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CORTICOSPINAL EXCITABILITY DURING IMAGINED AND OBSERVED DYNAMIC FORCE PRODUCTION TASKS: EFFORTFULNESS MATTERS

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Abstract—Research on motor imagery and action observation has become increasingly important in recent years particularly because of its potential benefits for movement rehabilitation and the optimization of athletic performance (Munzert et al., 2009). Motor execution, motor imagery, and action observation have been shown to rely largely on a similar neural network in motor and motor-related cortical areas (Jeannerod, 2001). Given that motor imagery is a covert stage of an action and its characteristics, it has been assumed that modifying the motor task in terms of, for example, effort will impact neural activity. With this background, the present study examined how different force requirements influence corticospinal excitability (CSE) and intracortical facilitation during motor imagery and action observation of a repetitive movement (dynamic force production). Participants were instructed to kinesthetically imagine or observe an abduction/adduction movement of the right index finger that differed in terms of force requirements. Trials were carried out with single- or paired-pulse transcranial magnetic stimulation. Surface electromyography was recorded from the first dorsal interosseous (FDI) and the abductor digiti minimi (ADM). As expected, results showed a significant main effect on mean peak-to-peak motor-evoked potential (MEP) amplitudes in FDI but no differences in MEP amplitudes in ADM muscle. Participants' mean peak-to-peak MEPs increased when the force requirements (movement effort) of the imagined or observed action

were increased. This reveals an impact of the imagined and observed force requirements of repetitive movements on CSE. It is concluded that this effect might be due to stronger motor neuron recruitment for motor imagery and action observation with an additional load. That would imply that the modification of motor parameters in movements such as force requirements modulates CSE. © 2015 The Authors. Published by Elsevier Ltd. on behalf of IBRO. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

Key words: corticospinal excitability, intracortical facilitation, dynamic force production, effort, motor imagery, action observation.

INTRODUCTION

There is a broad body of literature underpinning the concept of a functional equivalence between mental simulation states (S states) and the execution of actions (see Grèzes and Decety, 2001; Jeannerod, 2001, for reviews). One comprehensive account of the underlying brain mechanisms assumes that these cognitive motor states are based on one's own motor representations in the brain (Grush, 2004; Jeannerod, 1994, 2001). Jeannerod proposed an explanation for this in his mental simulation theory. This reveals that a movement possesses a covert action stage involving its characteristics as the goal, the means to achieve it, and its consequences (Jeannerod, 2001). Due to their covert nature, these actions are not executed but rather, mentally simulated. Exemplary situations for such covert activity are the conscious, self-intended simulation of one's own actions (motor imagery) or the perception of actions by others (action observation). However, the main difference between these two cognitive motor states is that motor imagery is generated internally, whereas action observation is driven by external stimuli (Munzert et al., 2008; Vogt et al., 2013). Therefore, the assumption of a functional equivalence between S states does not always imply a total congruency of the underlying processes (e.g., Lorey et al., 2013).

On a neural level, early positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) studies showed that these processes rely on a similar neural network in motor and motor-related cortical areas (Jeannerod, 2001; Porro et al., 1996; Lotze et al., 1999; Munzert et al., 2008), and that the neural activation patterns of these S states overlap with those of movement

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Abbreviations: ADM, abductor digiti minimi; ANOVA, analysis of variance; CSE, corticospinal excitability; EMG, electromyography; FDI, first dorsal interosseous; fMRI, functional magnetic resonance imaging; IC, imagery control; ICF, intracortical facilitation; IHF, imagery high force; IMF, imagery minimal force; M1, primary motor cortex; MEPs, motor-evoked potentials; MVC, maximal voluntary contraction; OBS, movement observation; rMT, resting motor threshold; S state, covert stages of action that share common representations with motor execution; SMA, supplementary motor area; TMS, transcranial magnetic stimulation; VC, visual control; VMIQ-2, vividness of movement imagery questionnaire 2.

execution. Brain imaging research has provided considerable evidence for neural activation of motor and motor-related brain areas during motor imagery and action observation (Filimon et al., 2007; Gazzola and Keysers, 2009; Munzert et al., 2009; Zentgraf et al., 2011; Lorey et al., 2013). This has indicated that specific action features such as accuracy affordances (Grosjean et al., 2007; Lorey et al., 2010) and effort (Decety and Jeannerod, 1996; Guillot et al., 2007) are also represented on a neural level.

