

available at [www.sciencedirect.com](http://www.sciencedirect.com)[www.elsevier.com/locate/brainres](http://www.elsevier.com/locate/brainres)
**BRAIN  
RESEARCH**

## Research Report

# Visual object cognition precedes but also temporally overlaps mental rotation

Haline E. Schendan\*, Lisa C. Lucia

Tufts University, USA

### ARTICLE INFO

#### Article history:

Accepted 15 July 2009

Available online 23 July 2009

#### Keywords:

Mental rotation

Parietal cortex

Temporal lobe

Visual object cognition

Spatial cognition

Event-related potentials

### ABSTRACT

Two-dimensional, mental rotation of alphanumeric characters and geometric figures is related to linear increases in parietal negativity between 400 and 800 ms as rotation increases, similar to linear increases with rotation in response times. This suggests that the frontoparietal networks implicated in mental rotation are engaged after 400 ms. However, the time course of three-dimensional object mental rotation using the classic Shepard–Metzler task has not been studied, even though this is one of the most commonly used versions in behavioral and neuroimaging work. Using this task, this study replicated a prior neuroimaging version using event-related potentials. Results confirmed linear mental rotation effects on performance and parietal negativity. In addition, a frontocentral N350 complex that indexes visual object cognition processes was more negative with mental rotation and showed linear trends at frontopolar sites from 200 to 700 ms and centrofrontal sites from 400 to 500 ms. The centrofrontal negativity has been implicated in object working memory processes in ventrolateral prefrontal and occipitotemporal areas. The frontopolar N350 has been implicated in processes that compute the spatial relations among parts of objects to resolve visual differences between object representations and enable an accurate cognitive decision involving a network of ventrocaudal intraparietal, ventral premotor, and inferotemporal cortices. Overall, the time course indicates that visual object cognition processes precede (200–500 ms) but also overlap the initial phase of mental rotation (500–700 ms) indexed by parietal negativity.

© 2009 Elsevier B.V. All rights reserved.

## 1. Introduction

The dorsal visual pathway has a well-established role in spatial cognition, and one of the most well-established spatial cognitive tasks is mental rotation. On the classic Shepard–Metzler mental rotation task (Shepard and Metzler, 1971), people see a pair of novel cube objects rotated relative to each other along an axis in one of three-dimensions (3D), and they decide whether the two objects are the “same” (i.e., identical objects) or “different” (i.e., left–right mirror images of each

other). The typical behavioral finding is that response time (RT) and errors increase linearly as the angular disparity between the two objects increases (Shepard and Cooper, 1982). This linear rotation curve has been interpreted as evidence that people imagine an object moving through space along the same continuous trajectory during mental rotation as if they were physically rotating it. Neuropsychological and neuroimaging findings implicate the intraparietal sulcus (IPS) in the critical process of mental rotation with Shepard–Metzler objects and other materials, like alphanumeric characters

\* Corresponding author. Department of Psychology, Tufts University, 490 Boston Avenue, Medford, MA 02155, USA. Fax: +1 617 627 3181.  
E-mail address: [Haline\\_E.Schendan@tufts.edu](mailto:Haline_E.Schendan@tufts.edu) (H.E. Schendan).  
URL: <http://www.ase.tufts.edu/psychology/vmn> (H.E. Schendan).

(e.g., Podzebenko et al., 2002; Podzebenko et al., 2005). Event-related brain potentials (ERPs) indicate that the mental rotation process for in-plane rotation (i.e., in two-dimensions, 2D) is indexed by slow parietal negativity between 400 and 800 ms or until the response (e.g., Heil, 2002; Rieccansky and Jagla, 2008). However, while the classic Shepard–Metzler mental rotation task has been studied using neuroimaging, the time course of this classic version has not been determined using ERPs, nor has 3D (in-depth) rotation been assessed. The present study replicated a prior fMRI study of Shepard–Metzler, object mental rotation in-depth (Schendan and Stern, 2007) with ERPs. Besides assessing the timing of parietal negativity, this study aimed to assess when visual object cognition processes contribute to object mental rotation, as some theories suggest that it precedes mental rotation (Corballis, 1988; Shepard and Cooper, 1982), while others suggest some limited overlap (Ruthruff and Miller, 1995). To do so, we assessed the timing of the frontocentral N350 complex between 200 and 500 ms that indexes visual object cognition processes (Schendan and Maher, 2009).

Neuropsychological studies of patients with parietal damage and neuroimaging research on mental rotation has focused primarily on anterior and superior parts of IPS in the superior parietal lobule (SPL). Neuroimaging shows mental rotation effects in parietal cortex with a variety of mental rotation stimuli and paradigms (as reviewed by Zacks, 2008). The SPL is consistently activated in Shepard–Metzler object and other mental rotation tasks, and this region is considered to be a component of the critical mental rotation process (Gauthier et al., 2002; Jordan et al., 2002; Kosslyn et al., 1998; Schendan and Stern, 2007; Tagaris et al., 1997; Zacks, 2008). However, parts of the SPL activated during mental rotation include the posterior eye fields (Schendan and Stern, 2007), and the SPL is commonly implicated as part of a working memory network of frontal and superior IPS regions (Courtney et al., 1998; Courtney, 2004) that is more involved in spatial than nonspatial working memory (Sayala et al., 2006), and may have an especially important role in actively maintaining spatial representations across a delay period (Postle, 2006). This raises the possibility that the SPL has a more generic role in mental rotation related to spatial transformation for saccade planning and/or spatial working memory.

