Different mental rotation strategies reflected in the rotation related negativity

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Abstract

In a mental rotation task of objects, typically, reaction time (RT) increases and the rotation related negativity (RRN) increases in amplitude with increasing angles of rotation. However, in a mental rotation task of hands, different RT profiles can be observed for outward and inward rotated hands. In the present study, we examined the neurophysiological correlates of these asymmetries in the RT profiles. We used a mental rotation task with stimuli of left and right hands. In line with previous studies, the behavioral results showed a linear increase in RT for outward rotations, but not for inward rotations as a function of angular disparity. Importantly, the ERP results revealed an RRN for outward rotated stimuli, but not for inward rotated stimuli. This is the first study to show that the behaviorally observed differences in a mental rotation task of hands is also reflected at the neurophysiological level.

Descriptors: Mental rotation, Motor imagery, Rotation related negativity, ERP

Over the past 4 decades, the mental rotation task has been studied intensively at both the behavioral and neuronal level. In a mental rotation task, participants have to judge rotated stimuli on their similarity with a reference picture (e.g., Shepard & Metzler, 1971) or on the laterality (*viz.*, is it left or right?) in case of hand (e.g., Sekiyama, 1982) or foot pictures (e.g., Parsons, 1987). Typically, reaction time (RT) increases with increasing angles of rotation. For hand stimuli, performance is influenced by biomechanical constraints as is evident from differences in RTs between laterally and medially rotated hand pictures (Parsons, 1994). Laterally rotated hands are rotated away from the body's midsagittal plane, and medially rotated hands are rotated towards the body's midsagittal plane. Medially rotated hand pictures are judged faster than laterally rotated pictures (Helmich, de Lange, Bloem, & Toni, 2007; Sauner, Bestmann, Siebner, & Rothwell, 2006; Shenton, Schwoebel, & Coslett, 2004; ter Horst, van Lier, & Steenbergen, 2010; Thayer & Johnson, 2006; Tomasino & Rumiati, 2004). The observed RT profiles mimic movement times for actually rotating one's hand laterally or medially, as rotating one's hand laterally is more difficult than rotating one's hand medially (Parsons, 1987, 1994). This process of mental movement is often referred to as motor imagery (MI), as it is a mental rehearsal or a simulation of a movement without actual overt movement (Decety, 1996).

As actual and simulated movements are similarly influenced by the biomechanical constraints of the performer, both are constrained by one's movement abilities. Indeed, different strategies or movement paths are thought to underlie the observed differences in RT profiles between laterally and medially rotated hands (Parsons, 1987). For laterally rotated hand stimuli, RTs increase with increasing angle of rotation, which points to the use of a mental rotation process (Sekiyama, 1982; Shepard & Metzler, 1971). For medially rotated hand stimuli, however, the RT curve does not increase with increasing angle of rotation, but is relatively unaffected by the rotational angle of the stimuli. Parsons (1987) showed that, during a hand laterality judgment task, hands are likely to be mentally rotated along two different paths. The first is the rotation-by-dimension path, in which hands are rotated in sequence along the three different main axes (longitudinal, sagittal, and frontal axis), see Figure 1. Hand rotations along this rather inefficient path result in the typically observed increasing RT with increasing angles of rotation. The rotation-by-dimension path is likely to be used for laterally rotated hand stimuli (Parsons, 1987). Alternatively, for medially rotated hand stimuli, participants are likely to use the shortest-path strategy, in which an imaginary axis is used to flip the observed hand 180° in order to covertly orient the own hand onto the observed hand's orientation, see Figure 1. This path results in a (nearly) horizontal RT curve as one only needs to (imaginarily) flip the own hand 180° over one axis for palm-view hand stimuli. The rationale for using two different strategies for laterally and medially rotated palm-view hand stimuli originates from the ability to adopt an observed hand posture. For laterally rotated stimuli, postures are difficult to adopt as rotations in several joints are required, especially for laterally rotated stimuli with angles between 90° and 180°. In contrast, for medially rotated palm-view stimuli, flexing the wrist together with a supination is sufficient (Parsons, 1987, 1994). Important to note is that the

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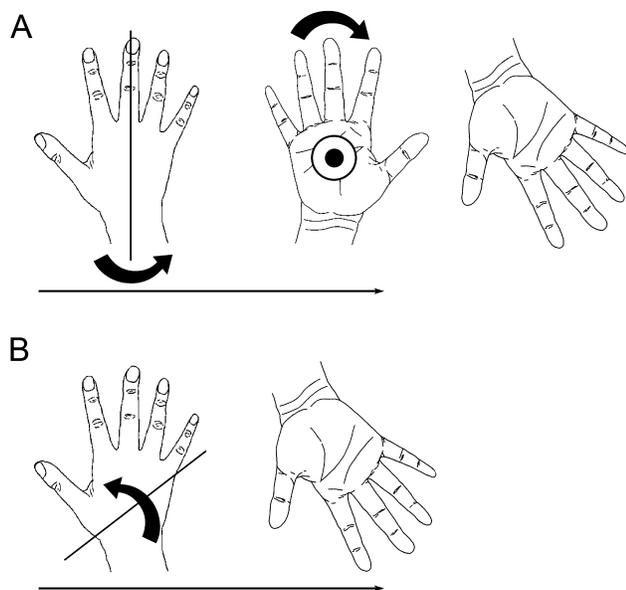
Figure 1. Examples of two paths along which a hand can be covertly rotated in a hand laterality judgment task. The first hand picture represents the (mental) starting position from which a mental movement is initiated. The final hand picture represents the end posture, i.e., the mentally imitated stimulus orientation. A: Rotation-by-dimension path, using a sequence of rotations along the main axes. At first, the hand, seen from the back, is rotated 180° along the longitudinal axis after which the hand, now seen from the palm, is rotated in-plane toward the stimulus orientation. B: Shortest path, in which an imaginary axis is used as rotational axis to rotate the hand 180°. This axis corrects for all orientation differences. Arrows indicate the direction of the rotation, and the straight lines and the bull's eye indicate rotational axes. Picture adapted from Parsons, 1987.

differences in RT profiles between lateral and medial rotations are most pronounced for palm-view stimuli and to a lesser extent for back-view hand stimuli (Parsons, 1987).

