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Visual image retention does not contribute to modulation of event-related potentials by mental rotation

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ABSTRACT

Rotation of a visual image in mind is associated with a slow posterior negative deflection of the event-related potential (ERP), termed rotation-related negativity (RRN). Retention of a visual image in short-term memory is also associated with a slow posterior negative ERP, termed negative slow wave (NSW). We tested whether short-term memory retention, indexed by the NSW, contributes to the RRN. ERPs were recorded in the same subjects in two tasks, a mental rotation task, eliciting the RRN, and a visual short-term memory task, eliciting the NSW. Over both right and left parietal scalp, no association was found between the NSW and the RRN amplitudes. Furthermore, adjusting for the effect of the NSW had no influence on a significant association between the RRN amplitude and response time, an index of mental rotation performance. Our data indicate that the RRN reflects manipulation of a visual image but not its retention in short-term memory.

1. Introduction

Visual imagery, the capacity to form and manipulate mental images, is an intriguing feature of the human mind. It is a major challenge for cognitive neuroscience to reveal how this process is accomplished by the brain. Among the varieties of visual imagery, the phenomenon of mental rotation has provided much insight into the nature of mental representations and visual-spatial reasoning (Cooper & Shepard, 1973; Corballis, 1997). Due to their high temporal resolution, event-related potentials (ERPs) are a particularly useful tool to assess the neural processing underlying mental rotation. Mental rotation is associated with a characteristic modulation of ERPs, referred to as rotation-related negativity (RRN, for a review see Heil, 2002). The RRN is a negative-going slow wave with peak amplitude located over the parietal scalp (Stuss, Sarazin, Leech, & Picton, 1983). It occurs with a latency of about 350 ms after the onset of visual stimuli that have to be rotated mentally and reduces the amplitude of the late positive complex. Therefore, the RRN is best detected as a difference negative wave when contrasting conditions that differ in rotation demands. The RRN is independent of stimulus type, as it has been observed for a variety of stimuli including abstract line figures (Desrocher, Smith, & Taylor, 1995; Inoue, Yoshino, Suzuki, Ogasawara, & Nomura, 1998; Ruchkin, Johnson, Canoune, & Ritter, 1991), 2D geometric shapes (Pierret, Peronnet, & Thevenet, 1994; Rösler, Heil, Bajric, Pauls, & Hennighausen, 1995; Rösler, Schumacher, & Sojka, 1990), symbols (Peronnet & Farah, 1989; Wijers, Otten, Feenstra, Mulder, & Mulder, 1989; Yan, Qiu, Zhu, & Tong, 2010), letter-like shapes (Núñez-Peña, Aznar, Linares, Corral, & Escera, 2005), drawings of hands (ter Horst, Jongsma, Janssen, van Lier, & Steenbergen, 2012; Thayer & Johnson, 2006; van Elk et al., 2010), and 3D perspective drawings of objects (Lamm, Fischmeister, & Bauer, 2005; Lamm, Windischberger, Leodolter, Moser, and Bauer, 2001; Schendan & Lucia, 2009; Vitouch, Bauer, Gittler, Leodolter, & Leodolter, 1997).

An important feature of the RRN is that its amplitude monotonically increases with increasing stimulus rotation angle. This corresponds strikingly well with the most salient behavioral finding in mental rotation tasks, which is a monotonous increase in response latencies as a function of stimulus angular deviation (Peronnet & Farah, 1989; Wijers et al., 1989). It has therefore been proposed that the RRN might be a specific ERP correlate of the mental rotation process proper. Further research was consistent with this idea (Rösler et al., 1990). For instance, Heil and co-workers

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demonstrated that the RRN is independent of stimulus classification (Heil, Bajric, Rosler, & Henninghausen, 1996). They also demonstrated that the RRN overlaps in time with the mental rotation process. For instance, the onset of the RRN is delayed when initial stimulus processing, which precedes mental rotation, is prolonged (Heil & Rolke, 2002). In our own previous study, we addressed the specificity of the RRN by studying individual differences in rotation ability (Riečanský & Jagla, 2008). We found that rotation skill, indexed by the time needed to solve the task, was predicted by the RRN amplitude. However, this was only true when EEG signals were averaged with respect to response, but not to stimulus onset (cf. Beste, Heil, & Konrad, 2010a and Beste, Heil, Domschke, and Konrad, 2010b). This indicates that neural processes of mental rotation are tapped better by response-aligned ERPs than by the more common approach to compute ERPs aligned with stimulus onset. In response-aligned ERPs the RRN was observed from about 600 ms before response and peaked at about 400 ms before response (Riečanský & Jagla, 2008).

