Mental rotation strategies reflected in event-related (de)synchronization of alpha and mu power

ARJAN C. TER HORST,[a,b] ROB VAN LIER,[a] AND BERT STEENBERGEN[b]

[a]Radboud University Nijmegen, Donders Institute for Brain, Cognition and Behaviour, Nijmegen, The Netherlands
[b]Radboud University Nijmegen, Behavioural Science Institute, Nijmegen, The Netherlands

Abstract

During a mental rotation task of hands, participants mentally rotate their hand into the orientation of the shown hand. These mental movements are subject to the body's biomechanical constraints. In this study, we investigated whether the involvement of motor processes during the mental rotation process, as reflected in mu-power desynchronization, is also influenced by one's movement capabilities. We performed an EEG study and used a delayed response mental rotation task of hands to examine the event-related desynchronization differences between movements that are biomechanically easy and difficult to perform. Our results show an increase in event-related desynchronization of the mu power for biomechanically easy compared to difficult-to-adopt postures. These findings provide further evidence for the notion that motor simulations can only be performed for movements that can already be performed overtly.

Descriptors: Mental rotation, Motor imagery, EEG, Event-related desynchronization, Event-related synchronization

During a mental rotation task, participants mentally rotate a shown stimulus, for example, a hand, in order to judge whether that stimulus is a left or a right hand. During the mental rotation of hands, participants typically imagine moving their own hand into the orientation of the shown stimulus in order to judge its laterality (Parsons, 1987, 1994; Sekiyama, 1982, 1987). The participant's performance during a mental rotation task of hands is influenced by one's own body posture (de Lange, Hagoort, & Toni, 2005; de Lange, Helmich, & Toni, 2006; Helmich, de Lange, Bloem, & Toni, 2007; Ionta & Blanke, 2009; Ionta, Fourkas, Fiorio, & Agliotti, 2007; Sirigu & Duhamel, 2001), movement constrictions (i.e., biomechanical constraints) (Parsons, 1987, 1994; ter Horst, van Lier, & Steenbergen, 2010, 2011; Tomasino & Rumiati, 2004), and pathologies related to the motor system (de Lange, Roelofs, & Toni, 2008; Funk & Brugger, 2008; Harris, Harris, & Caine, 2002; Helmich et al., 2007; Lust, Geuze, Wijers, & Wilson, 2006; Moseley et al., 2008; Mutsaarts, Steenbergen, & Bekkering, 2007; Nico, Daprati, Rigal, Parsons, & Sirigu, 2004; Sirigu & Duhamel, 2001; ter Horst, Cole, van Lier, & Steenbergen, 2012). These findings exemplify the embodied nature of the mental process during the mental rotation task of hands. This process is also referred to as motor imagery (MI). During MI, an action is internally simulated including the kinesthetic sensations but without the overt movement part (Decety, 1996a, 1996b; Guillot & Collet, 2010; Jeannerod, 1994). As stated in the simulation theory (Jeannerod, 2001), MI is similar to actual movements and has been shown to activate similar neuronal processes as actual movement (Jeannerod, 1994, 2001; see, for review, Jeannerod, 2006). In contrast to motor imagery, visual imagery (VI) encompasses mental visual transformations of (non-)corporeal objects without a kinesthetic sensation (Guillot & Collet, 2010). Consequently, VI is not subject to biomechanical constraints or postural changes (de Lange et al., 2005).