Although the reported fMRI studies offer a comprehensive picture of activation for the frontoparietal motor network as well as for subcortical regions during S states, some limitations are obvious, especially for primary motor cortex (M1) activation during motor imagery, for instance. The often reported level of 30–50% activation during motor imagery compared to movement execution may lead to no significant neural activations being found in M1 in fMRI studies, particularly when conservative thresholds are applied (Lotze and Zentgraf, 2010). These limitations may be overcome by studying corticospinal excitability (CSE) during cognitive motor states. Until now, several transcranial magnetic stimulation (TMS) studies have examined CSE during motor imagery and action observation within the same study. In general, they have demonstrated corticospinal facilitation for S states, even when specific results differ due to the application of different motor tasks, different instructions, and sometimes even different evaluation methods (Clark et al., 2003; Stinear et al., 2006; Léonard and Tremblay, 2007; Roosink and Zijdwind, 2010; Bianco et al., 2012). Nonetheless, these task-related result patterns illustrate a possible modulation of CSE during motor imagery and action observation.

Given the fact that S states are a covert stage of an action, it can be assumed that modulations of the motor task such as effort or accuracy will have an impact on neural activation as already reported in several fMRI studies (e.g., Winstein et al., 1997; Lorey et al., 2010). This makes it meaningful to ask whether different force requirements of imagined and observed actions will influence CSE in M1. The literature has already demonstrated that a higher force level within the same movement facilitates CSE (Alaerts et al., 2010; Mizuguchi et al., 2013). However, current evidence on this issue is inconsistent. Park and Li (2011) asked their participants to execute isometric finger flexions and extensions graded by force levels of 10–60% of the maximal voluntary contraction (MVC) followed by an imagery trial on which they had to imagine the same force level after a short delay. Whereas all imagined force levels showed corticospinal facilitation compared with a rest condition, there were no differences between imagined force levels. It has been argued that the missing effect for a graded corticospinal facilitation might be due not only to the time sequence of physically performed and imagined trials but also to a possible after effect of the physical contractions (Mizuguchi et al., 2013). This is why Mizuguchi and colleagues trained their participants to first produce 10%, 30%, and 60% of MVC in an isometric elbow flexion task. This training session was followed by a separate imagery session of the respective

force task. They found an increase of motor-evoked potential (MEP) amplitudes in the agonist muscles for higher force levels and significant differences between the 10% and the 60% force levels. This study provided evidence that the level of imagined isometric contraction modulates CSE.

To further clarify the influence of different force requirements, the present study aims to replicate and extend previous findings on movement simulation by investigating changes in M1 excitability and facilitation. The main objectives of the present study were as follows: First, we used a repetitive abduction/adduction movement of the right-index finger to be characterized as a dynamic force production task in the first dorsal interosseous (FDI). Second, we investigated CSE during motor imagery and action observation in the same experiment. Third, we applied single- and paired-pulse TMS to examine intracortical facilitation (ICF).

We applied a design with a total of three experimental conditions. Participants had to imagine the repetitive finger movement with two different force requirements. In addition, we implemented an observation condition with only high-force requirements of the same dynamic movement. Two control conditions (one each for the imagery and observation tasks) were applied in order to control the influence of perceptual-cognitive processes. We predicted that we would observe an increase in CSE and ICF during imagery of trials with higher mental force requirements. For the observation condition, we expected to observe an increase of CSE and ICF when compared to a visual control condition.

EXPERIMENTAL PROCEDURES

Participants and design

Eleven right-handed (Oldfield, 1971) participants with normal or corrected-to-normal vision volunteered to participate in this study (nine male, mean age = 25 years, $SD = 4.3$). Imagery ability was assessed with the Vividness of Movement Imagery Questionnaire 2 (VMIQ-2, Roberts et al., 2008). All participants reported no history of neurological disorders and no history and/or current use of psychoactive medication. The study was approved by the local ethics committee of the University of Queensland in accordance with the National Health and Medical Research Council's guidelines. All participants gave their informed written consent in accordance with the Declaration of Helsinki.