Despite these findings, however, conclusive evidence that the RRN indeed reflects the rotational operation proper is still missing. One hypothesis is that the RRN is related to maintenance of a visual image in short-term memory rather than to its manipulation. There is good evidence that mental images are maintained within short-term memory (Ganis & Schendan, 2011; Kosslyn, Ganis, & Thompson, 2001). This is consistent with current models of working memory, which postulate that short-term memory acts as a temporal buffer in which mental representations are accessible to cognitive operations (for recent review see, e.g., Baddeley, Eysenck, & Anderson, 2009). According to this view, retention of images in short-term memory is a prerequisite for mental image manipulation since only representations stored in short-term memory can be manipulated. A direct demonstration of the engagement of short-term memory in mental rotation was provided by Hyun and Luck (2007) who showed that retention of visual features in short-term memory interferes with mental rotation performance. In addition, the possibility that short-term memory retention contributes to the RRN is indicated by ERP studies of short-term memory which show that maintenance of information in visual short-term memory results in ERP modulations similar to those observed during mental rotation (see below). In short-term memory research, an ERP associated with short-term retention is usually referred to as the negative slow wave (NSW). Similarly to the RRN, the NSW (1) is a negative late slow potential, which peaks over posterior scalp, (2) shows amplitude increases with increasing task difficulty, and (3) reflects individual differences in cognitive ability (Lang, Starr, Lang, Lindinger, & Deecke, 1992; Mecklinger & Pfeifer, 1996; Ruchkin, Johnson, Grafman, Canoune, and Ritter, 1992; Ruchkin, Johnson, Grafman, Canoune, & Ritter, 1997; Ruchkin, Johnson, Canoune, and Ritter, 1990; Vogel & Machizawa, 2004; for reviews see Drew, McCollough, & Vogel, 2006; McCollough, Machizawa, & Vogel, 2007). In a recent study, Prime and Jolicoeur (2009) presented targets for mental rotation in the left or right visual hemifield, which evoked a negative sustained deflection over the contralateral hemisphere. This deflection closely resembled the lateralized NSW, which occurs when contralateral targets are maintained in short-term memory. However, it also had RRN characteristics, as its amplitude increased with stimulus angular deviation within the same time interval in which the RRN occurred. This suggests that the RRN might (at least in part) also reflect the activity related to retention in short-term memory and may not only be related to rotational operation (see also Pannebakker et al., 2011).

The aim of the present experiment was to directly test the hypothesis whether maintenance in short-term memory contributes to the RRN. We recorded ERPs in the same subjects in two tasks within one session. One task involved mental rotation of characters (Cooper & Shepard, 1973) and elicited the RRN. The other task was a delayed match-to-sample task and required precise retention of the orientation of characters in short-term memory. This task elicited the NSW during the delay interval. Our hypothesis was that if the RRN reflects both manipulation and retention of a visual image, we should find (1) a significant association between the NSW and the RRN, more specifically between the NSW amplitude and the increase in the RRN amplitude with increasing rotation demand, and (2) a contribution of the NSW to predictive power of the RRN modulation toward individual rotation ability.

2. Methods

2.1. Subjects

Thirty-two healthy volunteers (19 females, 13 males; mean age ± SD: 25.8 ± 3.5 years), mostly undergraduate students, participated in the experiment. Eight subjects were excluded as outliers since their task performance strongly deviated from the rest of the sample (see Section 2.6 for details). The final sample for analysis thus included 24 subjects (15 females, 9 males; mean age: 25.9 ± 4.2 years). The same participants were included for the analyses in both tasks. All subjects were right-handed (Oldfield, 1971), had normal or corrected-to-normal vision, and reported no history of mental or neurological disorders. All subjects signed informed consent with study participation. The study was conducted in accordance with the Declaration of Helsinki and local guidelines of the University of Vienna.

2.2. Procedure

The experiment was carried out in a darkened sound-attenuated EEG recording chamber. Subjects were seated in a comfortable chair. The experiment consisted of two tasks, a mental rotation (MR) task and a delayed match-to-sample task, which will hitherto be referred to as the delayed orientation discrimination (DOD) task. In both tasks, stimulus presentation was controlled by a PC using E-Prime 2.0 (Psychology Software Tools, Sharpsburg, Pennsylvania). Stimuli were displayed in the center of a CRT monitor screen. They were viewed binocularly from a distance of 114 cm and subtended 2° of visual angle. Subjects responded by pressing the keys 'F' and 'J' on a computer keyboard using their left and right index fingers respectively (see below for description of tasks including response options). Before the experiment, subjects were given written instructions how to perform the tasks and got acquainted with each task in a series of practice trials. For the MR task, blocks of 20 trials were introduced until the subject achieved at least 18 correct responses within the block. In these practice trials, no immediate feedback on the correctness of a response after a trial was provided. Many subjects reached this criterion already within the 1st practice block, and no subject required more than 3 blocks. This is a common finding, indicating that MR tasks as the one we used are usually easy to solve (Cooper & Shepard, 1973). For the DOD task, subjects were given as many practice trials as needed to feel confident in performing the task. The order of the tasks was counterbalanced across subjects.

2.3. Mental rotation task

The mental rotation (MR) task was a slightly modified version of the task used by Cooper and Shepard (1973) very similar to that used in our previous study (Riečanský & Jagla, 2008; Riečanský & Katina, 2010). Stimuli included the letters 'R', 'J', 'G', 'F', 'L', 'a', 'h', 'e', 'f', and 'r'. The letters were displayed in the upright position

(0°) or rotated clockwise by 90°, 135°, or 180°. In total there were 320 trials, i.e., 80 for each angular deviation. For each angle, each letter was presented four times in either canonical or mirror-reversed format. Presentation order of the stimuli was randomized. The subject's task was to judge whether the stimulus was presented in canonical or mirror-reversed format. According to previous evidence this required mental rotation in counter-clockwise direction (except for stimuli displayed at 0° rotation) (Cooper & Shepard, 1973; Liesefeld & Zimmer, 2011). Prior to stimulus presentation, a fixation cross was displayed for a time interval randomly varied between 1000 and 1500 ms (Fig. 1A). The character remained on the screen until the response was indicated (two-alternative forced choice). The response keys were counterbalanced across subjects. Breaks in stimulus presentation were included after 20 trials or whenever requested by the subject. Subjects were instructed to focus on precision while responding as fast as possible.