The influences of the biomechanical constraints on the mental rotation of hands has been studied extensively on a behavioral level by Parsons (1987, 1994). It was shown that participants are faster in judging the laterality of hands oriented in anatomically easier-to-adopt postures (i.e., medial rotations) than more difficult-to-adopt postures (i.e., lateral rotations). Medial and lateral rotations are hands rotated towards and away from the body's midsagittal plane, respectively, see Figure 1. The influence of biomechanical constraints on the mental rotation process is seen as evidence for the use of MI (Parsons, 1987, 1994; ter Horst, Jongsma, Janssen, van Lier, & Steenbergen, 2012; ter Horst et al., 2010, 2011). Parsons (1987) scrutinized the influence of the biomechanical constraints on the mental movements by showing that participants are likely to use different mental movement paths for internally rotating one's hands medially or laterally. The selection of a movement path is based on anatomically induced movement constraints. Medial rotations, especially when rotating one's hand with the palm in view, are biomechanically easy to perform. In contrast, lateral rotations are biomechanically difficult or even impossible to perform. From the literature, it is already known that experience with performing a movement is mandatory to be able to internally simulate that movement (Munzert, Lorey, & Zentgraf, 2009). Consequently, for medial rotations, it is likely that the corresponding motor simulations can be performed. For lateral rotations, on the other hand, experience with the movement is lacking, and hence it is unlikely that an accompanying motor simulation can be performed. The

Address correspondence to: Arjan C. ter Horst, Radboud University Nijmegen, Donders Institute for Brain, Cognition, and Behaviour, Centre for Cognition, P.O. Box 9104, 6500 HE Nijmegen, The Netherlands. E-mail: a.terhorst@donders.ru.nl
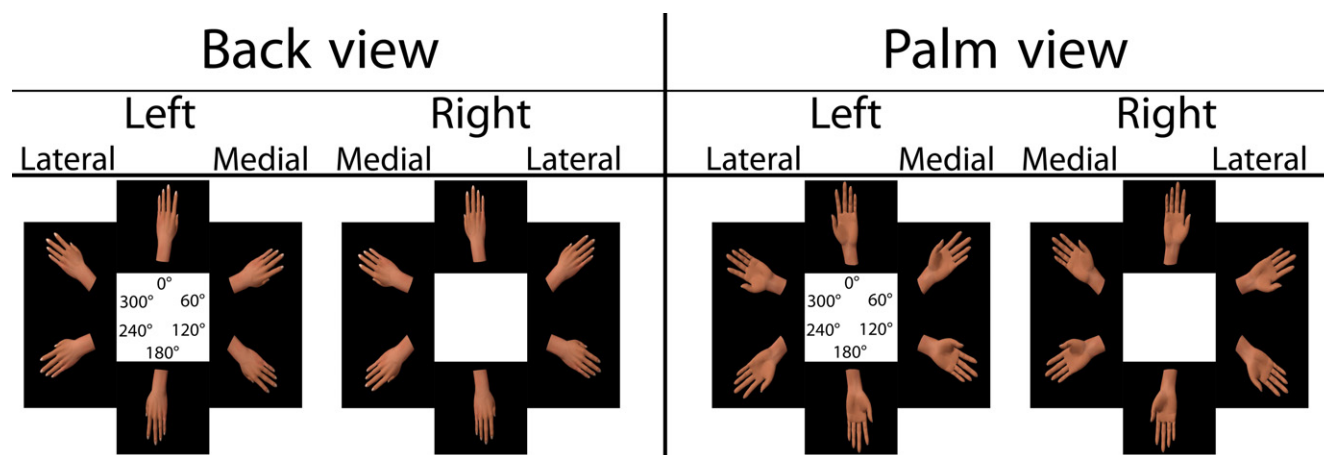
Figure 1. Stimuli used in the experiment.

latter is in line with recent findings from our lab (ter Horst, Jongsma et al., 2012). We found a remarkable resemblance between the mental rotation of laterally rotated hands and noncorporeal objects, typically inducing VI (de Lange et al., 2005), in both behavioral and electrophysiological tests.

