Effect of degree and direction of rotation in egocentric mental rotation of hand: an event-related potential study

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We explored the neural mechanisms of mental rotation of hand, which may invoke a mental transformation of viewer's own hands. It was found that, when a hand picture was presented at an orientation rotated from the upright orientation, participants' performance in making left or right hand judgment was affected by the degree and direction of rotation, with the direction effect being implicated as the evidence for egocentric mental rotation. Our event-related potentials measure supported the idea that amplitude modulation in the parietal cortex is a psychophysiological marker of the mental rotation of hand. Furthermore, the rotation-direction-dependent modulation of a positive wave was identified as possible neural correlate for the egocentric nature of such mental rotation. *NeuroReport* 00:000–000 © 2008 Wolters Kluwer Health | Lippincott Williams & Wilkins.

NeuroReport 2008, **00**:000–000

Keywords: biomechanical constrain, egocentric reference frame, mental rotation, motor imagery

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Received 4 September 2008 **accepted** 3 October 2008

Introduction

Mental rotation refers to a type of spatial ability in which a person imagines how an object or array would appear if rotated away from the presented orientation [1]. Humans use these visuospatial representations to address a range of reasoning problems in daily life, such as recognition, navigation, and action planning, among others [2]. In the early 1970s, using a three-dimensional (3D) nonsense armed objects and alphanumeric characters, Shepard and Metzer [3] conducted a series of experiments to investigate the process of mental rotation. The results showed that the time taken to decide the parity of a shape increased as a monotonic function of the angular disparity between the two objects. These results indicated that the participants performed the task by 'mentally rotating' the image of one object into correspondence with the other, or into its canonical view. In contrast, it has been shown that hands or bodies pictures as mental rotation stimuli in laterality tasks invoke egocentric mental transformation rather than object-centric one [4,5]. The results of the behavioral performance in these studies showed that mental rotation of the body and body parts seem to be constrained by the biomechanical properties of the physical rotation [6–9]. However, up to now, only a few studies have focused on whether the biomechanical constraints are also reflected in event-related potential amplitude.

Studies with event-related potentials (ERPs) have reported the existence of a psychophysiological marker of the mental rotation phenomenon when alphanumeric characters are used as stimuli [10]. A substantial number of studies conducted by Heil [11] have provided compelling evidence of the functional and temporal significance of this psychophysiological marker. The standard ERP effect most reliably obtained at parietal electrode leads consists of a pronounced positive component (P300) evoked by the presentation of characters, and the amplitude of this positivity is inversely related to character orientation. This implies that the amplitude becomes relatively more negative with the increasing angular disparity from the upright condition. While using hand pictures as mental rotation stimuli, Thayer and colleagues [1,12] found that mental hand rotation is associated with ERP amplitude modulations during two time windows (170 and 600–800 ms). Because of the limitation of the stimulus design and analysis, their studies overlooked the effect of rotation direction, which could be related to biomechanical constraints of the physical movement of hand. To date, few studies have examined whether the rotation direction-dependent modulations of negative slow wave exist.

Recently, several neuroimaging studies have been specifically conducted to investigate the motoric properties of mental hand rotation [7,13,14]. The results suggested that mental hand rotation engaged multiple brain regions including the primary motor cortex, parietal region, among others. These results showed that a difference exists

0959-4965 © 2008 Wolters Kluwer Health | Lippincott Williams & Wilkins DOI: 10.1097/WNR.0b013e32831c510a

between egocentric mental rotation and object-centric mental rotation. Moreover, egocentric-mental hand rotation is also a form of analogical reasoning with many sequential processing stages, such as perceptual encoding, identification/discrimination, mental rotation, judgment of the parity, response selection, and execution [4,5,11,15]. Because of the limitation of the temporal resolution of functional neuroimaging relative to the underlying neural events, it is difficult to discern the relationships between neuroimaging results and the stage of mental processes as the recorded differences could be the results of overlaps in the different stages of the mental processes. In contrast, it is possible to accurately record the time course of the electrical activity of the brain in the processing stages of mental rotation because of the high temporal resolution of ERPs.

