action occurred in the specified location in PC coincided with more agreement in IC (0.999). The clearer and more vivid the imagery in PC, the more clear and vivid it was in IC (0.897). And, more disagreement that there was concomitant kinesthetic imagery during PC coincided with more disagreement in IC (0.828).

4. Discussion

The present results expand the notion that action imagination brings about corticospinal facilitation by showing that the effect is present also during imagery of biologically impossible actions. This novel effect was muscle-specific in that there was no significant effect in ADM even though the stimulus intensity was defined using the rMT of ADM and we kept the muscles separate in the analysis to increase statistical sensitivity. The increase in excitability detected in the FDI SC–IC contrast is in keeping with the results of action observation studies using the same or similar stimuli (Avenanti et al., 2007; Romani et al., 2005). The difference between IC and PC noted in the post hoc of Condition, as opposed to the lack of difference in the same conditions in our action observation studies, is indeed a new finding.

The polychoric correlations suggest that some differences between imagery of the possible and impossible movements existed, particularly when kinesthetic imagery was used. We correlated responses across questions for each of the four blocks to assess if the items measured different concepts, i.e., had different trait definitions. It appears that the two movements were considered differently depending on whether they have to be imagined kinesthetically or visually. Indeed, while in kinesthetic imagery of impossible movements we found several correlations (5), which might suggest redundancy across items, the absence of a consistent *pattern* of redundancy across the same items in the PC kinesthetic (1 correlation) suggests differences in the trait definitions. An inverse pattern was found for the visual strategy, in which PC but not IC imagination showed a high number of correlated items (respectively, 5 and 2). Hence, for both imagery strategies, it seems the trait definition for an item can differ depending on whether the task involves imagery of a biologically possible or an impossible movement. However, the lack of statistical differences in the non-parametric analysis or in the interaction of the MEP data, indicates the overt influence of these differences in trait definitions was subtle.

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The main effect of factor Strategy revealed higher levels of corticospinal excitability in the target muscle when visuomotor imagery strategy was used. While this might seem counterintuitive, we would argue that it is not. Similar TMS evidence regarding visuomotor imagery was reported in Fourkas et al. (2006b). Stinear et al. (2006) reported that kinesthetic imagery induces more excitability than visuomotor imagery only if the imagery task focuses on the production of force, while non-force producing motor imagery tasks have similar levels of excitability regardless of strategy (visuomotor or kinesthetic). Moreover, kinesthetic imagery modulates excitability in expert athletes only during imagery of the task in which they are expert (Fourkas et al., 2008), and is increased by an intervention of physically training to do the task that is subsequently imagined (Takahashi et al., 2005). These data support the idea that conscious task familiarity, particularly with information regarding force, is important in order for kinesthetic imagery to modulate corticospinal excitability. More recent evidence related to task familiarity and motor imagery can be found in an fMRI study of elite and novice divers by Wei and Luo (2010).

Evidence that a biomechanically impossible movement is perceptually accessible is not new. Craske (1977), for example, has shown that vibration of a tendon may elicit an illusion of movement with amplitude beyond the limit of anatomical configuration of the related joint, suggesting that sensory limits of the individual are not set by anatomical configuration. Moreover, it has been recently demonstrated that amputee subjects can learn to imagine a formerly impossible movement of their phantom arm and thus modify profoundly their body image solely by means of internally generated mechanisms (Moseley and Brugger, 2009). Nevertheless, the notion that the motor system may play a role in simulating both possible and biomechanically impossible movements may seem in contradiction with evidence that motor structures activation occurs only when watching actions belonging into the observers' behavioral repertoire, for example during observation of dog biting but not barking movements (Buccino et al., 2004). However, while it may be very hard to map dog barking onto the human motor system, our biomechanically impossible movements can be considered exaggerated human gestures and thus conceptually possible. This property may allow the inclusion of the observed movement in the onlookers' conceptuo-motor repertoire and thus elicit motor mapping (Avenanti et al., 2007; Costantini et al., 2005; Romani et al., 2005). Research on action observation provides some clues as to how biomechanically impossible movements are processed within the motor system. Mirror neurones are active in premotor and parietal cortices of monkeys and humans during execution and observation of actions (Fogassi et al., 2005; Rizzolatti and Craighero, 2004). The somatotopic organization in these areas during observation of movements of different body parts correspond to that found when the same body parts are actually moved (Buccino et al., 2001).

It has been proposed that action observation in humans also involves an internal motor simulation of the observed complex action (Calvo-Merino et al., 2005). Our TMS research, however, demonstrated that the motor nodes of the mirror circuits underlying action observation are not involved in processing the biomechanical *plausibility* of the observed action (Romani et al., 2005). This result was further investigated in Avenanti et al. (2007) where repetitive TMS was used as a virtual lesion technique. Processing the plausibility of an action was unaffected by lesions to the primary motor cortex, supporting the results of Romani et al. (2005). Ventral premotor lesions selectively impaired corticospinal excitability associated with possible actions, while the excitability during observation of impossible actions was impaired with lesions in the primary somatosensory cortex. Moreover, neuroimaging has shown the involvement of frontal regions (particularly left precentral and inferior frontal regions) during both biomechanically possible and impossible movements, but activation of parietal areas (right BA areas 7 and 40) only during observation of biomechanically impossible movements (Costantini et al., 2005).