2.4. Delayed orientation discrimination task

In this task an image of a visually presented target stimulus had to be maintained in short-term memory during a delay interval in order to assess whether a probe stimulus presented after this interval was rotated with respect to the target. The target was the capital letter 'E, presented for 520 ms in an oblique orientation (45°, 135°, 270°, or 315°) randomly varied across trials (Fig. 1B). A single letter was used as target stimulus since pilot experiments had shown that the threshold for discrimination of orientation changes varied among different characters. The target presentation time was also chosen according to pilot tests, which had shown much compromised performance with shorter presentation times. The target was replaced by a random-dot mask, which was presented for a delay interval of 3000 ms. During this interval the subject had to keep the exact visual image of the probe stimulus in memory. The presentation of the mask was used to prevent formation of an afterimage and to increase similarity with the mental rotation task, where a stimulus was displayed on the screen until response. After the delay interval, the probe stimulus was presented. This was the same character but rotated by 2°, 4°, 6°, or 8° with respect to the target in either clockwise or counter-clockwise direction. The task was to judge in which direction the orientation of the probe deviated from that of the target. The probe stimulus remained on the screen until a response was given. The response keys were counterbalanced across subjects. In total 160 trials were presented, i.e., 40 for each target-to-probe offset (20 for leftward and 20 for rightward deviation).

2.5. EEG recording

The EEG signal was recorded from 61 equidistant scalp sites using sintered Ag-AgCl electrodes mounted on an elastic cap (EASYCAP GmbH, Herrsching, Germany). The scalp electrodes were referenced to a non-cephalic sternovertebral reference derivation (Stephenson & Gibbs, 1951). This is a joint lead from two electrodes, one placed over the sternal end of the right clavicula and the other over the processus spinosus of the vertebra prominens (7th vertebra), linked with an adjustable voltage divider (potentiometer). The potentiometer was adjusted individually to minimize intrusion of the electrocardiogram (ECG) into the EEG signal. Eye movements and blinks were monitored via electrooculograms (EOG) using bipolar montages (electrodes centered above and below the left eye for vertical EOG, electrodes placed on the outer canthi of each eye for horizontal EOG). The ground electrode was placed on the forehead. At each electrode the skin was scratched using a sterile needle and the electrodes were filled with degassed electrolyte gel to minimize skin potential artifacts and to lower electrode impedance, which was kept below 3 kΩ as verified by impedance measurements at the outset of the EEG experiment. The electrodes were connected to a 64-channel DC-amplifier (Ing. Zickler Ges.m.b.H., Pfaffstätten, Austria) and the signals were analog filtered in the range of 0–1000 Hz, sampled at 3000 Hz, and digitally down-sampled to 250 Hz resolution.

2.6. Data processing and statistical analyses

2.6.1. Behavioral data

2.6.1.1. MR task. Trials in which response time (RT) was shorter than 300 ms and longer than 3000 ms were discarded. For each subject, the percentage of correct responses and the mean RT of correct trials where calculated. Four subjects were excluded due

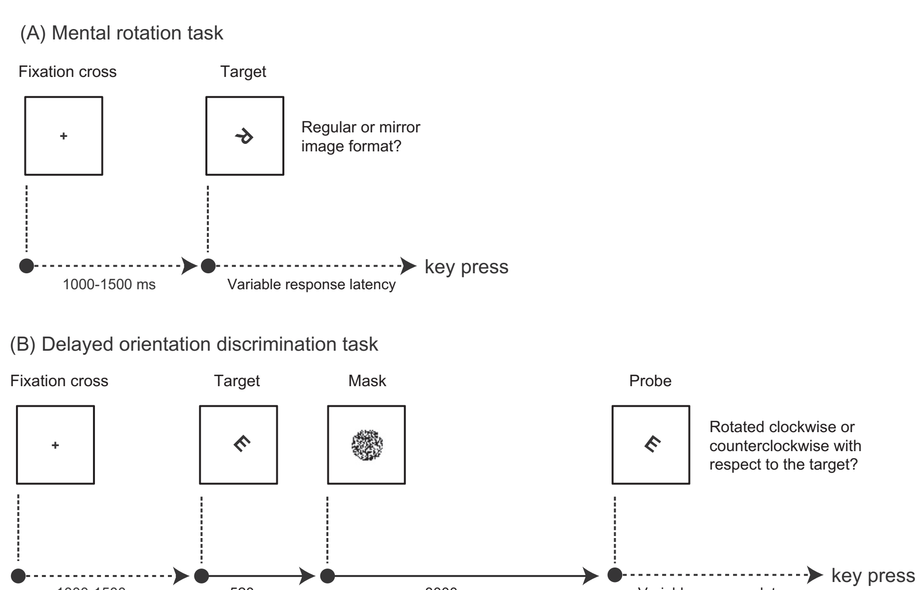

Fig. 1. A schematic depiction of the tasks. (A) mental rotation task; and (B) delayed orientation discrimination task. See text for detailed description of the stimuli and paradigms.

to exceptionally high number of errors or long RTs (exceeding the value $Q_3 + 1.5 \times IQR$, where Q_3 represents the 3rd quartile and IQR represents the interquartile range). One additional subject was excluded because he showed no increase in RT with increasing rotation angle, casting doubts on his compliance with task instructions and strategy. For the analyses in Sections 3.5, RT for the 0° condition was subtracted from RT at other angles (i.e., RT was centered to RT for the 0° location).