The aim of this paper is twofold. First, we aimed to find out whether the direction of rotation (in-rotation vs. out-rotation) affected both behavioral performances and brain activity during mental rotation process. We hypothesized that different electrophysiological resources were required as the hand imagery rotates laterally than when it rotates medially. Second, we also sought to confirm that using the hand as mental rotation stimulus could also evoke a psychophysiological marker of the mental rotation process.

This study differs from relevant earlier research [1,7,12] in a number of ways. First, to provide an unambiguous yet simplified visual display of the hand stimuli, we used computer generated 3-D models of the back of the left or right hand instead of line drawings [1] or photos [16]. Second, to make the visual features comparable across conditions, we only rotated the model of the hand in the picture plane and without any occlusion typically seen in other rotation planes.

Materials and methods

Participants

Sixteen neurologically normal adults (eight males and eight females; aged 18–24 years, with mean of 20.75) from Southwest University of China participated in this study and they were paid for their participation. They all signed an informed consent for the experiment. All participants were right handed, had normal or corrected-to-normal vision. They had no earlier experience in similar experiments.

Visual displays

The experiment was carried out on a Dell P_{IV} computer using E-Prime 1.1 software. (Psychology Software Tools, Pittsburgh, Pennsylvania, USA). The stimuli were displayed on the center of a 15″ SVGA monitor with a resolution of 800×600 pixels. The participants were seated in front of the screen from a distance of 75 cm.

The stimuli of the left or right hands' picture were all created in 3D graphics software and had a height of 14 cm, subtending 10.73° of the vertical visual angle. Each virtual hand (with the back of the hand facing participants) was presented at the three orientations of 45°, 90°, and 135° rotated clockwise or counter-clockwise from canonical upright orientation. Instead of describing the hand rotation in clockwise or counter-clockwise fashion, the directions of rotation can be described in terms of in-rotation (rotated medially) and out-rotation (rotated laterally) (see Fig. 1). For the left hand, in-rotation means that the hand is rotated clockwise in the range of 0–180°, whereas out-rotation means that it is rotated counter-clockwise in the range of 180–360°. On the contrary, for the right hand, out-rotation is clockwise rotation in the range of 0–180°, and in-rotation is counter-clockwise rotation in the range of 180–360°. The left and right hands were mirror images of each other, and they were otherwise identical for each view. The participants were instructed to judge whether the presented single picture was the right hand or the left one.

Fig. 1

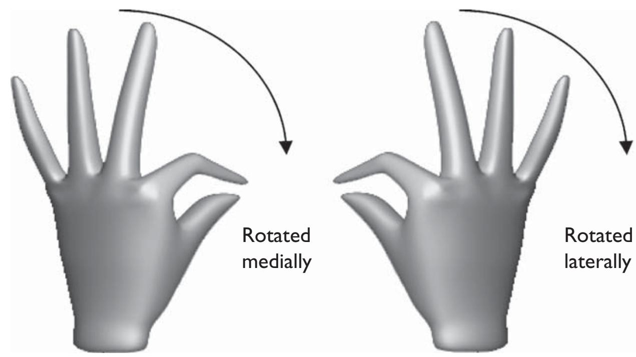


Illustration of stimuli used in left or right hand discrimination task. Note that only one hand was shown in a given time during experiment.

Procedure

Each trial began with the presentation of a white fixation point ' + ' at the center of a black screen for 200 ms, and then followed by a presentation of blank screen for a randomly selected duration between 500 and 1000 ms. After this, a left or right rotated hand was presented and remained on the screen until the participant responded. If no response was made within 5000 ms, the stimulus automatically disappeared, and that trial was coded as 'no response'. The participants made judgments by pressing the keyboard: if the presented picture was the right hand, then they pressed the 'J' key using their right hand, whereas if the presented picture was the left hand, they pressed the 'F' key using their left hand. Blank screen of 1000 ms was presented between trials.