The mental rotation process itself was shown to be reflected in a modulated positive waveform approximately between 300 to 800 ms and is inversely related to the rotational angle of the stimulus, with decreasing amplitudes for increasing angles of rotation (Heil, 2002; Heil, Rauch, & Hennighausen, 1998; Heil & Rolke, 2002; Peronnet & Farah, 1989). This gradual decrease in amplitude is thought to be caused by a superimposed negativity on the simultaneously prevailing P300 complex (Peronnet & Farah, 1989; Wijers, Otten, Feenstra, Mulder, & Mulder, 1989) and is referred to as rotation related negativity (RRN) (Lust, Geuze, Wijers, & Wilson, 2006; Nunez-Pena & Aznar-Casanova, 2009; Nunez-Pena, Aznar, Linares, Corral, & Escera, 2005). The RRN has been shown to be an electrophysiological correlate of the mental rotation process (Heil, 2002; Heil et al., 1998; Heil & Rolke, 2002). Notwithstanding the differences between the mental rotation of corporeal and noncorporeal objects on both the behavioral and the neurological level, the RRN was present during the mental rotation of both types of objects (Heil, 2002; Lust et al., 2006; Tao et al., 2009; Thayer & Johnson, 2006; Thayer, Johnson, Corballis, & Hamm, 2001). In line with the RRN for noncorporeal objects, the RRN in a hand laterality judgment task gradually increases in amplitude with increasing angle of rotation. This provides converging evidence that the RRN is an electrophysiological marker for the mental rotation process itself.

Despite the well-studied electrophysiological processes of the RRN for both corporeal and noncorporeal objects, the electrophysiological correlates of the use of different strategies (i.e., rotation-by-dimension and shortest-path) in a hand laterality judgment task, due to the engagement in MI, have not been addressed in the literature. That is, our study is the first to focus on the electrophysiological reflection of the use of different mental rotation paths (i.e., rotation-by-dimension path and shortest path) as a function of the direction of rotation. The use of different mental rotation paths reveals the influence of biomechanical constraints on the simulated movements (i.e., MI) and hence reflects the embodied nature of the task. An important aspect of MI is its tight link with executed actions (Jeannerod, 2001). Studying the processes involved in MI allows one to explore the internal dynamics of motor control such as planning and preparation without sensory or motor interferences related to motor execution (de Lange, Roelofs, & Toni, 2008). The current study focuses on the modulation of the RRN as a function of the rotational direction of palm-view hand stimuli (i.e., laterally or medially). We hypothesized that for lateral rotations a typical RRN would be observed and that, in contrast, for medial rotation no such RRN would be observed, as the RT profiles of the latter do not imply the use of a gradual rotational process. In the present study, we used a mental rotation task of hands. We used palm-view stimuli because these stimuli were shown to elicit different rotational strategies for the different rotational directions more prominently than back-view stimuli (Parsons, 1987). In addition, we used back-view stimuli filler trials, as the use of a single view has been shown not to elicit the use of MI (ter Horst et al., 2010). The participants' engagement in MI is crucial to elicit the use of different strategies between laterally and medially rotated hand stimuli. During the task, we measured RTs and electroencephalogram (EEG) signals. From the latter, we calculated event-related potentials (ERPs). The use of different mental rotation strategies is assumed to reflect the influence of biomechanical constraints. The RRN, in turn, is shown to reflect the mental rotation process. Consequently, the hypothesized differences in the presence of an RRN between laterally and medially rotated stimuli is likely to reflect the embodied nature of the task at the neural level.

Method

Participants

Fourteen 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. None of the participants reported a history of neurological or psychiatric disorders. Due to error rates exceeding 20%, the data of two participants were excluded from further analyses. Data of the remaining twelve participants (one male) aged 18–26 years ($M = 20.5$, $SD = 2.46$) were used for analysis. The study was approved by the local ethics committee, in accordance with the Helsinki Declaration.

Stimuli

Stimuli were black and white line drawings of left and right hands. Both back- and palm-view stimuli were shown. Hands were presented from two views (i.e., from the back and front) in 10 different orientations, starting at 0° (fingers pointing up) and rotated clockwise to 40°, 75°, 110°, 145°, 180°, 215°, 250°, 285°, 320° yielding a total of 40 different stimuli, see Figure 2. All stimuli were
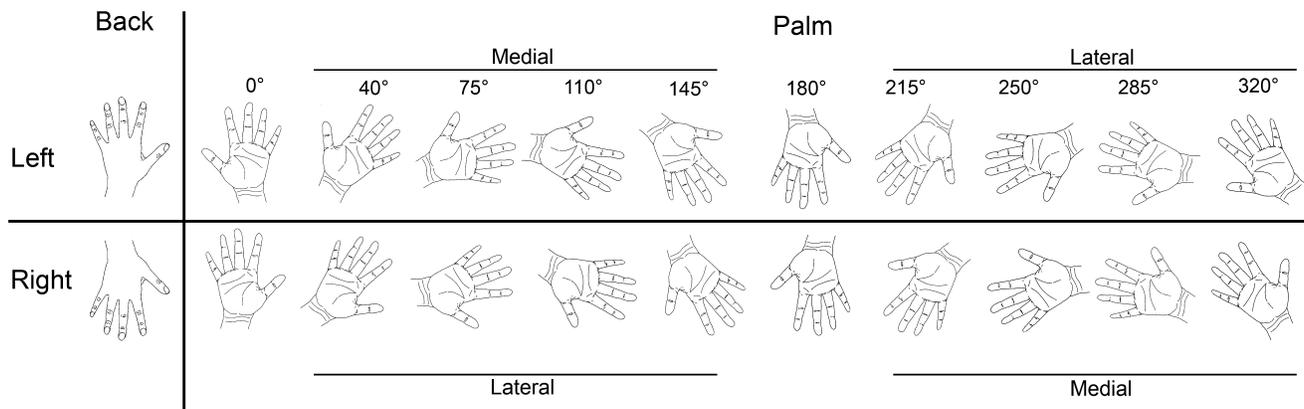
Figure 2. Examples of stimuli. Every orientation (0°, 40°, 75°, 110°, 145°, 180°, 215°, 250°, 285°, 320°), laterality (left, right) and view (back, palm) are shown.

displayed on a 19″ LCD computer screen, at a distance of approximately 70 cm from the participants' eyes, resulting in a visual angle of approximately 6°.