Thus, the significant increase of MEPs amplitude in IC vs. PC we found in the present study might be explained considering that, because of the violation of biomechanical constraints, more complex sensorimotor computations during imagery of impossible movements were required. This process could be particularly relevant since first person imagery – unlike action observation – strongly requires an embodied perspective. Thus, imagery of simple possible actions can be based on mere reactivation of known motor plans. By contrast, imagery of impossible actions may imply that biomechanical constraints, motor plans, and associated somatic sensations are re-elaborated and computed to accomplish the task.

Several imagery studies have illustrated that biomechanical constraints, largely focused on proprioceptive afferents, can, for example, alter response times (Shenton et al., 2004) and corticospinal excitability (Fourkas et al., 2006b; Vargas et al., 2004). Mental rotation of body parts is a well-known example of being able to use imagery to position a body part in extremely awkward orientations; indeed it is arguable that some of the orientations would be impossible to reach using a first person perspective unless one ignored joint constraints, for example rotating one's foot 180° so that it is pointing backward or one's view of the little finger 270°. Here also, premotor and posterior parietal activation are commonly detected. Complementing the action observation results of Costantini et al. (2005) described above, imagery studies that actively manipulate proprioceptive afferents during the imagery task have shown modulation of the hemodynamic response in the posterior parietal lobe. Activation in the intraparietal sulcus during mental rotation of body parts is reportedly related to the rotation process itself (Vingerhoets et al., 2002) with activity increasing as biomechanical difficulty increases, i.e., as the orientation changes to one which would be physically awkward to actually adopt (de Lange et al., 2005, 2006). More recently, Lorey et al. (2009) have shown that during first person kinesthetic imagery, but not third person visual imagery, the inferior parietal lobe (parietal operculum, SII) is more activated when hand posture is compatible with imagined hand action than when it is incompatible. Thus the mental simulation/rehearsal of actions, either through observation or imagination, involves activation of motor areas while, in contrast, the plausibility of the action appears to be assessed upstream in parietal regions capable of addressing the conflict between vision and proprioception.

Finding a higher increase of corticospinal excitability during imagery of impossible actions, a condition in which – given the biomechanical constraints – brain activity cannot be translated into muscle activity, may seem counterintuitive. However, in keeping with our previous action observation studies (Avenanti et al., 2007; Costantini et al., 2005), the M1 facilitation may depend on computations and processes that take place in different (although strictly interconnected) nodes of the neural network involved in action observation and imagination.

In our action observation studies involving biologically impossible stimuli, it was consistently reported that subjects experience a sense of physical aversion to the impossible stimuli. Six of our subjects described IC kinesthetic as unpleasant, suggesting that it may have engaged the somatosensory system more intensely in these subjects than in the others (by contrast, only 2 said IC visual was unpleasant which can probably be attributed to their cognitive interpretation of the task rather than be explained by primary somatosensory activation). It remains, however, that 1 subject found IC kinesthetic 'funny' and 6 others had no opinion about (un)pleasantness. The difference between the two tasks (observation and imagery), and hence the subject's subjective experience of the task, may be a function of physiology. In action observation there is a strong afferent component as the observer witnesses the

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stimuli, which in the case of biologically impossible actions induces a sense of aversion. Action observation arguably serves an evolutionary purpose which enables our ability to empathize with others and embody their emotional as well as physical pain, which allows us to more accurately understand their actions (Minio-Paluello et al., 2009; Rizzolatti et al., 2009). Yet the action being observed (and in the case of the current study, imagined) is essentially an exaggeration of an action which can be performed. As discussed elsewhere (Avenanti et al., 2007), even without exposure to the possible movement condition subjects can still use their existing motor repertoire to generate a feed-forward model of the ~1 Hz paced 35° finger abduction–adduction performed in this study.

In summary, we found that the imagination of biomechanically impossible movements of the FDI muscle increased corticospinal excitability in FDI above that recorded during the imagination of biomechanically possible movements. And, the imagination of both possible and impossible movements increased excitability relative to imagination of the static hand. This novel motor imagery finding expands on results we previously reported using an action observation paradigm (Avenanti et al., 2007; Romani et al., 2005). Moreover, we have replicated that visual imagery can increase excitability more than kinesthetic imagery (Fourkas et al., 2006b). Finally, we have incorporated the use of polychoric correlations in addition to non-parametric analysis of the subjective reports. The combination of these procedures has allowed us better scrutinize how subjects performed the completely covert mental activity of motor imagery. Indeed, although no significant differences were found in non-parametric testing, the correlations suggested differences in the two kinesthetic, but not visual, tasks. And, quite importantly for researchers of motor imagery, we found evidence that the trait definitions underlying questionnaire items used to assess kinesthetic and visual imagery can differ with the motor task.

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