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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