There were 360 trials in total, with 60 trials per condition. The participants were instructed to withhold eye blinks and other body movements during the trials. They were also required to respond as accurately and quickly as possible.

Electroencephalography recording and analysis

The Electroencephalography was recorded from 64 scalp sites by tin electrodes mounted in an elastic cap (Brain Product Inc.), with references to the left and right mastoids. In addition, a ground electrode (GND) was placed on the medial aspect of the frontal lobe (on the middle line, between Fz and Fcz). The horizontal and vertical electrooculograms (EOGs) were recorded. The electroencephalography and EOG were amplified using a DC approximately 100 Hz bandpass and were continuously sampled at 500 Hz/channel. All interelectrode impedance was maintained below 5 kΩ. The average of the ERPs was computed offline.

The average epoch for ERPs was 1000 ms including a 200 ms prestimulus baseline, and only epochs associated with correct responses were included in the analyses. Trials with EOG artifacts (this refers to an EOG voltage exceeding $\pm 80\,\mu V$) and those contaminated trials with artifacts because of amplifier clipping were excluded from averaging. Grand averages were digitally filtered with a zero phase shift fourth-order Butterworth filter with a bandpass filter of 0.01–16 Hz.

Because our focus was the differences between in-rotation (rotated medially) and out-rotation (rotated laterally), we collapsed all conditions into six grand mean ERPs (two directions of rotation: in-rotation/out-rotation × three magnitudes of rotation: 45°, 90° and 135°). Furthermore, to improve the signal-to-noise ratios, the data of the left and right hands were collapsed according to orientation of the hand (e.g., combining data for left hand 45° and right hand 315°). The average amplitude of the epoch 200–800 ms after stimuli presentation was used as the dependent variable. A 2 × 3 × 15 repeated measures analysis of variance (ANOVA) was performed on the ERP amplitude at 15 electrodes (F7, F3, Fz, F4, F8, T7, C3, Cz, C4, T8; P7, P3, Pz, P4, P8) with factors of direction of rotation (in-rotation and out-rotation), degree of rotation (45°, 90°, 135°), and 15 electrodes.

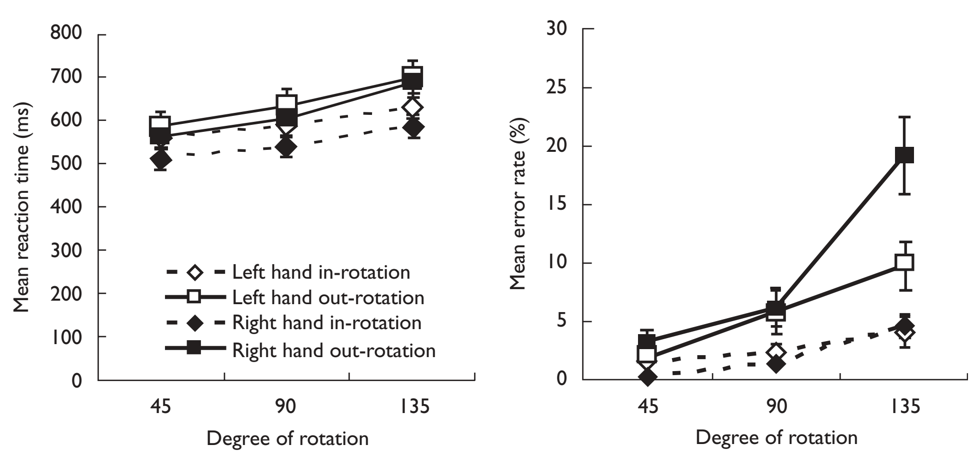
Results

Behavioral performance

Mean accuracy and response times were calculated for each participant under each condition. Fig. 2 shows the mean reaction times (RT) for the correct responses (Fig. 2a) and the mean error in percentages (Fig. 2b) of all 16 participants. In both rotation directions, the response times and error rates increased systematically as a function of angular disparity from the upright condition. Participants' reaction times were shorter in the in-rotation condition than in the out-rotation condition, whereas their performances were more accurate under the in-rotation condition than in the out-rotation condition.