In the current study, we explore the possible differential involvement of motor processes between mentally rotating one's hand laterally and medially. That is, for laterally, but not medially, rotated hands, the mental rotation process might rely more on VI than on MI. This is also intuitively feasible as lateral rotations are difficult to perform and, as such, a visual strategy might be more efficient. We used electroencephalography (EEG) to measure oscillatory power in the upper alpha frequency range to study MI and VI engagement during the mental rotation of hands. We did so by obtaining event-related synchronization (ERS) and event-related desynchronization (ERD) in the upper alpha frequency range at an individual level, as the exact range of the individual alpha frequency is highly subject specific (Klimesch, 1999). ERD/ERS in the upper alpha frequency range has been shown to exert a higher spatial focus than lower alpha ERD/ERS. Furthermore, changes in upper alpha power are less sensitive to general cognitive demands as attention processes compared to changes in lower alpha ERD/ERS (Klimesch, 1997, 1999; Studer, Koeneke, Blum, & Jancke, 2010). The use of EEG provides an excellent opportunity to distinctively investigate the contributions of visual and motor processes during mental rotation. In particular, EEG power in the upper alpha frequency range at occipital and central electrode sites was shown to provide a valid measure to uncover the relationship between the task and the involvement of visual and motor processes, respectively (Neuper, Scherer, Reiner, & Pfurtscheller, 2005; Pfurtscheller, Brunner, Schlogl, & Lopes da Silva, 2006; Pfurtscheller & Neuper, 1997; Pfurtscheller, Neuper, Andrew, & Edlinger, 1997; Pineda, 2005; van der Helden, van Schie, & Rombouts, 2010). We refer to oscillatory power in the upper alpha frequency range at occipital and central electrode sites as alpha power and mu power, respectively. In the literature, there is an abundance of evidence showing the relation between mu-power ERD and the involvement of motor processes during action execution, action observation, and imagined actions (see, for review, Pineda, 2005). By the same token, it has been shown that the alpha rhythm, which is strongest over occipital electrode sites, desynchronizes during tasks that require visual attention, such as a mental rotation task of noncorporeal objects (Michel, Kaufman, & Williamson, 1994). Measuring ERD/ERS in the upper alpha frequency range enables us to study possible differences in the involvement of motor processes between imagined lateral and medial hand rotations. We used a similar mental rotation task of hands as in ter Horst, Jongsma et al. (2012), but now with a delayed response to prevent potential confounding of motor preparations on the mu-power ERD.

To test our hypothesis, we calculated the ERD/ERS in the alpha frequency range at both central and occipital electrode sites for laterally and medially rotated hand stimuli, reflecting the involvement of MI and VI processes, respectively. We expected to find a stronger ERD for medial rotations than for lateral rotations at central electrode sites as medial rotations are biomechanically possible to perform, whereas lateral rotations require more awkward and biomechanically difficult-to-perform (mental) movements. This would reflect a stronger involvement of motor processes in biomechanically easy than in biomechanically difficult-to-perform (mental) movements. Furthermore, we did not expect to find differences in alpha-power ERD at occipital electrodes between medially and laterally rotated hands as MI encompasses VI (de Lange et al., 2005), at least partly (Pelgrims, Andres, & Olivier, 2009).

Method

Participants

Seventeen healthy individuals participated in the experiment after written informed consent was acquired. All participants had normal or corrected-to-normal vision and were right-handed. Right hand preference was found in all participants (laterality quotient $M = 94.2$, $SD = 11.8$). None of the participants reported a history of neurological or psychiatric disorders. Due to incorrect task compliance, the data of one participant was excluded from further analyses. Data of the remaining sixteen participants (two male) aged 18–22 years ($M = 19.6$, $SD = 1.31$) were used for analysis. The study was approved by the local ethics committee, in accordance with the Helsinki Declaration.

Stimuli

We used a custom made 3D hand model designed in a 3D image software package (Autodesk Maya 2009, USA). From this realistic

model, we constructed all stimuli that were used in the experiments. Both back and palm view stimuli were shown of left and right hands. These stimuli were presented in six different orientations, starting at 0° (fingers pointing up) and rotated clockwise to 60°, 120°, 180°, 240°, and 300°, yielding a total of 24 different stimuli, see Figure 1. All stimuli were displayed on a 19" LCD computer screen, at a distance of approximately 60 cm from the participants' eyes, resulting in a vertical visual angle of approximately 6° with the fingers pointing up.