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 left and right buttons corresponded to a left- and right-hand judgment of the observed stimulus, respectively. No instructions on possible strategy use were given. The experiment consisted of 10 consecutive blocks of 90 trials each. We presented back- and palm-view hand stimuli in a 1:8 ratio. Palm-view stimuli were repeated 40 times. Back-view stimuli served as filler trials. Stimuli were shown sequentially by custom developed software in the Presentation software package (Neurobehavioral Systems, Albany, CA) and were randomized and counterbalanced for every block and counterbalanced over subjects. Trials started with a white fixation cross, shown for 0.5–1.5 s, followed by a stimulus. When a response was given, the stimulus disappeared. Interstimulus intervals (ISI) lasted for 1.5–2.5 s and varied randomly.

Participants were seated in a sound-shielded room in front of a computer screen. Participants were asked not to make eye movements or eye blinks during trials, but to consistently blink a few times immediately after a response was given. In between blocks, participants could rest. RTs and judgments (left/right) were recorded. The actual blocks were preceded by a 60-stimuli test trial to familiarize the subject with the task.

EEG Recordings

EEG signals were recorded with a 64-channel actiCAP (Brain Products GmbH, Munich, Germany) 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 .016 Hz (i.e., 10 s time-constant) and 250 Hz. Horizontal and ver-

tical electrooculograms (EOGs) were recorded from the remaining three electrodes, placed on the outer canthi and below the right eye.

Data Analysis

Behavioral data. Trials with RTs below 300 ms or above 3500 ms were excluded from analysis. These boundaries were chosen based on former studies using a hand laterality judgment task (de Lange, Helmich, & Toni, 2006; Ionta, Fourkas, Fiorio, & Aglioti, 2007; ter Horst et al., 2010; ter Horst, van Lier, & Steenbergen, 2011). From the remaining data set, erroneous responses were used to calculate the error rate for individual subjects. Incorrect trials are those with left responses for right-hand stimuli and vice versa. Only correct responses for palm-view stimuli were used for further analysis of the RTs. To assess whether participants used MI during the task, we tested for the influence of biomechanical constraints. To that aim, the differences in RTs between laterally and medially rotated hand stimuli were analyzed (Parsons, 1987, 1994; ter Horst et al., 2010). Laterally rotated stimuli consisted of 40°, 75°, 110°, and 145° rotated right-hand stimuli and 215°, 250°, 285°, and 320° rotated left-hand stimuli. Medially rotated hand stimuli consisted of 215°, 250°, 285°, and 320° rotated right-hand stimuli and 40°, 75°, 110°, and 145° rotated left-hand stimuli, see Figure 2. In the following, we will refer to this distinction between lateral and medial rotations as direction of rotation (DOR).

A 2 × 4 repeated measures analyses of variance (ANOVA) was performed to test for the influence of rotational angle and biomechanical constraints on the RTs with the following design: 2 within-subject factors (Angle, DOR), with 4 levels for Angle (40°, 75°, 110°, and 145°) and 2 levels for DOR (Lateral, Medial). A significant effect of Angle, accounted for by increasing RTs with increasing angles of rotation, would indicate that participants mentally rotated the hand stimuli (Kosslyn, DiGirolamo, Thompson, & Alpert, 1998; Sekiyama, 1982; Shepard & Metzler, 1971; ter Horst et al., 2010). A significant DOR effect would indicate that RTs were subject to biomechanical constraints and hence the use of MI (Parsons, 1994; ter Horst et al., 2010). The erroneous responses were analyzed separately in an identical ANOVA. Alpha level was set at $p = .05$, and Bonferroni correction was applied when appropriate.

ERP data. Offline processing of the ERP data was conducted in BrainVision Analyzer version 1.05 (Brain Products GmbH). Only

ERPs corresponding to correct palm-view trials were analyzed. ERPs were calculated relative to stimulus onset from −200 to 700 ms. ERPs were filtered between 0.016 and 80 Hz. Baseline correction was applied using a −150 to 0 ms prestimulus interval. Trials with movement artifacts were excluded from analysis on the basis of careful visual inspection of the raw data. Ocular artifacts were corrected using a semiautomatic correction procedure based on the logarithm of Gratton, Coles, and Donchin (1983). Grand averages were calculated for the same angles as used in the RT data analysis (i.e., 40°, 75°, 110°, 145°) for both lateral and medial rotations.

Visual inspection of the grand averages showed a parietal P300 peak followed by the expected RRN between 450 and 600 ms. Furthermore, during visual inspection, we found an unexpected P290 peak from 280 to 300 ms with changing amplitudes as a function of our experimental manipulations. Both peaks were most pronounced at parietal electrode sites. Consequently, and in accordance with the literature, ERPs for both the P290 and RRN were quantified at the parietal region of interest (ROI) containing the electrodes P3, Pz, and P4 (Beste, Heil, & Konrad, 2010; Gootjes, Bruggeling, Magnee, & Van Strien, 2008; Heil, 2002; Heil & Rolke, 2002; Prime & Jolicoeur, 2009).