2.6.1.2. DOD task. Trials in which RT was shorter than 300 ms and longer than 3000 ms were discarded. For each subject, the percentage of correct responses was calculated for each target-to-probe angular disparity (2°, 4°, 6°, and 8°). In two subjects, the expected increase in accuracy as a function of angular disparity was not evident. In two other subjects, response accuracy even at the largest disparity did not exceed 75%, the cut-off value for random responding. Therefore, these 4 subjects were excluded (note that one of these subjects had also been identified as an outlier in the MR task).

2.6.2. EEG data

Processing and analysis of the EEG data was carried out using the EEGLAB toolbox (Delorme & Makeig, 2004) and MATLAB (The MathWorks, Massachussets). EEG signals were digitally filtered in the range 0.1–80 Hz. Data were carefully inspected and portions of data containing coarse artifacts were removed. Next, independent component analysis was performed (Delorme & Makeig, 2004). Components that separated artifactual signals (eye movements, eye blinks, ECG, muscle activity) were identified based on activity time course, topography and spectrum, and were eliminated from the data (Jung et al., 2000). Since previous research suggested that eye movements might be associated with mental rotation (Beste et al., 2010a and Beste, Heil, Domschke, and Konrad, 2010b) this procedure ensured that all explored ERP components were void of eye movement-related activity. Each epoch was then baseline corrected to the mean activity within 300 ms preceding target onset. Error trials were eliminated. ERPs were calculated by averaging single trial signals with respect to specific events. In the MR task, ERPs were calculated with respect to button press for each stimulus angular deviation. The rotation-related negativity (RRN) was calculated for the rotation conditions (90°, 135°, and 180°) by subtracting the ERPs of the non-rotation condition (0°). Average ERPs were calculated for right and left parietal regions of interest (ROI) defined based on the RRN topography (see Fig. 2). In the DOD task, epochs were truncated at the time of the onset of the probe stimulus and ERPs were calculated across all trials with signals aligned to the onset of the target stimulus. For quantitative analysis, mean amplitudes were calculated within selected time intervals for the parietal ROIs. Extreme values were winsorized (Wilcox, 2011) into the range $\langle Q_1 - 1.5 \times IQR, Q_3 + 1.5 \times IQR \rangle$, where Q_1 and Q_3 represent the 1st and the 3rd quartile respectively and IQR represents the interquartile range.

2.6.3. Statistical analyses

The statistical analyses were performed with R (R Development Core Team, 2012). All univariate null hypotheses about the equality of means where tested against two-sided alternatives at significance level $\alpha = 0.05$ by F-tests of repeated measures analysis of variance (ANOVA) and analysis of covariance (ANCOVA) models with fixed effects (as a univariate output of multivariate analysis of variance (MANOVA) and multivariate analysis of covariance (MANCOVA) models, respectively). The Greenhouse–Geisser correction was used in case the null hypothesis about sphericity had been rejected, using Mauchly's test. All multivariate hypotheses about zero association were tested against two-sided alternative at significance level $\alpha = 0.05$ by F-tests of the multivariate linear regression model (MLRM). Details of the models tested are presented in Appendix. The numbering of the models presented in the results section refers to the numbering as listed in Appendix.

3. Results

3.1. Performance

In the MR task, RT increased as a function of stimulus rotation angle (group mean ± SD, 0°: 804 ± 135 ms, 90°: 909 ± 178 ms, 135°: 987 ± 221 ms, 180°: 1235 ± 280 ms; Model 1: $F(3,69) = 99.666$, $\varepsilon_{GG} = 0.529$, $p < 0.001$). Response accuracy was very high and decreased slightly only at the largest angular deviation of stimuli (0°: 94 ± 5%, 90°: 92 ± 5%, 135°: 91 ± 6%, 180°: 84 ± 9%). This ceiling effect of the response accuracy is typical for mental rotation of characters and indicates that RT is the only informative performance indicator.