There were three experimental conditions: Two kinesthetic imagery conditions in which two levels of force were required to be imagined (imagery high force: IHF; imagery minimal force: IMF) and only one movement observation (OBS) condition in which the force requirements reflected those of the high-force condition of the imagery trials as changes in movement kinematics are difficult to recognize during observation tasks in general. These imagined or observed actions consisted of 10 repetitive movements (1 Hz) of horizontal abduction/adduction of the right index finger resulting in a dynamic force production in FDI. In the

minimal force condition participants simply had to imagine the index finger movement without any particular resistance. To achieve higher force needs in the IHF condition, participants performed the movement against a spring as a resistor to enforce a higher force level for contraction in an earlier familiarization session. The tip of the index finger was attached to the spring that was fixed onto an apparatus. The tension of the spring was chosen based on an earlier pilot experiment where participants reported additional movement effort while executing the abduction/adduction movement. The experimental imagery conditions (IHF, IMF) were contrasted to an imagery control (IC) condition in which the participants *imagined* a fixation cross on a black screen, and the OBS condition to a visual control (VC) condition in which participants *observed* a fixation cross on a black screen. The aim of such a conservative control paradigm was to exclude a general effect of changes in excitability for imagery and observation. We suggest that cognitive processes can potentially effect a generalized increase in CSE levels. For this reason, the present study contrasted the motor imagery conditions with a movement unspecific imagery and the OBS condition with a movement unspecific observation condition.

Conditions were presented in blocks of 30 trials in a pseudo-randomized order. All experimental and control conditions included an auditory metronome.

The following instructions were given in the different conditions. IHF: *Close your eyes and imagine performing the high-force task and what it would feel like.* IMF: *Close your eyes and imagine performing the minimal force task and what it would feel like.* OBS: *Observe the video.* IC: *Close your eyes and imagine the fixation cross.* VC: *Fixate on the cross.*

Procedure

Prior to the experimental block (approx. 15 min), participants attended a training session to ensure they had adequate imagery skills and to enable them to familiarize themselves with the experimental setting. They were trained to imagine a minimal or high force-related index finger movement as applied in the different experimental imagery conditions. First, participants observed video trials of the adduction/abduction movement of the index finger (1 Hz, guided through an auditory metronome) while simultaneously executing the index finger movement in either the high force or minimal force condition. Subsequently, they started to imagine the action in time with the 1-Hz auditory metronome. The following instruction was given before each imagination trial: *“Please close your eyes and imagine the index finger movement and what it would feel like!”* Participants performed a total of 12 training trials (six high force, six minimal force) and rated their vividness of imagery for each trial on a 5-point scale taken from the VMIQ-2.

During the experiment, participants were seated in a comfortable chair in front of a computer screen with support for their right arm and hand. This support was necessary to ensure participants remained comfortable

with their hand in a pronated position throughout the experiment. Each condition consisted of 30 trials with pseudo-randomized single- or paired-pulse TMS (15 trials each). A catchphrase was used to give the instruction for each block. All trials in each condition started with a fixation cross. This was displayed for 1 s on the screen before the tones were presented and the corresponding task started. Visual stimuli were generated with Cogent 2000 Graphics (http://www.vislab.ucl.ac.uk/cogent_2000.php) running in MATLAB 7.5. Trials of 10-s duration were carried out with single- or paired-pulse TMS delivered 50 ms before the sixth metronome sound according to the occurrence of FDI contraction either in the imagery or the observation task (Stinear et al., 2006). Vividness of imagery scores were requested for all trials in the IHF and the IMF condition. The timing of the stimuli for all conditions is illustrated in Fig. 1.

Electromyography (EMG)

Surface EMG was recorded from the FDI of the right hand as the movement-relevant muscle and the abductor digiti minimi (ADM) as a control using a pair of 24-mm diameter disposable Ag–AgCl electrodes following standard skin preparation techniques. The EMG signal was amplified, band-pass filtered between 30 and 1 kHz (Grass P511 isolated amplifier), sampled at 2000 Hz, and stored on a computer. The auditory tones guiding the timing of the imagined action were time locked to the EMG signal and also sampled at 2000 Hz.