Amplitudes averaged over the electrodes within the parietal ROI were analyzed in repeated measures ANOVAs with the factors Angle and DOR, with 4 levels for Angle (40°, 75°, 110°, and 145°) and 2 levels for DOR (Lateral, Medial). This ANOVA design was used for the P290 and RRN ERP data. Alpha level was set at $p = .05$, and Bonferroni correction was applied when appropriate.

Results

Behavioral Data

The total number of erroneous responses over all participants (i.e., 3.2% of all trials) corresponds to former studies (de Lange et al., 2006; ter Horst et al., 2010). The ANOVA on erroneous responses revealed no significant effects or interaction.

The ANOVA on the RT data revealed a significant main effect of Angle $[F(3,33) = 7.201; \ p < .01; \ \eta^2 = 0.396; \ \varepsilon = 0.839]$ and DOR $[F(1,11) = 38.080; p < .001; \eta^2 = 0.776; \varepsilon = 1.00]$. The DOR effect was accounted for by a smaller mean RT for medially (986 ms) compared to laterally (1138 ms) rotated stimuli. The interaction of DOR × Angle was also significant $[F(3,33) = 6.648; p < .001; \eta^2 = 0.377; \varepsilon = 0.951]$. Planned further analysis revealed a significant simple Angle effect for lateral $[F(3,33) = 9.898; p < .001; \ \eta^2 = 0.474; \ \varepsilon = 0.986]$, but not medial rotations $(F(3,33) = 1.876; p = .187)$, see Figure 3. For lateral rotations, RTs increased linearly $(p < .005)$. *Ad hoc* analyses revealed that RTs for 40° (1077 ms) and 75° (1129 ms) differed significantly from 145° (1301 ms) $(p < .05)$. RT differences between 110° (1197 ms) and 145° failed to reach conventional levels of significance after correction for multiple comparisons $(p = .055)$.

ERP Data

The ERPs elicited at the electrodes within the ROI are depicted in Figure 4. The ANOVA on the ERP P290 data revealed a significant main effect of DOR $[F(1,11) = 6.721; p < .05; \eta^2 = 0.379; \varepsilon = 0.656]$ and a significant interaction of Angle × DOR $[F(3,33) = 4.176; p < .02; \eta^2 = 0.275; \varepsilon = 0.797]$. Simple effects analyses revealed a significant Angle effect for medial $[F(3,33) = 4.908; p < .01; \eta^2 = 0.309; \varepsilon = 0.873]$, but not for lateral
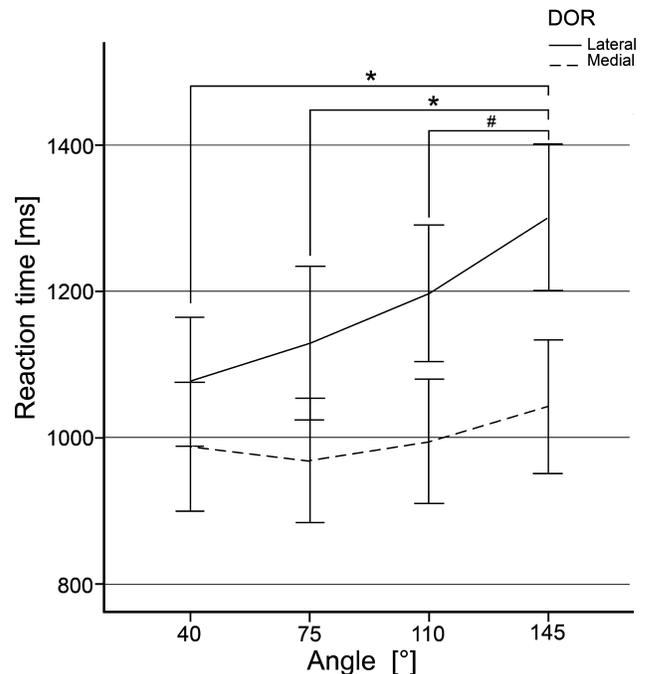

Figure 3. Reaction times as a function of rotational axes, shown per rotational direction (i.e., lateral and medial). *$p < .05$. #$p = .055$. Error bars denote standard error of the mean.

rotations $(F(3,33) = 1.998; p = .143)$, see Figure 5. Further analyses on medially rotated stimuli revealed a significant difference between 40° and 110° rotated stimuli $(p < .02)$. The amplitude difference between 40° and 145° rotated stimuli did not result in a significant difference after Bonferroni correction $(p = .077)$. See also Figure 5.

The ANOVA on the RRN ERP data revealed a significant main effect of Angle $[F(3,33) = 4.645; \ p < .02; \ \eta^2 = 0.267; \varepsilon = 0.739]$ and a significant two-way interaction of Angle × DOR $[F(3,33) = 3.612; p < .05; \eta^2 = 0.247; \varepsilon = 0.730]$. The significant two-way interaction indicates a modulated amplitude as a function of angular disparity between laterally and medially rotated stimuli, see Figure 6. Further analysis revealed a significant simple effect of Angle for lateral $[F(3,33) = 7.698; \ p < .005; \ \eta^2 = 0.412; \varepsilon = 0.876]$, but not medial rotations $(F(3,33) = 0.990; p = .404)$. Further analyses on the lateral rotations revealed significant difference between 40° and 110° and 145° (all $p < .05$). The decrease in amplitude with increasing angle of rotation was found to be linear $(p < .01)$. No quadratic or cubic trends were found significant (all $p > .2$). See also Figure 6.