The RTs for the correct trials were analyzed in a two (hand picture: left hand vs. right hand) × two (In-rotation vs. Out-rotation) × three (45° rotation, 90° rotation, and 135° rotation) repeated measures ANOVA. The significant main effects of the hand picture [$F(1,15) = 4.657$, $P = 0.048$], direction of rotation [$F(1,15) = 17.785$, $P = 0.001$], and degree of rotation [$F(2,30) = 62.248$, $P = 0.000$] were obtained. For interactions, only the interaction between the direction of rotation and the degree of rotation was significant [$F(2,30) = 4.752$, $P = 0.016$]. Fig. 2 shows that RTs were significantly shorter for the in-rotation than for out-rotation (572.981 vs. 632.473 ms). Moreover, RTs increased gradually as the hand rotated further from the upright condition (562.312 vs. 593.248 vs. 652.620 ms).

Fig. 2



Mean reaction time and error rate for the rotation as a function of the degree and direction of rotation.

The same ANOVA was conducted on error rate, and it was found that there was a significant main effect of direction of rotation [$F(1,15) = 16.963$, $P = 0.001$], with more error for the out-rotation than for the in-rotation (8.368 vs. 2.396%). Furthermore, the main effect of degree of rotation [$F(2,30) = 28.059$, $P = 0.000$] was found, with more error as the hand was rotated farther from the upright condition (1.823 vs. 4.167 vs. 10.156%). The main effect of the hand picture was not significant [$F(1,15) = 3.008$, $P = 0.103$]. Finally, there was a significant interaction between the direction of rotation and the degree of rotation [$F(2,30) = 22.701$, $P = 0.000$], hand picture and direction of rotation [$F(1,15) = 5.372$, $P = 0.035$], and hand picture and degree of rotation [$F(2,30) = 11.616$, $P = 0.000$].

As the interaction between the direction of rotation and degree of rotation for both reaction time and error rate was significant, we conducted multivariate analysis of variance to conduct further analysis. The result of simple effect analysis for reaction time showed that for all 45°, 90° and 135° conditions, the direction of in-rotation was quicker than that of out-rotation [$F(1,15) = 9.94$, $P = 0.007$; $F(1,15) = 11.12$, $P = 0.005$; $F(1,15) = 17.51$, $P = 0.001$]. The result of simple effect analysis for error rate showed that the difference between in-rotation and out-rotation was significant at 90° and 135° [$F(1,15) = 6.51$, $P = 0.022$, $F(1,15) = 28.39$, $P = 0.000$], whereas it was not at 45° [$F(1,15) = 3.62$, $P = 0.077$].