TMS

Single- and paired-pulse transcranial magnetic stimuli were delivered using two Magstim 200 stimulators through a BiStim module (Magstim Whitland, Dyfed, UK) via a figure-of-eight coil (outer diameter of each wing 85 mm). The coil was positioned over the left M1 at the optimal site for producing responses in the right FDI muscle. This site was marked to ensure consistent coil placement. The coil was held tangential to the scalp with the handle pointing backward and laterally at approximately 45° from the midline. Resting motor

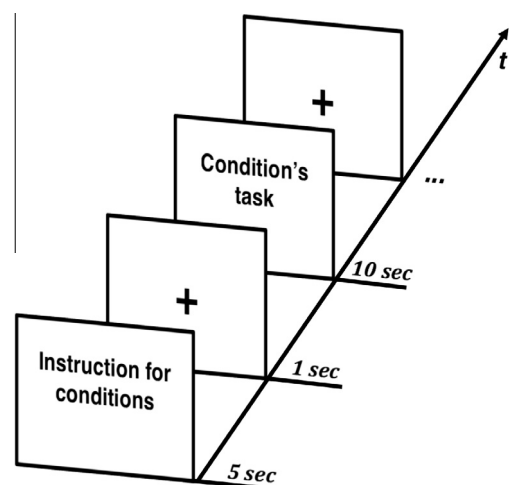


Fig. 1. Temporal structure. Timing of the stimuli for all conditions.

threshold (rMT) was defined by the lowest stimulation intensity that could reliably elicit a peak-to-peak MEP of ~ 0.05 mV in the FDI muscle (agonist in imagery and observation conditions). During the experiment, participants were stimulated with an intensity of 120% of rMT for single-pulse TMS. The inter pulse interval (IPI) for paired-pulse stimulation was 12 ms (Marinovic et al., 2014). The test stimulus was set at 120% of rMT and the intensity of the conditioning stimuli at 70% of rMT.

Data analysis

We visually inspected the MEPs and discarded trials (6.9%) in which any sign of increased background EMG activity occurred within the 400 ms prior to the test pulse. Mean peak-to-peak MEP amplitudes (mV) of FDI and ADM muscles were determined for each participant under each condition. A repeated measures analysis of variance (ANOVA) was used to determine effects of imagery conditions (IHF, IMF, IC) for a single-pulse TMS. A Tukey's honestly significant difference test ($p > 0.05$) was conducted post hoc to determine the locus of significant differences involving more than two means.

Increases in CSE for the experimental observation task OBS compared to the VC condition were examined with t tests. ICF was examined across the ratio between single- and paired-pulse TMS for FDI and ADM. Therefore, t tests were used to determine effects of the IHF, the IMF and the OBS condition.

RESULTS

Motor imagery vividness

Average scores on the VMIQ-2 ranged from 1.17 to 4.58 ($M = 1.98$, $SD = 0.95$) for the kinesthetic imagery section, from 1.25 to 4.75 ($M = 2.2$, $SD = 0.92$) for the internal visual imagery section, and from 1.17 to 4.83 ($M = 2.42$, $SD = 1.14$) for the external visual imagery section on a scale from 1 (*perfectly clear and vivid as*

normal vision) to 5 (*no image at all, you only know that you are thinking of the skill*). The results for the kinesthetic imagery section showed that participants had very good to good imagery abilities. This was supported by the participants' average scores on imagery vividness ($M = 2.0$, $SD = 0.69$) during the training session.

Statistical analyses of the imagery vividness scores during the experiment revealed a significant difference between the IHF and IMF condition, $t(10) = 2.39$, $p < 0.05$, with higher imagery scores for IHF, $M_{IHF} = 1.82$ ($SD = 0.75$) and $M_{IMF} = 2.18$ ($SD = 0.41$). Both mean scores revealed good to very good subjective self-evaluation of imagery performance during the experiment. According to the vividness scale of the VMIQ-2 (Roberts et al., 2008) each task was imagined about as "clear and reasonably vivid" as the other.

CSE for experimental conditions

A repeated measures ANOVA for MEP amplitudes in FDI of the imagery conditions (IHF, IMF, IC) revealed a significant main effect in CSE, $F(2,20) = 15.45$, $p < 0.001$. The post hoc test showed that IHF had higher mean peak-to-peak MEP amplitudes in comparison to the IMF and IC conditions (IHF vs. IMF: $p < 0.01$, IHF vs. IC: $p < 0.001$). Results of the t tests for the observation conditions (OBS, VC) showed a similar pattern. Mean peak-to-peak MEP amplitudes of OBS were significantly higher in comparison to VC, $t(10) = 1.92$, $p < 0.05$. A comparison of the imagery (IHF, IMF) and observation (OBS) conditions with t tests showed a significant difference for IHF versus OBS, $t(10) = 3.19$, $p < 0.01$, but not for IMF versus OBS, $t(10) = 0.047$, $p = 0.48$. MEPs for imagery and observation conditions for one representative participant are represented in Fig. 2A, B. Group mean MEP amplitudes for all conditions are depicted in Fig. 3. Tests of the ICF ratios across the imagery (IHF, IMF)