In the DOD task, proportion of correct responses increased as a function of target-probe angular disparity (2°: 65 ± 7%, 4°: 79 ± 9%, 6°: 88 ± 7%, 8°: 93 ± 7%). While judgments for the lowest disparity

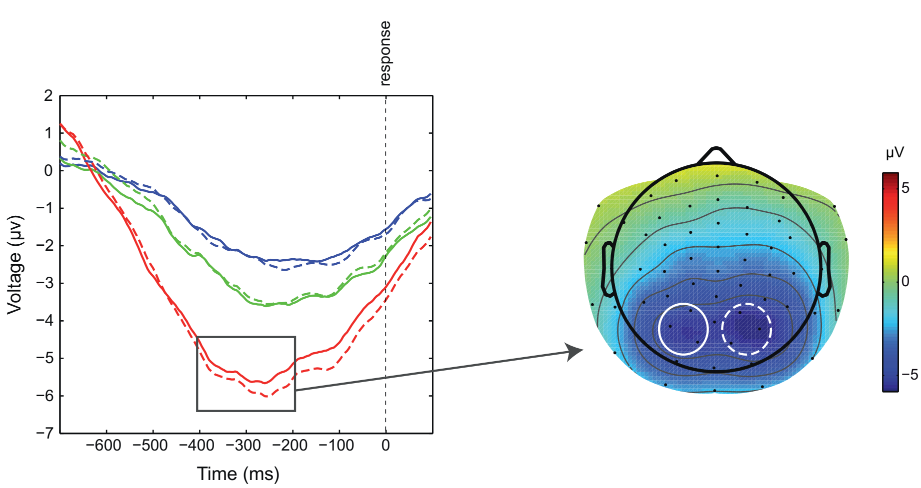

Fig. 2. The RRN recorded in the MR task (group average, $n = 24$). ERPs were calculated with respect to manual response; ERP of the non-rotation condition (0°) was subtracted from ERP of rotation conditions. Blue: 90°, green: 135°, red: 180°, solid line: average within the left ROI, dashed line: average within the right ROI. Vertical line indicates the time of the manual response. The topographical plot depicts the group mean RRN (180° – 0°) within 400–200 ms before response and the parietal ROIs from which ERP signals were analyzed.

were very close to chance level (50%), they were clearly above chance level for higher disparities.

3.2. The RRN

Fig. 2 depicts group average RRNs for both the right and left parietal ROIs and topography of the mean RRN calculated within 400–200 ms before response. The RRN amplitude increased as a function of stimulus rotation angle. For each subject and ROI, the mean RRN was calculated within 400–200 ms before response. The effect of rotation angle was highly significant (right ROI, Model 2.1: $F(2,46) = 21.962$, $\varepsilon_{GG} = 0.732$, $p < 0.001$; left ROI, Model 2.2: $F(2,46) = 18.061$, $\varepsilon_{GG} = 0.685$, $p = 0.001$). Modulation of the RRN with increasing rotation angle was larger over the right ROI (compare solid red with dashed red line in Fig. 2; Model 2.3: $F(2,46) = 3.666$, $\varepsilon_{GG} = 0.928$, $p = 0.037$).

3.3. The NSW

The group average ERP for the DOD task is shown in Fig. 3. A sustained negative deflection, the NSW, occurred during the delay period with latency of about 500 ms after mask onset and lasted till the onset of the probe stimulus. Since the voltage of the sustained wave was determined by a preceding large positive component the NSW amplitude was assessed as the difference between the mean ERP voltage within the interval 500–1000 ms (baseline) and 2000–3000 ms following mask onset (see the windows depicted in Fig. 3). The amplitude of the NSW within the ROIs was significantly negative (right ROI, Model 3.1: $F(1,23) = 29.713$, $p < 0.001$; left ROI, Model 3.2: $F(1,23) = 26.245$, $p < 0.001$) and was not significantly different between the ROIs (Model 3.3: $F(1,23) = 0.924$, $p = 0.346$).

3.4. The relationship between the NSW and the RRN

The NSW was unrelated to the RRN for both the right and left ROIs (right ROI, Model 4.1: $r = 0.402$; $F(3,20) = 1.287$, $p = 0.306$; left ROI, Model 4.2: $r = 0.325$, $F(3,20) = 0.788$, $p = 0.515$). Crucially, the NSW amplitude was also unrelated to the modulation of the RRN with increasing rotation angle (interaction of angle and the NSW; right ROI, Model 4.3: $F(2,44) = 0.423$, $\varepsilon_{GG} = 0.736$, $p = 0.598$; left ROI, Model 4.4: $F(2,44) = 0.806$, $\varepsilon_{GG} = 0.692$, $p = 0.413$).

3.5. The relationship between RT and the RRN: the effect of the NSW

RT increases with stimulus rotation angle and the magnitude of this increase are established indicators of individual mental rotation skill, with small RT increases indicating high rotation ability (Cooper & Shepard, 1973). The RRN also increases with increasing stimulus rotation angle. To properly assess the association between the increases in RT and the RRN with rotation angle, a multivariate correlation coefficient was calculated for matrices of differences between adjacent rotation angles, denoted RTd and RRNd, respectively. A significant association between the RTd and the RRNd was found for both the right and left ROIs (right ROI, Model 5.1: $r = 0.49$, 95% CI = (0.11, 0.75), $p = 0.015$; left ROI, Model 5.2: $r = 0.42$, 95% CI = (0.02, 0.71), $p = 0.040$). This association was negative as indicated by the Pearson's correlation coefficients, which were all negative at both levels of differences for both ROIs (values not shown). In order to determine the contribution of the NSW to this association, the correlation between the RTd and the RRNd was calculated using residuals of a multivariate linear regression of the RRNd on the NSW (Models 5.3 and 5.4). Such residuals, denoted "adjusted RRNd" (adjRRNd; since the RRNd is adjusted for the effect of the NSW), represent the portion of the RRNd which is unrelated to the NSW. Compared with the association between the RTd and the RRNd, the correlation between the RTd and the adjRRNd was only slightly weaker (right ROI, Model 5.5: $r = 0.48$, 95% CI = (0.10, 0.74), $p = 0.018$; left ROI, Model 5.6: $r = 0.40$, 95% CI = (0.00, 0.69), $p = 0.054$). Moreover, the correlation between the RRNd and the adjRRNd was very high (right ROI, Model 5.7: $r = 0.99$, 95% CI = (0.98, 1.00), $p < 0.001$; left ROI, Model 5.8: $r = 0.98$, 95% CI = (0.95, 0.99), $p < 0.001$). These findings indicate that the NSW does not contribute to the relationship between the increases in RT and RRN amplitudes with increasing rotation angle.