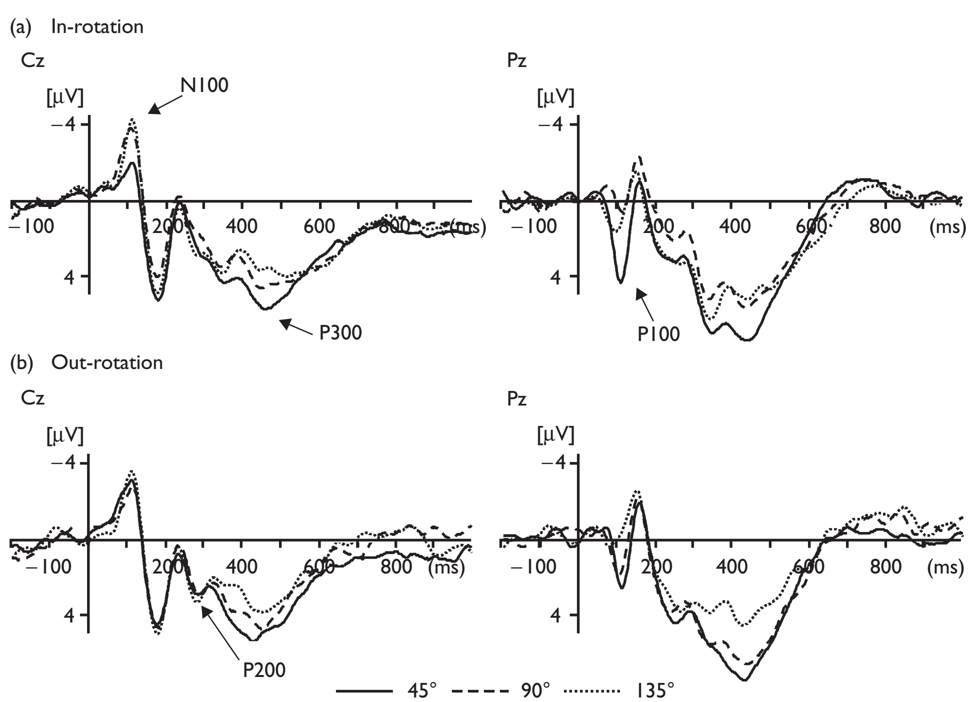
The effect of angle in this study exhibits the standard behavioral signature of mental rotation processing in this task: a monotonic increase in RT and error rates as a function of increasing angular disparity from the upright orientation. Meanwhile, the effect of out-rotation (that is, a laterally rotated hand was recognized more slowly and less accurately than a medially rotated hand) supports the idea that the processing of mental hand rotation in the left-right task is limited by the biomechanical constraints of the corresponding physical rotation. Thus, it is very likely that the participants employed an egocentric (motor imagery) mental rotation strategy to complete the task.

Event-related potentials results

As shown in Fig. 3, P1, N1, and P2 were elicited at Cz and Pz by all six conditions. The usual pattern of voltage for angle effect was found: an increase in degree of rotation resulted in a decrease in the amplitude of the slow wave's negative at a latency of 350–500 ms in both in-rotation and out-rotation conditions. The peak of P1 also showed this pattern in the parietal cortex.

The ANOVA results for the 50 ms windows from 200 to 800 ms indicated that the main effect of the direction of rotation reached statistical significance only in the time window of 250–300 ms [$F(1,15) = 5.139$, $P = 0.039$], but the direction of rotation and electrode interaction was also significant [$F(1,15) = 2.107$, $P = 0.018$]. The results

Fig. 3



Grand average event-related potentials at Cz and Fz as a function of the degree and direction of rotation.

of further simple effect analysis showed that the difference between in-rotation and out-rotation reached significance (all $P < 0.05$) in frontal (F7, F3, Fz, F4, F8) and central electrode (T7, C3).

The main effect of the degree of rotation was obtained during 350–500 ms [$F(2,30) = 3.262$, $P = 0.052$; $F(2,30) = 6.668$, $P = 0.004$; $F(2,30) = 4.337$, $P = 0.022$]. The amplitude was more positive for 45° than 90° ($P < 0.01$) and 135° ($P < 0.01$); the amplitude was also more positive for 90° than 135° ($P < 0.05$), which confirms that an amplitude of the time window 350–500 ms central, parietal sites' ERP is a monotonically decreasing function of angular disparity from the upright condition. The analysis of the peak amplitude of P1 also showed the significant main effect of the degree of rotation in the parietal cortex [$F(1,15) = 3.583$, $P = 0.039$]. During the time window 250–800 ms, all selected channels reached significance, with the maximum amplitude over midline located at Cz, Pz. To test the laterality of the effects, additional repeated measures ANOVA was run with three factors, namely, direction of rotation, laterality, and four electrodes (excluding three midline and other four frontal electrodes of 15 selected electrodes: left hemisphere, T7, C3, P7, P3; right hemisphere, C4, T8, P4, P8) during the time window 350–500 ms. The results show that there was no significant main effect nor was there an interaction in the hemisphere (all $P > 0.05$).