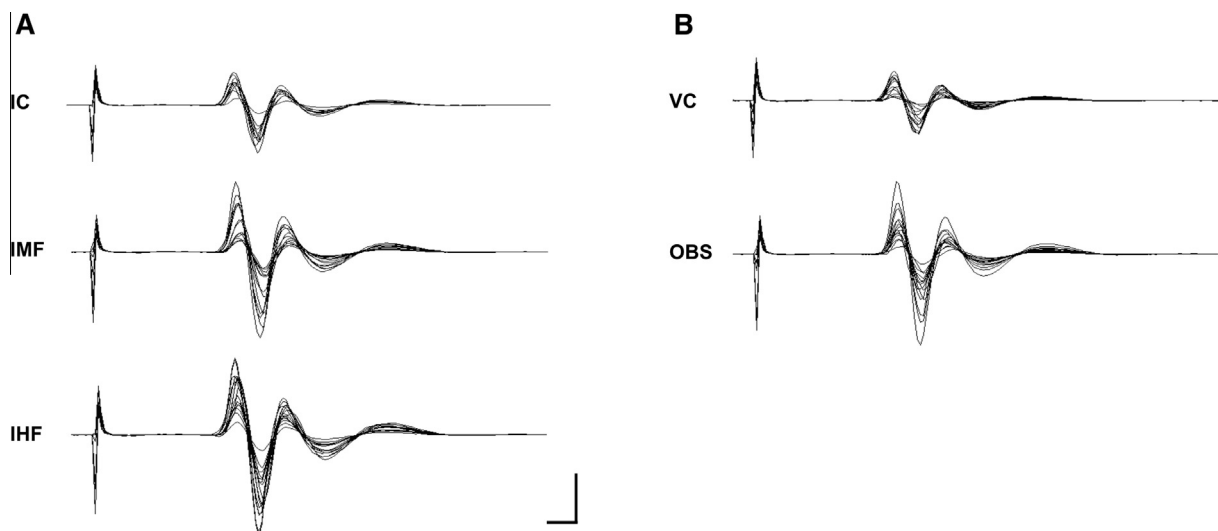


Fig. 2. Representative result pattern. Motor-evoked potentials recorded in FDI muscle for a representative subject (15 MEPs superimposed per condition) for imagery conditions (A) and observation conditions (B) during single-pulse TMS. IC = imagery control, IMF = imagery minimal force, IHF = Imagery high force, VC = visual control, OBS = movement observation. Calibration bar: 1 mV, 10 ms.

and observation (OBS) conditions revealed a significant effect only for the IHF condition: IHF, $t(10) = 3.11$, $p < 0.012$, IMF, $t(10) = 1.13$, $p = 0.28$, OBS, $t(10) = 2.0$, $p = 0.07$. In contrast, for the ADM muscle, we found no evidence of differences in MEP amplitudes among conditions for single-pulse TMS in the imagery conditions, $F(2,20) = 0.34$, $p = 0.72$, and the OBS condition, $t(10) = 0.9$, $p = 0.2$.

To make sure differences in MEP amplitudes found for the FDI muscle were not a result of larger background EMG in the IHF and OBS condition, we compared the RMS error of the EMG signal for 400 ms prior to the TMS pulse. The repeated measures ANOVA for pretrigger background EMG revealed no significant main effect among experimental conditions, $F(4,40) = 2.14$, $p = 0.094$. Moreover, the background EMG levels observed in all conditions were well within normal background activity at rest.

DISCUSSION

The present study used TMS to investigate changes in CSE of M1 during motor imagery and action observation of repetitive finger movements (dynamic force production) with different force requirements. The use of a “conservative strategy” for the selection of control conditions allows an interpretation of the present results as movement specific effects. In general, results replicate previous findings showing an increased CSE in the target muscle (FDI) during both the imagery and observation of human hand movements (Fadiga et al., 1999; Clark et al., 2003; Vargas et al., 2004; Stinear et al., 2006; Alaerts et al., 2009; Bianco et al., 2012). Our main findings are as follows: First, the CSE during imagery of a repetitive finger abduction/adduction movement depends on the imagined effort of the movement. Second, the CSE during observation of the same movement is increased in comparison to the VC condition. Third, the imagery and observation conditions differ only when the imagery high force condition is compared with the OBS condition.