Discussion

In this study, we analyzed RTs and ERPs from a hand laterality judgment task. It is well known that such a task induces the use of a mental rotation process of the own hands (de Lange et al., 2008; Parsons, 1994; ter Horst et al., 2010). Parsons (1987) showed that participants use different mental rotation strategies for medially and laterally rotated stimuli. In the present study, we examined whether these different rotational strategies are also reflected at the neural level as assessed by electrophysiological measurements. Due to the close relation between increasing RT with increasing angles of rotation and the mental rotation process, we hypothesized
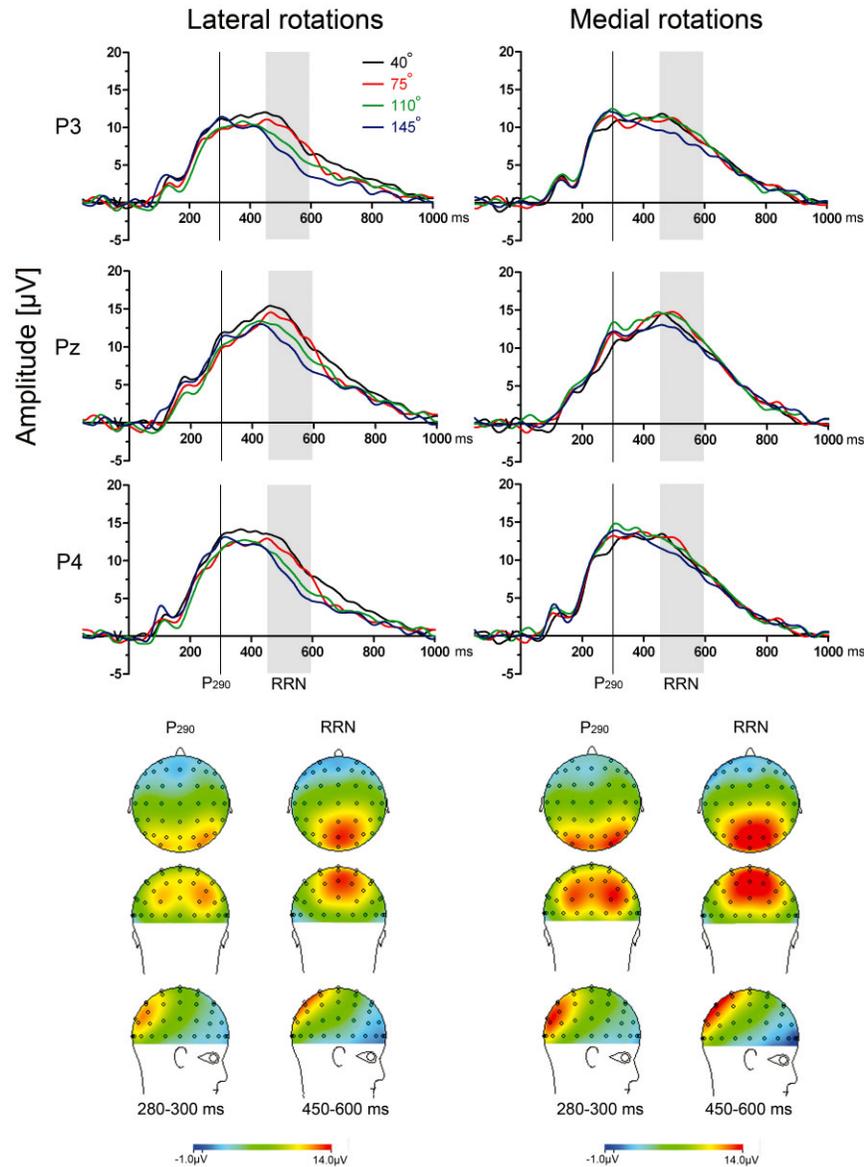
Figure 4. ERP's relative to stimulus onset for laterally rotated hand stimuli (left panel) and medially rotated hand stimuli (right panel). Scalp topographies represent the ERP amplitude at the P290 time interval (left panel) and RRN time interval (right panel).

that the RRN would be present only for lateral rotations and not for medial rotations.

Behavioral data. We replicated the finding of Parsons (1987), by showing an increase in RT for increasing angles of rotations for lateral, but not medial rotations, see Figure 3. The increase in RT for lateral rotations is likely to originate from the used rotation-by-dimension process, as pointed out by Parsons (1987). Due to the awkward posture of laterally rotated hands, participants use an inefficient (but effective) strategy to mentally move their own hand to the stimulus' orientation. For medially rotated hands, the body's movement abilities allow an effective and efficient strategy, reflecting the ability to rotate one's hand over different angles by supination and flexion of the wrist (i.e., shortest-path rotation).

ERP data. In accordance with our hypothesis and in line with previous studies, we found a significant general effect of increasing

negativity with increasing angle of rotation of the RRN. Importantly, this RRN was present only for laterally and not medially rotated stimuli, see Figure 6. For lateral rotations, the observed amplitude decreased linearly with increasing angle of rotation. This RRN for lateral rotations is likely to reflect the in-plane rotation process during the rotation-by-dimension method. This is in line with the literature on the mental rotation of noncorporeal objects and letters (Heil, 2002), showing that the in-plane mental rotation of the stimulus is reflected in the RRN. Additionally, the observed RRN for lateral rotations fits our behavioral data as they show an increase in RT as a function of angle for lateral rotations. Consequently, our findings further confirm the close relation between the RRN and the in-plane mental rotation process.