Experimental Procedure

A hand laterality judgment task was used to implicitly evoke MI (de Lange et al., 2008; ter Horst et al., 2010). Participants had to decide whether a given stimulus was a left or right hand by pressing one of two buttons with their index fingers and were instructed to do so as accurately and quickly as possible. The participants had to press one of the two buttons situated on the left and right, for the laterality judgment. No instructions on possible strategy use were given. The experiment consisted of five consecutive blocks of 54 trials each. We presented back and palm view hand stimuli in a 1 : 8 ratio. Unique conditions of palm view stimuli were repeated 20 times (i.e., 20 repetitions per unique stimulus). Back view stimuli served as filler trials. Stimuli were shown sequentially by custom developed software in the Presentation software package (Neurobehavioral Systems, Albany, USA). The angle of rotation, view, and side of the stimuli were randomized and counterbalanced for every block and over subjects. A trial started with the presentation of a black screen for 2,000 ms, followed by a white fixation cross that was presented on a black background randomly between 1,000 ms and 1,200 ms. After the fixation cross disappeared, a hand stimulus was presented. The participants were instructed to withhold their response until one of the two possible response screens was presented after 2,000 ms. The response screens were replaced by a new black screen for the next trial after a response was given, see Figure 2. The response screens consisted of the words "left" and "right" (in that order) in 50% of the trials or "right" and "left" in the other 50% of the trials, see Figure 2. The participants were

instructed to press the button corresponding to the side of the word which they thought represented the laterality of the shown hand stimulus. For example, when participants thought that a left hand was shown, they had to press the left button when the upper response screen in Figure 2 was visible. When the lower response screen in Figure 2 was presented, the participant had to press the right button. The participants used their left and right hand for the left and right button, respectively.

Participants were seated in a sound-shielded room in front of a computer screen. They were asked not to make eye movements or eye blinks during the presentation of the fixation cross and hand stimuli, but to consistently blink a few times immediately after a response was given. In between blocks, participants could rest. The EEG signals, reaction times, and judgments (left/right) were recorded. The actual blocks were preceded by a 24-stimuli test block to familiarize the subject with the task.

EEG Recordings

EEG signals were recorded with a 64-channel ActiCap (MedCaT B.V., the Netherlands) according to the International 10–20 system, on a computer running Brain Vision Recorder, and were amplified by two 32-channel BrainAmp DC EEG amplifiers. A ground electrode was placed over AFz, and all electrodes were referenced to the left mastoid online and rereferenced offline to linked mastoids. Electrode impedance was kept below 5 kΩ. The signal was digitized at 500 Hz and filtered online between 0.016 Hz (i.e., 10-s time constant) and 250 Hz. Horizontal and vertical electrooculograms (EOG) were recorded from the remaining three electrodes, placed on the outer canthi and below the right eye.