4. Discussion

In this study, we assessed the effects of visual short-term memory retention on ERP indicators of mental rotation. Performance and ERP measures recorded in both the short-term memory DOD task and the MR task were in good agreement with previous findings. In the MR task, RT and the RRN amplitude increased with increasing rotation demands, which are both defining features of mental rotation. In agreement with our own work (Riečanský & Jagla, 2008), we also found a significant association between the RRN amplitude and RT. Extent of the increase in RT with increasing

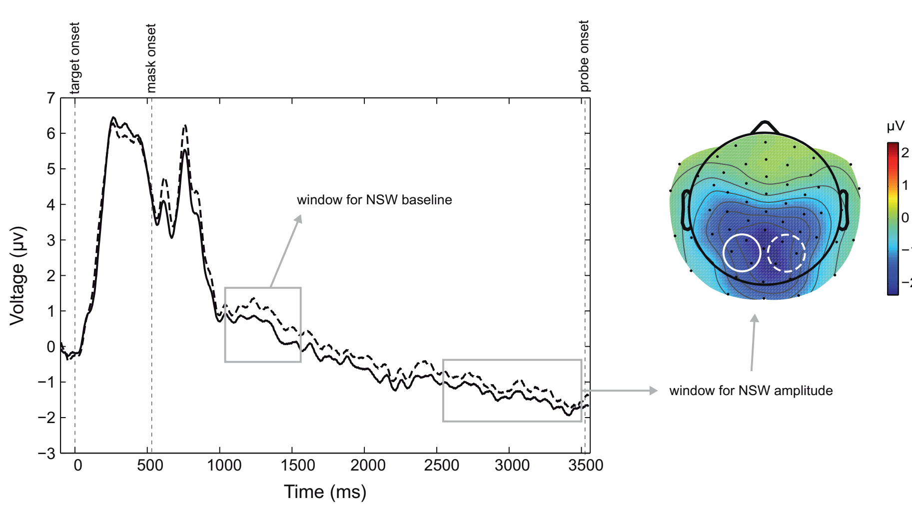

Fig. 3. ERPs recorded in the DOD task (group average, $n = 24$). Vertical lines indicate times of the onset of the target, mask, and probe stimuli. Windows indicate time intervals selected for baseline and amplitude assessment of the NSW. Solid line: average within the left ROI, dashed line: average within the right ROI. The topographical plot depicts the group mean NSW.

stimulus rotation angle represents an index of individual rotation ability, which is free of mental rotation-unspecific factors, such as basic psychomotor speed. The negative relationship between the increases in RT and the RRN indicates that brain processing related to mental rotation is more efficient in subjects with high rotation skill (Lamm, Bauer, Vitouch, & Gstättner, 1999; Rösler et al., 1995, for a general review see Neubauer & Fink, 2009). This association was a little stronger over the right than the left parietal cortex, which fits with evidence that mental rotation shows right hemispheric dominance (for a review see Corballis, 1997).

It is widely agreed that slow negative deflection of the ERP over the parietal cortex is linked to the processing of the MR task. However, there is controversy whether this reflects the computation of mental rotation per se. In particular, it is unclear how the RRN relates to short-term memory since retention of a visual image in short-term memory, which is exploited by mental rotation, is also associated with a posterior slow negative deflection of the ERP (Drew et al., 2006; McCollough et al., 2007). Furthermore, functional neuroimaging studies show that both maintenance in visual short-term memory and mental rotation activate several brain regions in common, in particular the posterior parietal cortex (mental rotation: Alivisatos & Petrides, 1997; Gogos et al., 2010; Milivojevic, Hamm, & Corballis, 2009; Podzebenko, Egan, & Watson, 2002; Weiss et al., 2009, for a review of mental rotation studies see Zacks, 2008; visual short-term memory retention, e.g.: Kaiser et al., 2010; Pollmann & von Cramon, 2000; Xu & Chun, 2006; for a review of short-term memory studies see Wager & Smith, 2003).