Furthermore, the time window in which the RRN was significant for lateral rotations in our study (i.e., 450–600 ms) corresponds with the literature. The observed time window for the RRN differs between studies and extends from 300 to 800 ms (Milivojevic, Hamm, & Corballis, 2009; Thayer & Johnson, 2006).
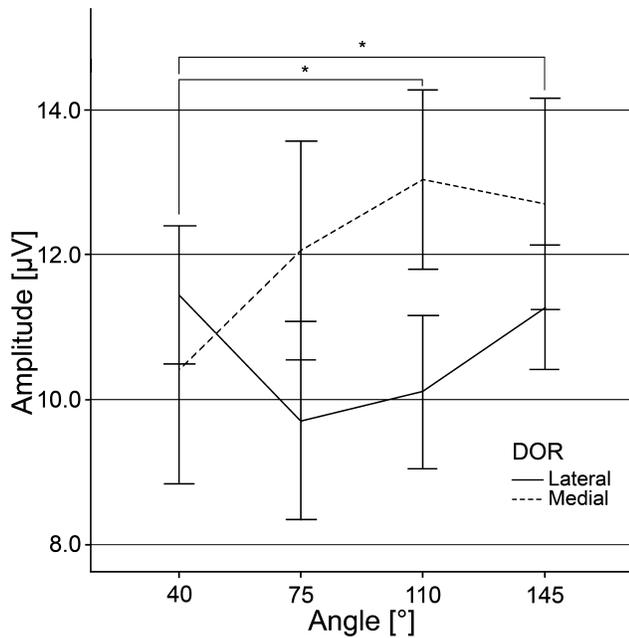
Figure 5. Mean P290 amplitudes within the ROI (i.e., P3, Pz, and P4) per direction of rotation as function of angle. *p < .05. Error bars denote standard error of the mean.

Additionally, the observed distribution of the RRN over the parietal electrodes is also in agreement with former literature (Heil, 2002; Heil et al., 1998; Heil & Rolke, 2002; Parsons, 2003; Prime & Jolicoeur, 2009; Tao et al., 2009; Thayer & Johnson, 2006; Thayer et al., 2001). In fMRI studies on the mental rotation task, the superior parietal cortex has been shown to be active during mental rotation tasks (de Lange, Hagoort, & Toni, 2005; de Lange et al., 2006; Harris & Miniussi, 2003; Vingerhoets, de Lange, Vandemaele, Deblaere, & Achten, 2002). The superior parietal cortex is regarded as an essential brain region for mental rotation. This area is involved in aspects of spatiovisual processing (de Lange et al., 2005; Graziano, Cooke, & Taylor, 2000) and is thought to relate observed objects to egocentric or allocentric frames of reference (Parsons, 2003). The latter is of specific relevance during a mental rotation task.

We also obtained a P290 peak, reflecting a modulated influence of angle between the rotational directions. In contrast to the RRN, the P290 revealed that the rotational angle influences ERP amplitudes for medial, but not lateral rotations. The amplitude at the P290 for medial rotations increases with increasing angle of rotation. Hence, the observed effect cannot be attributed to an earlier onset of the RRN, which is described as a negative-going process superimposed on the P300 waveform (Wijers et al., 1989). This relatively early process is thought to reflect early visuospatial processing (Gootjes et al., 2008), with the increase in amplitude possibly reflecting an increase in mental effort with increasing angle of rotation (Pritchard, 1981; Ullsperger, Metz, & Gille, 1988).

The dissociation between the task-dependent processing of laterally and medially rotated stimuli is in line with former research, stating that prior to the mental rotation process itself a strategy is selected (Desrocher, Smith, & Taylor, 1995; Ruchkin, Johnson, Canoune, & Ritter, 1991). The differences between the processing of angular disparity for lateral and medial rotations in both behav-

ioral and electrophysiological data are likely to relate to the use of different strategies as supposed by Parsons (1987). The remarkable resemblance in both RT as well as ERP data between the mental rotation of noncorporeal objects (e.g., Heil, 2002) and laterally rotated hands might point to the use of a more visually based strategy for laterally rotated hands compared to medially rotated hands. This is also intuitively feasible as lateral rotations are difficult to perform and, as such, a nonmotor-based strategy might be more efficient. For medial rotations, a motor-based strategy is highly efficient due to the ability to rotate the own hand medially. However, this remains speculative as it goes beyond the scope of the current study. In future research, it might be interesting to study Mu-band synchronization and desynchronization between lateral and medial rotations as a measure for the involvement of an embodied-based imagery (i.e., MI) (Pineda, 2005).

In a recent study on the neurophysiological correlates of the hand laterality judgment task, no modulated difference in the RRN was found between lateral and medial rotations (Tao et al., 2009). The apparent contrast between the study of Tao et al. and our results is likely to be caused by differences in stimulus sets. Tao et al. (2009) used only back-view stimuli. As shown by Parsons (1987), performance for back-view stimuli is less affected by biomechanical constraints compared to palm-view stimuli.

In our study, eleven female and one male participant were included. In the literature, gender differences have been observed during mental rotation tasks (Johnson, McKenzie, & Hamm, 2002; Parsons et al., 2004; Seurinck, Vingerhoets, de Lange, & Achten, 2004). Parsons et al. (2004) showed that the generally observed RT advantage of men over women is present only for 2-dimensional (2D) presented 3-dimensional (3D) objects and is not present in mental rotation tasks of 3D presented 3D objects. This finding implies that the male advantage does not apply to the mental rotation process *per se*, but rather in the derivation of 3D objects from 2D objects (Neubauer, Bergner, & Schatz, 2010; Parsons
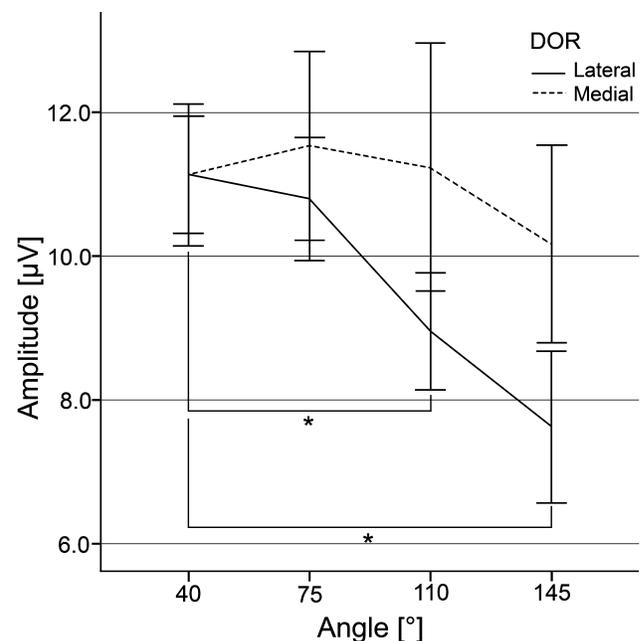

Figure 6. Mean RRN amplitudes within the ROI (i.e., P3, Pz, and P4) per direction of rotation as function of angle. *p < .05. Error bars denote standard error of the mean.

et al., 2004). In this case, our results might be applicable to both sexes, as our study focuses on the mental rotation process itself. However, the onset of the RRN for women has been shown to differ from that of men (Gootjes et al., 2008). Furthermore, although no gender differences in the pattern of parietal activation were found in an fMRI study (Seurinck et al., 2004), EEG studies showed contradicting results concerning P300 amplitude differences between male and female participants (Desrocher et al., 1995; Johnson et al., 2002). Given these findings, caution should be taken in generalizing our results to both genders.