Data Analysis

Offline processing of the EEG data was conducted in BrainVision Analyzer version 1.05 (Brain Products GmbH, Munich). Only data corresponding to correct palm view trials were analyzed. We focused on palm view stimuli as these exhibit the most pronounced differences in mental movement paths between lateral and medial
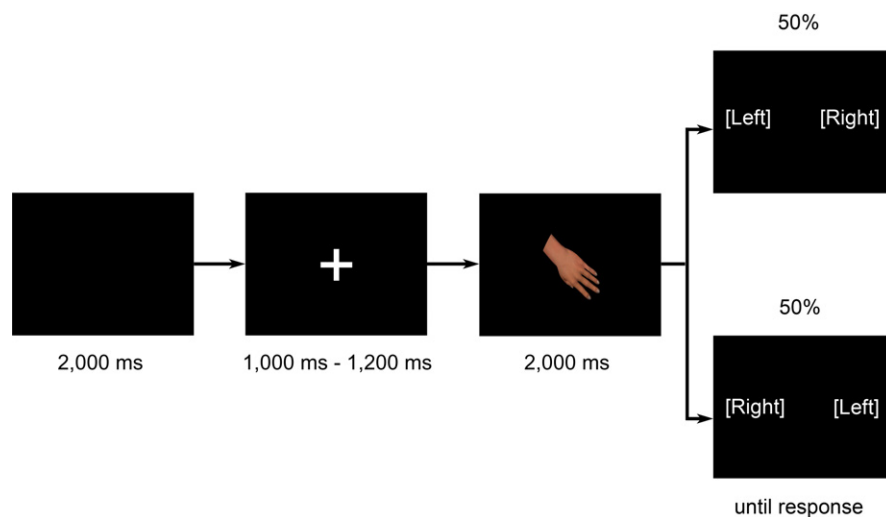
Figure 2. Sequence of events during the experiment. First, a black screen was presented for 2,000 ms, after which a fixation cross was presented between 1,000 and 1,200 ms. After the fixation cross, a stimulus was presented for 2,000 ms. Participants were instructed not to respond until one of the two response screens appeared. In 50% of the trials, the upper response screen was shown, and in the other 50% of the trials, the lower response screen was shown. Participants had to press the button at the same side as the word describing the correct laterality of the shown stimulus.
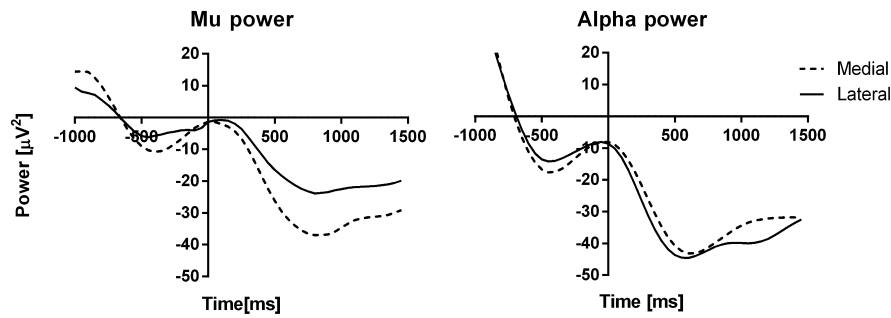
Figure 3. Grand averages of alpha and mu power as function of time for all ROIs.

rotations (Parsons, 1987; ter Horst, Jongsma et al., 2012). Trials with movement artifacts were excluded from analyses on the basis of careful visual inspection of the raw data. Trials with ocular artifacts during the presentation of the fixation cross or hand stimuli were also excluded from further analyses.

Individual upper alpha frequency bands were determined by first denoting the dominant individual alpha frequency (IAF) between 8 and 12 Hz. The lower and upper bound of the individual upper alpha band was set at the IAF and IAF + 2 Hz, respectively (Klimesch, 1999). Consequently, the quantification of ERD/ERS was performed in four steps (Pfurtscheller & Lopes da Silva, 1999). We first applied an individual band-pass filter in the upper alpha frequency range, after which we determined the power by squaring and averaging over the trials. Averages were calculated for lateral and medial rotations. Laterally rotated stimuli consisted of 60° and 120° rotated right hand stimuli and 240° and 300° rotated left hand stimuli. Medially rotated hand stimuli consisted of 240° and 300° rotated right hand stimuli and 60° and 120° rotated left hand stimuli, see Figure 1. In the following, we will refer to this distinction between lateral and medial rotations as direction of rotation (DOR). The ERD/ERS was expressed as percentage power decrease (ERD) and increase (ERS) with respect to a 1,000-ms reference interval prior to stimulus onset (Pfurtscheller et al., 2006; Pfurtscheller & Lopes da Silva, 1999).

For statistical analyses, bilateral regions of interest (ROI) were identified for alpha power (PO7, PO3, and O1; PO8, PO4, and O2) and mu power (C5, C3, and C1; C6, C4, and C2). In the literature, mu- and alpha-power ERD/ERS has been shown to be most pro-nounced over central and occipital electrode sites, respectively (Pfurtscheller & Neuper, 1997; Pfurtscheller et al., 1997; van der Helden et al., 2010). Furthermore, we focused our analyses on the time interval between 300 and 800 ms poststimulus onset. This time interval has been shown to specifically reflect the mental rotation process itself (Heil, 2002; Heil & Rolke, 2002; Milivojevic, Hamm, & Corballis, 2009; Overney, Michel, Harris, & Pegna, 2005; Tao et al., 2009; ter Horst, Jongsma et al., 2012; Thayer & Johnson, 2006; Thayer, Johnson, Corballis, & Hamm, 2001).