In the present study, the DOD task simulated the type of short-term memory engagement, i.e. visual image retention, exploited in mental rotation. The DOD task was designed to match the MR task as closely as possible. This not only required matching visual stimulation but also task difficulty and reliability of performance. The display of a masking pattern (rather than a blank screen) during the delay interval of the DOD task intended to approximate visual stimulation during the MR task, in which a visual stimulus was displayed until the judgment was indicated. Our pilot behavioral measurements showed that the judgments were highly variable when different letters were used as targets in the DOD task. Therefore, we decided to use a single target letter in oblique orientations. We do not expect that this exerts any influence on the results or the compatibility of the tasks since there is no evidence that neural processes of visual image retention differ among objects of a particular category, such as letters or digits, or other symbols and abstract two-dimensional objects (Ganis & Schendan, 2011). The duration of the target stimulus was also optimized based on pilot measurements and subjects' reports confirmed comparable difficulty of both tasks. An additional important aspect was that both tasks were performed within one EEG session.

In the DOD task, the judgment accuracy monotonically increased with increasing angular deviation between target and probe stimuli. This indicates that the subjects followed given instructions and appropriately carried out the task. Within the delay interval of the DOD task, during which a visual image of the target had to be maintained in short-term memory, the NSW was observed, as predicted from previous ERP studies on visual short-term memory (Drew et al., 2006; McCollough et al., 2007). The NSW was clearly present within the ROIs of the RRN confirming the possibility indicated by previous studies (in particular, Prime & Jolicoeur, 2009) that the NSW could contribute to the RRN. However, our analysis showed that the amplitude of the NSW was unrelated to the modulation of the RRN with increasing rotation angle, the defining feature of the RRN. Furthermore, the relationship between the RRN difference and rotation ability was not decreased after the RRN difference was adjusted for the effect of the NSW, which means that rotational manipulation, not retention, underlies the predictive utility of the RRN amplitude modulation toward mental rotation skill. Both findings indicate that the RRN does not reflect maintenance of a visual image in short-term memory, but rather indexes rotational manipulation upon it, as repeatedly suggested, but not directly tested, by previous work. At the same time, the results further support the idea that the NSW is a specific ERP correlate of short-term memory retention (Drew et al., 2006; McCollough et al., 2007).

Of course, this is not the end of the debate about the cognitive and neural processes underlying the RRN. For instance, it remains to be investigated whether the RRN selectively reflects rotational operation. Rotational operation seems to be a unique neurocognitive process. For instance, deficits in mental rotation may occur without concurrent impairment of other kinds of mental spatial transformation (Bricolo, Shallice, Priftis, & Meneghello, 2000). Therefore, it is conceivable that the RRN is a specific ERP correlate of rotational neural computation. In line with this hypothesis, Muthukumaraswamy, Johnson, and Hamm (2003) identified ERP differences between mental rotation and mental size-transformation and Milivojevic, Johnson, Hamm, and Corballis (2003) reported that ERPs associated with mental rotation and mental paper folding are not identical. However, to our knowledge, no study so far analyzed differences in ERPs between mental rotation and mental translation of objects, which are similar but not identical mental spatial transformations. In addition, the relationship between the RRN and central executive processes engaged in mental rotation remains to be established (Pannebakker et al., 2011). Our study shows that one useful approach to investigate the nature of the RRN may be to apply multivariate regression analyses to ERP data recorded in selected tasks in the same sample of subjects.

In conclusion, the results of our study indicate that the RRN relates to the manipulation of a visual image but not to its retention in short-term memory.

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Appendix

Here, we provide details about the statistical models used throughout this paper. Models are presented in a (slightly) modified version of Rogers–Wilkinson notation (Wilkinson & Rogers, 1973) and are described in the form of *endpoint* $\approx$ *predictor*(*s*) followed by the model abbreviation in brackets, dimensions of the variables, and tested hypotheses of interest (null hypothesis – H_0, alternative hypothesis – H_1). The first dimension reflects the number of subjects. For RTd, RRNd, and adjRRNd the second dimension is equal to 2 since having three rotations angles we get two differences (difference #1: 135° – 90° and difference #2: 180° – 135°). The numbers of the models correspond to the numbering in the results section.

1. *Model 1: RT* $\approx$ *rotation angle* [ANOVA], RT (vector 24×1) at 4 rotation angles, H_0: the means of RT at each rotation angle are equal, H_1: there is at least one pair of rotation angles for which the means of differences of RT are not equal.
2. *Model 2.1: RRN*(*right ROI*) $\approx$ *rotation angle* [ANOVA], RRN (vector 24×1) at 3 rotation angles, H_0: the means of RRN(right ROI) at each rotation angle are equal, H_1: there

is at least one pair of rotation angles for which the means of differences of RRN(right ROI) are not equal.

Model 2.2: RRN(left ROI) ≈ rotation angle [ANOVA], RRN (vector 24 × 1) at 3 rotation angles, H_0: the means of RRN(left ROI) at each rotation angle are equal, H_1: there is at least one pair of rotation angles for which the means of differences of RRN(left ROI) are not equal.

Model 2.3: RRN(right ROI) – RRN(left ROI) ≈ rotation angle [ANOVA], RRN (vector 24 × 1) at 3 rotation angles, H_0: the differences of the means between RRN(right ROI) and RRN(left ROI) at each rotation angle are equal, H_1: there is at least one pair of rotation angles for which the means of differences between RRN(right ROI) and RRN(left ROI) are not equal.