In sum, our findings show that the behaviorally observed differences between lateral and medial rotations are also reflected in differences at the neural level. The electrophysiological processes concerning the processing of angular differences for lateral and medial rotations differ in onset latency, and for lateral rotations, an RRN is observed. For medially rotated hand stimuli, however, no increase in RT with increasing angle of rotation was found in the RRN interval, pointing to the absence of a typical in-plane mental rotation process. Instead, an increase of a P290 was observed with an increase in rotational angle. These observed differences between medial and lateral rotations are likely to reflect the use of different strategies for the different rotational directions due to the embodied nature of the hand laterality judgment task.

References

Beste, C., Heil, M., & Konrad, C. (2010). Individual differences in ERPs during mental rotation of characters: Lateralization, and performance level. *Brain Cognition, 72*, 238–243. doi: 10.1016/j.bandc.2009.09.005

de Lange, F. P., Hagoort, P., & Toni, I. (2005). Neural topography and content of movement representations. *Journal of Cognitive Neuroscience, 17*, 97–112. doi: 10.1162/0898929052880039

de Lange, F. P., Helmich, R. C., & Toni, I. (2006). Posture influences motor imagery: An fMRI study. *NeuroImage, 33*, 609–617. doi: 10.1016/j.neuroimage.2006.07.017

de Lange, F. P., Roelofs, K., & Toni, I. (2008). Motor imagery: A window into the mechanisms and alterations of the motor system. *Cortex, 44*, 494–506. doi: 10.1016/j.cortex.2007.09.002

Decety, J. (1996). The neurophysiological basis of motor imagery. *Behavioural Brain Research, 77*, 45–52. doi: 10.1016/0166-4328(95)00225-1

Desrocher, M. E., Smith, M. L., & Taylor, M. J. (1995). Stimulus and sex differences in performance of mental rotation: Evidence from event-related potentials. *Brain Cognition, 28*, 14–38. doi: 10.1006/brcg.1995.1031

Gootjes, L., Bruggeling, E. C., Magnee, T., & Van Strien, J. W. (2008). Sex differences in the latency of the late event-related potential mental rotation effect. *NeuroReport, 19*, 349–353. doi: 10.1097/WNR.0b013e3282f519b3

Gratton, G., Coles, M. G., & Donchin, E. (1983). A new method for off-line removal of ocular artifact. *Electroencephalography and Clinical Neurophysiology, 55*, 468–484. doi: 10.1016/0013-4694(83)90135-9

Graziano, M. S., Cooke, D. F., & Taylor, C. S. (2000). Coding the location of the arm by sight. *Science, 290*, 1782–1786. doi: 10.1126/science.290.5497.1782

Harris, I. M., & Miniussi, C. (2003). Parietal lobe contribution to mental rotation demonstrated with rTMS. *Journal of Cognitive Neuroscience, 15*, 315–323. doi: 10.1162/089892903321593054

Heil, M. (2002). The functional significance of ERP effects during mental rotation. *Psychophysiology, 39*, 535–545. doi: 10.1017/S0048577202020449

Heil, M., Rauch, M., & Hennighausen, E. (1998). Response preparation begins before mental rotation is finished: Evidence from event-related brain potentials. *Acta Psychologica (Amsterdam), 99*, 217–232.

Heil, M., & Rolke, B. (2002). Toward a chronopsychophysiology of mental rotation. *Psychophysiology, 39*, 414–422. doi: 10.1017/S0048577202001105

Helmich, R. C., de Lange, F. P., Bloem, B. R., & Toni, I. (2007). Cerebral compensation during motor imagery in Parkinson's disease. *Neuropsychologia, 45*, 2201–2215. doi: 10.1016/j.neuropsychologia.2007.02.024

Ionta, S., Fourkas, A. D., Fiorio, M., & Aglioti, S. M. (2007). The influence of hands posture on mental rotation of hands and feet. *Experimental Brain Research, 183*, 1–7. doi: 10.1007/s00221-007-1020-2

Jeannerod, M. (2001). Neural simulation of action: A unifying mechanism for motor cognition. *Neuroimage, 14*, S103–109. doi: 10.1006/nimg.2001.0832

Johnson, B. W., McKenzie, K. J., & Hamm, J. P. (2002). Cerebral asymmetry for mental rotation: Effects of response hand, handedness and gender. *NeuroReport, 13*, 1929–1932.