Discussion

This study sought to investigate the neural correlates of the mental rotation of human hands by focusing on whether the direction of rotation in in-rotation hand versus out-rotation hand results in different amplitude modulations during mental rotation processing. We also examined whether such mental rotation processing evoked a typical psychophysiological marker. The in-rotation effect was established through the following behavioral evidence: the significant difference between in-rotation and out-rotation on reaction time and accuracy showed that the direction of rotation had a strong effect on the judgment of the left or the right hand. Similar results were found in earlier research [7,9], which suggested mechanism of the biomechanical constraints of the human hand and indicated that when an external stimulus had to be compared with an internal representation of the hand, the participants will usually rely on their own hands and imagine rotations from their current position to the state of the stimulus to be judged. The imagined spatial trajectories they 'used' are very similar to the ones they would take physically. Accordingly, more difficult postures require longer, more awkward movements as well as longer times for execution and imagination.

The result of our high-density ERP recordings not only replicated but also extended observations from earlier studies using alphanumeric data as stimuli. It confirmed a parietal distribution for a 350–500 ms latency component that is considered to be an electrophysiological marker of mental rotation. Furthermore, it was found that the degree of rotation effect extends to the central and occipital cortex. Similar results were found in earlier studies [17]. In comparison with Thayer's research [1], however, our study found a shorter latency for the psychophysiological marker of mental rotation. This could be because that in our study we used a 3D picture of the back of the hand instead of pictures of both back and palm as stimuli. Meanwhile, the interesting result also revealed the orientation effect shown on the amplitude of P1, which was attributed to the early stage of encoding's visual processing or to visuoperceptual analysis over the parietal lobe. Therefore, early-stage visual encoding might be different when the rotated hand pictures were presented to the participants. In our research, this late negative amplitude was observed at 350–500 ms with a distinct distribution on the bilaterally central, parietal, and occipital cortex.

In addition, we did not find any significant difference between the left and right hemisphere. This result is consistent with some earlier findings (for example see Ref. [1]) of lack of lateralization using a similar task and the same ERP measure. The evidence for lateralization for mental rotation is, however, mixed in the literature. For example, a left lateralized activity was demonstrated for egocentric mental rotation [2,4,5,18] when body or body parts were used as mental rotation stimuli. The reason for the inconsistency between studies is unclear. It is conceivable that the probability of isolating difference between hemispheres (if there is any) could be affected by many factors such as the type of measurement, complexity of the stimuli, the sex of the participants, and so on.

The most important aspect of this experiment is the ERP components manifesting the effect of the rotating direction, which were distributed over the central cortex. As expected, the amplitude of the slow wave was less negative for the in-rotation hand stimuli than that for the out-rotation hand stimuli. These results also indicate that the rotating imagery of own-hand movement modulates the amplitude of rotation-related negativity. When the hand stimuli were presented, the encoding stage for in-rotation was the same as that for out-rotation. In contrast, in the stage of imaging the rotation of the participants' own hand, in-rotation elicited a more positive late slow wave than out-rotation most likely because of biomechanical constraints. This suggests that it is easier to imagine rotation under the in-rotation condition.

Conclusion

We showed that amplitude modulation over the parietal cortex can serve as a psychophysiological marker of the mental rotation of the hand in the left or right judgment task. The rotation-direction-dependent modulations of a positive slow wave provide evidence for the egocentric nature of the mental process (motor imagery).

Acknowledgements

This research was supported by grants from National Key Discipline of Basic Psychology in Southwest University (Grants NSKD05001, XGZ413062) and the Natural Sciences and Engineering Research Council of Canada.

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