Amplitudes averaged over the electrodes within the ROIs were analyzed in a repeated measures analysis of variance (ANOVA) with the factors DOR, location, and hemisphere; with 2 levels for DOR (lateral, medial), 2 levels for location (central, occipital) and 2 levels for hemisphere (left, right). Threshold level was set at $p = 0.05$, and Bonferroni correction was applied when appropriate.

Results

The amount of erroneous responses for all participants consisted of 7.3% of all trials. The grand average mu and alpha ERD/ERS over all ROIs are shown in Figure 3 and 4. The analysis showed a significant main effect of location, $F(1,15) = 24.145$; $p < .001$; $\mu^2 = 0.617$; $\varepsilon = 0.996$. Importantly, the analysis also revealed a significant interaction of DOR by location, $F(1,15) = 10.897$; $p < .005$; $\mu^2 = 0.421$; $\varepsilon = 0.869$. In line with our hypothesis, post hoc analyses revealed a larger ERD for medial than for lateral rotations at the central ROIs, as reflected in a significant DOR
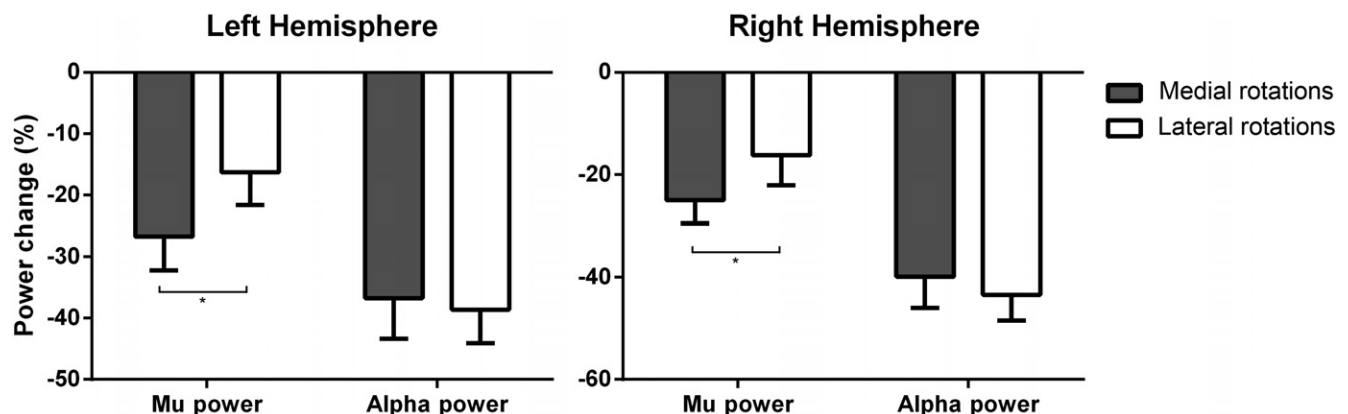

Figure 4. Effects on alpha and mu power. Left graph represents the alpha and mu power for the left hemisphere. The right graph represents the alpha and mu power for the right hemisphere. *significance at the $p < 0.05$ level. Error bars represent the standard error of the mean.

effect, $F(1,15) = 5.091$; $p < .05$; $\mu^2 = 0.253$; $\varepsilon = 0.560$, at the central ROIs. The DOR effect at the occipital locations was not significant ($p > .43$). No other effects were found significant.

Discussion

In the current study, we investigated the possible differential involvement of motor processes between lateral and medial rotations in a hand laterality judgment task. We focused on oscillatory power in the individual upper alpha frequency range (Klimesch, 1999) and found a larger ERD in the mu power at central electrode sites for medial rotations compared to lateral rotations.