Kosslyn, S. M., DiGirolamo, G. J., Thompson, W. L., & Alpert, N. M. (1998). Mental rotation of objects versus hands: Neural mechanisms revealed by positron emission tomography. *Psychophysiology, 35*, 151–161. doi: 10.1017/S0048577298001516

Lust, J. M., Geuze, R. H., Wijers, A. A., & Wilson, P. H. (2006). An EEG study of mental rotation-related negativity in children with developmental coordination disorder. *Child: Care, Health, and Development, 32*, 649–663. doi: 10.1111/j.1365-2214.2006.00683.x

Milivojevic, B., Hamm, J. P., & Corballis, M. C. (2009). Hemispheric dominance for mental rotation: It is a matter of time. *Neuroreport, 20*, 1507–1512. doi: 10.1097/WNR.0b013e32832ea6fd

Neubauer, A. C., Bergner, S., & Schatz, M. (2010). Two- vs. three-dimensional presentation of mental rotation tasks: Sex differences and effects of training on performance and brain activation. *Intelligence, 38*, 529–539. doi: 10.1016/j.intell.2010.06.001

Nunez-Pena, M. I., & Aznar-Casanova, J. A. (2009). Mental rotation of mirrored letters: Evidence from event-related brain potentials. *Brain Cognition, 69*, 180–187. doi: 10.1016/j.bandc.2008.07.003

Nunez-Pena, M. I., Aznar, J. A., Linares, D., Corral, M. J., & Escera, C. (2005). Effects of dynamic rotation on event-related brain potentials. *Brain Research. Cognitive Brain Research, 24*, 307–316. doi: 10.1016/j.cogbrainres.2005.02.004

Parsons, L. M. (1987). Imagined spatial transformations of one's hands and feet. *Cognitive Psychology, 19*, 178–241.

Parsons, L. M. (1994). Temporal and kinematic properties of motor behavior reflected in mentally simulated action. *Journal of Experimental Psychology: Human Perception and Performance, 20*, 709–730.

Parsons, L. M. (2003). Superior parietal cortices and varieties of mental rotation. *Trends in Cognitive Science, 7*, 515–517. doi: 10.1016/j.tics.2003.10.002

Parsons, T. D., Larson, P., Kratz, K., Thiebaux, M., Bluestein, B., & Buckwalter, J. G. (2004). Sex differences in mental rotation and spatial rotation in a virtual environment. *Neuropsychologia, 42*, 555–562. doi: S0028393203002380 [pii]

Peronnet, F., & Farah, M. J. (1989). Mental rotation: An event-related potential study with a validated mental rotation task. *Brain Cognition, 9*, 279–288.

Pineda, J. A. (2005). The functional significance of mu rhythms: Translating "seeing" and "hearing" into "doing." *Brain Research. Brain Research Review, 50*, 57–68. doi: 10.1016/j.brainresrev.2005.04.005

Prime, D. J., & Jolicoeur, P. (2009). Mental rotation requires visual short-term memory: Evidence from human electric cortical activity. *Journal of Cognitive Neuroscience, 22*, 2437–2446. doi: 10.1162/jocn.2009.21337

Pritchard, W. S. (1981). Psychophysiology of P300. *Psychological Bulletin, 89*, 506–540. doi: 10.1037/0033-2909.89.3.506

Ruchkin, D. S., Johnson, R., Jr., Canoune, H., & Ritter, W. (1991). Event-related potentials during arithmetic and mental rotation. *Electroencephalography and Clinical Neurophysiology, 79*, 473–487.

Sauner, D., Bestmann, S., Siebner, H. R., & Rothwell, J. C. (2006). No evidence for a substantial involvement of primary motor hand area in handedness judgements: A transcranial magnetic stimulation study. *European Journal of Neuroscience, 23*, 2215–2224. doi: 10.1111/j.1460-9568.2006.04731.x

Sekiyama, K. (1982). Kinesthetic aspects of mental representations in the identification of left and right hands. *Perception & Psychophysics, 32*, 89–95.

Seurinck, R., Vingerhoets, G., de Lange, F. P., & Achten, E. (2004). Does egocentric mental rotation elicit sex differences? *NeuroImage, 23*, 1440–1449. doi: 10.1016/j.neuroimage.2004.08.010

Shenton, J. T., Schwoebel, J., & Coslett, H. B. (2004). Mental motor imagery and the body schema: Evidence for proprioceptive dominance. *Neuroscience Letters, 370*, 19–24. doi: 10.1016/j.neulet.2004.07.053

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

Tao, W., Liu, Q., Huang, X., Tao, X., Yan, J., & Teeter, C. J. (2009). Effect of degree and direction of rotation in egocentric mental rotation of hand: An event-related potential study. *NeuroReport, 20*, 180–185. doi: 10.1097/WNR.0b013e32831c510a

ter Horst, A. C., van Lier, R., & Steenbergen, B. (2010). Mental rotation task of hands: Differential influence number of rotational axes. *Experimental Brain Research, 203*, 347–354. doi: 10.1007/s00221-010-2235-1

ter Horst, A. C., van Lier, R., & Steenbergen, B. (2011). Spatial dependency of action simulation. *Experimental Brain Research, 212*, 635–644. doi: 10.1007/s00221-011-2748-2

Thayer, Z. C., & Johnson, B. W. (2006). Cerebral processes during visuo-motor imagery of hands. *Psychophysiology, 43*, 401–412. doi: 10.1111/j.1469-8986.2006.00404.x

Thayer, Z. C., Johnson, B. W., Corballis, M. C., & Hamm, J. P. (2001). Perceptual and motor mechanisms for mental rotation of human hands. *NeuroReport, 12*, 3433–3437.

Tomasino, B., & Rumiati, R. I. (2004). Effects of strategies on mental rotation and hemispheric lateralization: Neuropsychological evidence. *Journal of Cognitive Neuroscience, 16*, 878–888. doi: 10.1162/089892904970753

Ullsperger, P., Metz, A. M., & Gille, H. G. (1988). The P300 component of the event-related brain potential and mental effort. *Ergonomics, 31*, 1127–1137.

Vingerhoets, G., de Lange, F. P., Vandemaele, P., Deblaere, K., & Achten, E. (2002). Motor imagery in mental rotation: An fMRI study. *Neuro-Image, 17*, 1623–1633. doi: 10.1006/nimg.2002.1290

Wijers, A. A., Otten, L. J., Feenstra, S., Mulder, G., & Mulder, L. J. (1989). Brain potentials during selective attention, memory search, and mental rotation. *Psychophysiology, 26*, 452–467.