3. *Model 3.1: NSW(right ROI) ≈ mean* [ANOVA], NSW (vector 24 × 1), H_0: the mean of NSW(right ROI) is equal to zero, H_1: the mean of NSW(right ROI) is not equal to zero.

   Model 3.2: NSW(left ROI) ≈ mean [ANOVA], NSW (vector 24 × 1), H_0: the mean of NSW(left ROI) is equal to zero, H_1: the mean of NSW(left ROI) is not equal to zero.

   Model 3.3: NSW(right ROI) – NSW(left ROI) ≈ mean [ANOVA], NSW (vector 24 × 1), H_0: the difference of the means between NSW(right ROI) and NSW(left ROI) is equal to zero, H_1: the difference of the means between NSW(right ROI) and NSW(left ROI) is not equal to zero.

4. *Model 4.1: RRN(right ROI) ≈ NSW(right ROI)* [MLRM], RRN (matrix 24 × 3), NSW (vector 24 × 1), H_0: multivariate correlation coefficient of RRN(right ROI) and NSW(right ROI) is equal to zero, H_1: multivariate correlation coefficient of RRN(right ROI) and NSW(right ROI) is not equal to zero.

   Model 4.2: RRN(left ROI) ≈ NSW(left ROI) [MLRM], RRN (matrix 24 × 3), NSW (vector 24 × 1), H_0: multivariate correlation coefficient of RRN(left ROI) and NSW(left ROI) is equal to zero, H_1: multivariate correlation coefficient of RRN(left ROI) and NSW(left ROI) is not equal to zero.

   Model 4.3: RRN(right ROI) ≈ rotation angle + rotation angle: NSW(right ROI) [ANCOVA], RRN (vector 24 × 1) at 3 rotation angles, NSW (vector 24 × 1, the same for all 3 rotation angles), H_0: the slopes of three regression lines (at each rotation angle) of RRN(right ROI) on NSW(right ROI) are equal; H_1: there is at least one pair of rotation angles, for which the slope of regression line of a difference of RRN(right ROI) on NSW(right ROI) is not equal to zero.

   Model 4.4: RRN(left ROI) ≈ rotation angle + rotation angle: NSW(left ROI) [ANCOVA], RRN (vector 24 × 1) at 3 rotation angles, NSW (vector 24 × 1, the same for all 3 rotation angles), H_0: the slopes of three regression lines (at each rotation angle) of RRN(left ROI) on NSW(left ROI) are equal, H_1: there is at least one pair of rotation angles, for which the slope of regression line of a difference of RRN(left ROI) on NSW(left ROI) is not equal to zero.

5. *Model 5.1: RRNd(right ROI) ≈ RTd* [MLRM], RRNd (matrix 24 × 2), RTd (matrix 24 × 2), H_0: multivariate correlation coefficient of RRNd(right ROI) and RTd is equal to zero, H_1: multivariate correlation coefficient of RRNd(right ROI) and RTd is not equal to zero.

   Model 5.2: RRNd(left ROI) ≈ RTd [MLRM], RRNd (matrix 24 × 2), RTd (matrix 24 × 2), H_0: multivariate correlation coefficient of RRNd(left ROI) and RTd is equal to zero, H_1: multivariate correlation coefficient of RRNd(left ROI) and RTd is not equal to zero.

   Model 5.3: RRNd(right ROI) ≈ NSW(right ROI) [MLRM], RRNd (matrix 24 × 2), NSW (vector 24 × 1), the residuals of this model, denoted adjRRNd(right ROI), are used in the model 5.5.

   Model 5.4: RRNd(left ROI) ≈ NSW(left ROI) [MLRM], RRNd (matrix 24 × 2), NSW (vector 24 × 1), the residuals of this model, denoted adjRRNd(left ROI), are used in the model 5.6.

   Model 5.5: adjRRNd(right ROI) ≈ RTd [MLRM], adjRRNd (matrix 24 × 2), RTd (matrix 24 × 2), H_0: multivariate correlation coefficient of adjRRNd(right ROI) and RTd is equal to zero, H_1: multivariate correlation coefficient of adjRRNd(right ROI) and RTd is not equal to zero.

   Model 5.6: adjRRNd(left ROI) ≈ RTd [MLRM], adjRRNd (matrix 24 × 2), RTd (matrix 24 × 2), H_0: multivariate correlation coefficient of adjRRNd(left ROI) and RTd is equal to zero, H_1: multivariate correlation coefficient of adjRRNd(left ROI) and RTd is not equal to zero.

   Model 5.7: adjRRNd(right ROI) ≈ RRNd(right ROI) [MLRM], adjRRNd (matrix 24 × 2), RRNd (matrix 24 × 2), H_0: multivariate correlation coefficient of adjRRNd(right ROI) and RRNd(right ROI) is equal to zero, H_1: multivariate correlation coefficient of adjRRNd(right ROI) and RRNd(right ROI) is not equal to zero.

   Model 5.8: adjRRNd(left ROI) ≈ RRNd(left ROI) [MLRM], adjRRNd (matrix 24 × 2), RRNd (matrix 24 × 2); H_0: multivariate correlation coefficient of adjRRNd(left ROI) and RRNd(left ROI) is equal to zero; H_1: multivariate correlation coefficient of adjRRNd(left ROI) and RRNd(left ROI) is not equal to zero.

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