Our results indicate that the modulation of CSE in M1 during motor imagery and action observation resembles the changes of cortical excitability occurring during motor execution. This underpins the notion that S states are a covert stage of an action and its characteristics. Furthermore, our data suggest that the functional characteristics differ to some extent between the different S states, because there is a detectable difference in M1 excitability between the IHF and the OBS condition. However, it should be noted that the main focus of the present study was not on comparing the impact of different force requirements for imagery and observation. Further studies will have to clarify the functional commonalities and differences between motor imagery and action observation with respect to M1 excitability. The following sections will now discuss the present data in detail.

The effect of movement effort on CSE

One central assumption of action simulation theory in neural terms is the similarity between the state in which an action is merely simulated (i.e., an S state) and the execution of that action. Within this framework, the present results demonstrate a force-dependent cortical excitability increase during motor imagery resembling the increasing M1 activity related to the level of contractile force demonstrated for movement execution in several studies involving animals (Evarts, 1968) and humans (Dai et al., 2001). Such increased neural activation is not reported exclusively for M1 or S1, but also for supplementary motor area (SMA), pontine micturition center (PMC), parietal areas, and the cerebellum in humans (Dai et al., 2001).

Until now, few studies have used isometric force production tasks to examine cortical excitability changes when a movement with different force levels is being imagined (e.g., Park and Li, 2011; Mizuguchi et al., 2013). For example, Mizuguchi and colleagues (2013) found significant force-dependent differences in MI for an isometric elbow flexion force production task. This is

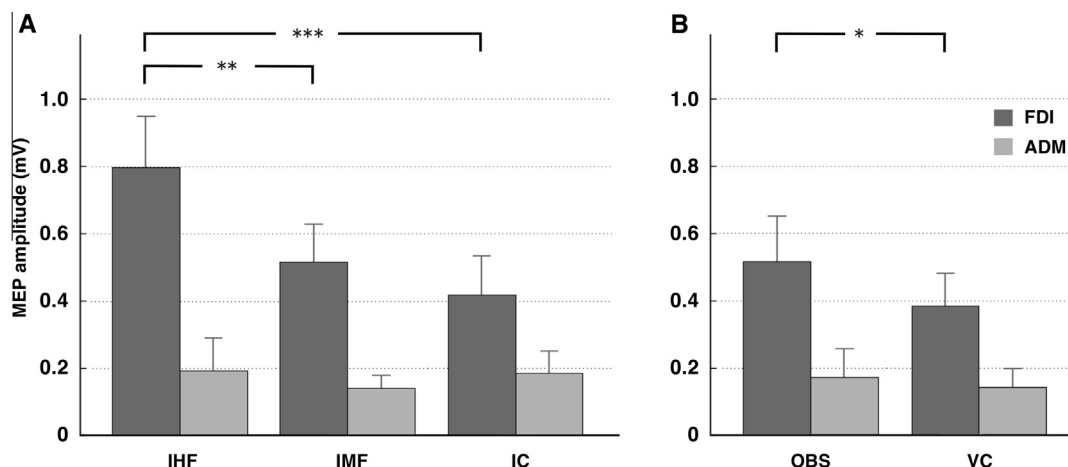


Fig. 3. Average amplitude values. Mean peak-to-peak amplitude values recorded in FDI and ADM muscle for single-pulse TMS for imagery conditions (A) and observation conditions (B). IC = imagery control, IMF = imagery minimal force, IHF = imagery high force, VC = visual control, OBS = movement observation. Error bars represent SE of the group mean.

in line with our results for a dynamic force production task. They underpin the notion that imagining a movement with a higher force level recruits more output- and interneurons in M1, and this triggers stronger MEPs in the target muscle (Reis et al., 2008). This assumption underlines the well-established concept that force is generated in cortical areas (Yue and Cole, 1992; Carroll et al., 2006; Lee and Carroll, 2007). Because the present study did not use isometric force production tasks (Park and Li, 2011; Mizuguchi et al., 2013), it further clarifies questions on the mental simulation of different movement characteristics by applying a dynamic movement with different force levels and a specific movement trajectory.