Mu-band ERD is shown to reflect the activity of motor processes (Pineda, 2005). Therefore, a larger mu-power ERD during the laterality judgment of medially compared to laterally rotated hands shows that the involvement of motor processes is more pronounced for medial rotations than for lateral rotations. Interestingly, there is also a clear ERD of the mu power for lateral rotations, see Figure 3. Consequently, it is likely that there is also an involvement of motor processes during the laterality judgment of lateral rotations, though not as pronounced as for medial rotations.

The differential involvement of MI between biomechanically easy and more difficult-to-adopt postures begs the question as to how the brain distinguishes between both conditions and how the brain selects the appropriate consecutive strategy. The implicitly induced use of MI is likely to be the key process for distinguishing between the continued use of MI for medially rotated hands and a transition from MI to VI for laterally rotated hands. That is, MI can be seen as a process due to which a selection of the appropriate movement is made in the action-planning process on the basis of the biomechanical constraints (Craje et al., 2010; Johnson, 2000; Mutsaarts et al., 2007). That is, at the start of the laterality judgment process, MI is implicitly induced as a consequence of the presentation of corporeal objects (Parsons, 1994). When medially rotated hands are shown, MI can be used throughout the entire judgment process as the movement falls within the body's movement capabilities. For lateral rotations, however, it is biomechanically possible to rotate one's hand a few degrees, but further lateral rotations are biomechanically complex or even impossible. Consequently, the MI process is likely to be padded with VI. This is in line with our current results as they show that motor processes are involved for lateral rotations, though not as pronounced as for medial rotations. Furthermore, recent studies have shown that early in the laterality judgment process (i.e., around 300 ms poststimulus onset) a distinction is made between medial and lateral rotations (Overney et al., 2005; ter Horst, Jongsma et al., 2012), possibly corresponding to a differential processing of laterally and medially rotated hands.

The transition from MI to VI for lateral rotations might be induced by the time-consuming simulation of complex and awkward lateral rotations, which is inefficient. However, it is more likely that the experience with rotating one's hand laterally plays a crucial role in the use of VI instead of MI. As laterally rotating one's hand is biomechanically difficult or even impossible, it is likely that participants have no proper experience with performing such movements. Consequently, these movements cannot be simulated properly using MI, because having experience with a certain movement is conditional to simulate that movement (Grush, 2004; Mulder, Zijlstra, Zijlstra, & Hochstenbach, 2004).

Recently, a study showed that different cerebral networks are active during imagery of skilled and novel movements (Ionta, Ferretti, Merla, Tartaro, & Romani, 2010). They showed that, for unfamiliar movements, lower level structures such as the basal ganglia are more active than for the imagery of familiar movements for which higher level structures are more active. The novelty of a movement and the biomechanical aspects of that movement are likely to be related. That is, movements that are biomechanically more difficult to perform are not likely to be executed, resulting in a lack of experience with that movement. Whether the observed differences in mu-power ERD between hand rotations in the current study is a result of different cerebral networks being activated cannot be concluded from the current study.

We did not find a difference in alpha-power decrease between both rotational directions. This is in line with the notion that MI (partly) encompasses VI processes (de Lange et al., 2005; Pelgrims et al., 2009). Furthermore, we did obtain a difference in overall ERD in the upper alpha frequency range between occipital and central electrode sites from which the former showed a more profound ERD. This is in line with former literature (e.g. van der Helden et al., 2010).

In conclusion, our findings show that the behavioral and ERP differences between laterally and medially rotated hands are also reflected in nonphase-locked electrophysiology. We found that the use of motor imagery is more pronounced for biomechanically easy-to-adopt postures (i.e., medial rotations) than for biomechanically difficult or even impossible postures (i.e., lateral rotations). Medial rotations are biomechanically possible to perform, and hence MI can be used to simulate this movement. For the lateral rotations, it is likely that there is no experience in rotating one's hands laterally, and hence MI cannot be used to completely simulate this movement. Therefore, VI is likely to be used to complete the lateral mental rotations. This difference reflects the role of MI during movement planning in differentiating between biomechanically possible and impossible movements. Hence, these findings provide further evidence for the embodied nature of MI and show that the involvement of motor processes during imagery rely on movement experience.

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