Research on the observation of actions has shown that humans are able to recognize the effort of a model that is displayed by only the kinematics of a few joints depicted as a point-light display, for example, when lifting objects of different weights (Runeson and Frykholm, 1981; Bingham, 1987). TMS studies on movement observation have shown that the observed movement-related effort modulates CSE in a transitive reach-grasp-lifting task (Alaerts et al., 2010, 2012). Within this framework, we found a significant difference between the observation of an effort-related movement and a VC condition. This confirms a general effect of CSE for action observation (Strafella and Paus, 2000; Maeda et al., 2002). Furthermore and more importantly, we compared the CSE associated with the motor imagery of movements at different force levels with the observation of

the high-force-level condition. We found that the mean MEP values of the OBS condition were similar to the MEP values of the IMF condition. These results are in line with Bianco et al. (2012) who report a stronger excitability for motor imagery compared to movement observation. This clearly shows that motor imagery and action observation differ to some extent with regard to increased CSE despite their assumed functional equivalence (Lorey et al., 2013). Conceptually, it could be stated that motor imagery and action observation are distinct processes in the framework of action simulation that pursue different underlying goals and intentions. For motor imagery, it has been reasoned that it is a motor preparation-like process generated internally and built up by specific motor representations with the aim of predicting a precise image of the movement and its characteristics (Lorey et al., 2010, 2013) – especially when participants are instructed to imagine movements kinesthetically. However, considering the process of action observation, it springs to mind that observation is first and foremost driven by external stimulation with the aim of understanding the observed action. In the present experiment, we used a simple, intransitive, and repetitive movement with no explicit modulated intention or object manipulation. This could be one reason for the differences in M1 excitability during imagery and observation of the same force requirement. A second reason for the observed differences between imagery and observation might be the characteristics of the present motor task. More precisely, we used a

Table 1. Average MEP amplitudes. Mean peak-to-peak amplitude values in mV for single-pulse and paired-pulse TMS for each individual participant. IC = imagery control, IMF = imagery minimal force, IHF = imagery high force, VC = visual control, OBS = movement observation

Participant	IHF		IMF		IC		OBS		VC	
	Single Mean (SD)	Paired Mean (SD)	Single Mean (SD)	Paired Mean (SD)	Single Mean (SD)	Paired Mean (SD)	Single Mean (SD)	Paired Mean (SD)	Single Mean (SD)	Paired Mean (SD)
S01	0.170 (0.11)	0.185 (0.07)	0.028 (0.04)	0.010 (0.02)	0.013 (0.01)	0.014 (0.01)	0.118 (0.14)	0.122 (0.14)	0.065 (0.07)	0.094 (0.10)
S02	0.575 (0.17)	0.644 (0.09)	0.507 (0.16)	0.652 (0.12)	0.313 (0.19)	0.452 (0.10)	0.545 (0.07)	0.565 (0.05)	0.433 (0.07)	0.459 (0.14)
S03	0.735 (0.40)	0.771 (0.44)	0.686 (0.61)	0.739 (0.60)	0.543 (0.18)	0.508 (0.25)	0.351 (0.15)	0.483 (0.25)	0.567 (0.29)	0.546 (0.26)
S04	0.254 (0.12)	0.287 (0.15)	0.228 (0.15)	0.243 (0.13)	0.099 (0.07)	0.109 (0.05)	0.169 (0.08)	0.204 (0.12)	0.081 (0.04)	0.099 (0.05)
S05	0.481 (0.26)	0.652 (0.27)	0.347 (0.26)	0.365 (0.28)	0.028 (0.02)	0.053 (0.04)	0.057 (0.04)	0.069 (0.04)	0.103 (0.11)	0.081 (0.07)
S06	1.102 (0.97)	0.983 (0.84)	0.289 (0.27)	0.385 (0.57)	0.152 (0.06)	0.233 (0.17)	0.118 (0.07)	0.193 (0.15)	0.104 (0.06)	0.137 (0.09)
S07	1.032 (0.76)	1.185 (0.76)	0.724 (0.65)	0.581 (0.61)	0.790 (0.60)	1.287 (1.28)	1.082 (1.10)	0.705 (0.61)	1.025 (1.03)	0.470 (0.47)
S08	1.010 (0.96)	1.289 (1.17)	0.649 (1.15)	0.675 (0.41)	0.524 (0.53)	0.795 (0.61)	0.771 (1.00)	0.907 (1.12)	0.349 (0.21)	0.710 (0.60)
S09	0.327 (0.27)	0.561 (0.31)	0.097 (0.08)	0.231 (0.16)	0.097 (0.08)	0.198 (0.14)	0.194 (0.29)	0.219 (0.20)	0.127 (0.16)	0.405 (0.37)
S10	1.226 (0.79)	1.512 (0.76)	0.860 (0.53)	1.185 (0.92)	1.057 (0.76)	1.262 (0.90)	0.896 (0.75)	1.070 (0.78)	0.606 (0.37)	0.822 (0.53)
S11	1.852 (0.76)	2.147 (0.72)	1.268 (0.84)	1.347 (0.61)	0.975 (0.48)	1.126 (0.59)	1.352 (0.88)	1.314 (0.64)	0.761 (0.48)	0.859 (0.40)
Mean	0.797 (0.51)	0.929 (0.51)	0.517 (0.43)	0.583 (0.40)	0.417 (0.27)	0.549 (0.38)	0.514 (0.41)	0.532 (0.37)	0.384 (0.26)	0.426 (0.28)

repetitive finger movement task. It is obvious that differences in effort are more visible in movements such as weight lifting that display changes in movement kinematics more obviously than repetitive finger moving tasks that change only with respect to movement effort. This line of reasoning is supported by the finding that effortful whole-body gymnastic movements reveal similar neural activation in M1 for motor imagery and action observation (Munzert et al., 2008).

Increased MEPs – a result of cortical or spinal facilitation

As stated above, a central issue in the discussion of increased MEPs is whether they result from increased cortical and/or spinal facilitation. Within this framework, Reis et al. (2008) demonstrated that increased MEPs reflect both cortical and spinal excitability. Thus, the present effects of motor imagery might also be caused on a spinal level. Our results on paired-pulse TMS (see Table 1) showed a significant proportion of ICF in the IHF condition for the target muscle FDI. It has been stated that the effect of ICF might be due to the facilitation of M1 output and M1 interneurons (Hallett, 2007; Reis et al., 2008; Di Lazzaro and Ziemann, 2013). Therefore, ICF in particular provides a general explanation for cortical proportions of corticospinal facilitation even when the essential mechanism for ICF has yet to be fully understood (Di Lazzaro and Ziemann, 2013).

Clinical implications

A broad body of literature underpins the notion that motor imagery techniques might well become powerful tools for neurological rehabilitation processes (cf. Lotze and Cohen, 2006; Lotze and Halsband, 2006; Mulder, 2007) as well as motor skill learning (cf. Feltz and Landers, 1983; Fansler, 1985; Linden, 1989; Yue and Cole, 1992; Munzert et al., 2009) by inducing plastic changes in M1 (Pascual-Leone et al., 1995; Debarnot et al., 2011). Within this framework, the present data revealed that CSE, ICF, and subjective imagery scores were increased in the IHF compared to IMF condition. These data highlight that the subjective data are related to their objectives. Such a similar relationship has been demonstrated for fMRI data. (Lorey and colleagues, 2011) showed that the perceived vividness of motor imagery is parametrically associated with neural activity within motor and sensorimotor areas. Despite this relationship, it is difficult to assume a causal link between neural activation and the subjective measurements. Our results showed that motor imagery of effortful movements is perceived more easily than movements with lower effort due to the higher kinesthetic sensations that are also present during internal simulations (Stinear et al., 2006; Roberts et al., 2008; Munzert et al., 2009). For instance, Stinear et al.'s (2006) imagery study demonstrated that kinesthetic but not visual imagery modulates the CSE of M1. Against this background, these and the present results suggest that it is especially motor imagery of movements with high effort that might be useful in the context of training and neurorehabilitation.

Conclusions

The present data revealed that modifications of motor parameters such as force requirements modulate CSE and ICF in a specific target muscle during motor imagery of an intransitive repetitive movement (dynamic force production). The effects for action observation were smaller, but also showed significant differences compared to a VC condition. The present data support the notion of a functional equivalence between the execution of action and S states such as motor imagery and action observation. These data also revealed differences between the different processes states. Turning to the embedding of motor imagery in an applied context such as athletic training or neurological rehabilitation, we consider that there are strong indications for using motor imagery of movements involving an increased effort because it is particularly the imagination of effortful movements that reveals an impact on M1 excitability.

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