Another candidate region for the critical mental rotation process is the ventral caudal IPS (vcIPS) region, which includes the right vcIPS proper and the adjacent transverse occipital sulcus (TOS) bilaterally. Functional magnetic resonance imaging (fMRI) studies using the Shepard–Metzler object mental rotation task indicate that this vcIPS region is a critical region for the spatial transformation process in mental rotation as it contributes to the scaling of mental rotation task performance with angular disparity. fMRI studies with a parametric design have found that activity in the vcIPS region increases linearly with larger angles of rotation, similar to the behavioral findings (Carpenter et al., 1999; Harris et al., 2000; Podzebenko et al., 2002; Zacks, 2008). This vcIPS region is a dorsal object-sensitive region that is more active for intact than scrambled objects (Schendan and Stern, 2007), and activated for unusual than canonical views and more than less rotated views on object categorization and recognition tasks (Gauthier et al., 2002; Schendan and Stern, 2008). Related behavioral findings show

that RTs increase as objects are rotated farther from their canonical (“best”) or a studied view (Tarr and Pinker, 1989; Schendan and Kutas, 2003; Schendan and Stern, 2008; Schendan and Lucia, submitted for publication-a). This is consistent with multiple-views-plus-transformation accounts of visual object cognition (Tarr and Pinker, 1989), which predict that spatial transformation processes critical for mental rotation should be activated for unusual or noncanonical views in order to bring them into alignment (or spatial correspondence) with stored view representations in memory, while canonical views do not require this additional spatial transformation. Altogether, these findings suggest that the vcIPS region has the most common, critical, and important role in scaling of object cognition performance depending upon how much spatial transformation is needed in order to achieve a match between perceived and/or mental representations of objects, that is, in object mental rotation, categorization, and recognition tasks.

The present study aimed to assess a subcomponent of the N350 complex with a frontopolar scalp distribution that seems to index this vcIPS region, as well as ventral premotor (PMv; BA 44/6) and inferotemporal sulcus (ITS) regions that are part of a frontal–posterior network for computing the relative spatial relations among parts of objects, and, if necessary, transforming the visual spatial structure of objects to facilitate pattern matching (Schendan and Stern, 2008; Schendan and Lucia, submitted for publication-b). The frontocentral N350 complex is thought to index core processes for visual object cognition, including object model selection: selecting the best match in memory for the visual structure of the perceived object (Schendan and Maher, 2009). Accordingly, this ERP complex is modulated with the success of this matching process, as negativity is greater to less than more successfully categorized pictures of known objects (Folstein and Van Petten, 2004; Gratton et al., 2009; Schendan and Kutas, 2002; Schendan and Maher, 2009). The functional significance of the N350 complex is described in the two-state interactive account of visual object cognition that posits object model selection occurs after the initial, fast, bottom-up pass (the first state) through the ventral stream, during a second state of prefrontal and posterior interactions after 200 ms, indexed by the frontocentral N350 complex (Schendan and Kutas, 2007; Schendan and Stern, 2008; Schendan and Maher, 2009). This state can be considered a second state of perceptual encoding of the object (i.e., perceptual analysis of object shape, including the spatial configuration of features and perhaps also orientation determination) that involves recurrent and feedback inputs to neurons along the ventral stream from other brain structures, such as prefrontal and parietal cortex. Such neural computations are crucial for reactivating memory about the object to support diverse object cognition tasks, like categorization and recognition, as well as for visual object learning (Carpenter et al., 1992; David et al., 2005; Lamme and Roelfsema, 2000; Scott et al., 2006). Such processes would also be expected to play a critical role in perceptual analysis for object mental rotation.

The spatiotemporally overlapping but functionally distinct subcomponents of this ERP complex are: at frontopolar sites, a P250 (200–300 ms), N350 (300–400 ms), and N450 (400–500 ms), and, at centrofrontal sites, an N350 (300–400 ms), and N390 (390–500 ms), and these can have occipitotemporal

counterparts with inverted polarity (Ganis et al., 1996; Ganis and Kutas, 2003; McPherson and Holcomb, 1999; Schendan and Kutas, 2003; Schendan and Maher, 2009). While the centrofrontal subcomponents have a greater role in categorization, the frontopolar subcomponents have a more task-general role in visual object cognition. The frontopolar P250 and N350 subcomponents index model selection of more perceptually-specific object knowledge, while the frontopolar N450 and centrofrontal subcomponents index model selection of more abstract (i.e., less perceptually-specific) object knowledge (Ganis and Kutas, 2003; Schendan and Maher, 2009). The frontopolar ERPs are larger for unusual than canonical views by 200 ms post-stimulus onset during categorization and recognition tasks (Schendan and Lucia, submitted for publication-a; Schendan and Kutas, 2003). This suggests that an orientation-dependent process, such as the spatial transformation computation in the vCIPS region, occurs during the N350, and facilitates object model selection to achieve visual constancy of cognitive performance (i.e., accurate cognitive decisions despite changes in viewing conditions, like orientation changes). This is consistent with one prior ERP mental rotation study that reported greater negativity for more than less rotation on a similar frontal negative-going ERP (Ruchkin et al., 1991). Thus, here, we focused on the frontopolar N350, and predicted greater negativity with mental rotation.

Prior ERP studies have focused on a late parietal negativity between 400 and 800 ms that increases monotonically as stimuli require increasing degrees of mental rotation (reviewed by Heil, 2002). The negativity is maximal over parietal scalp locations, and increases as rotation in-plane increases away from the normal upright, starting from ~250 to 420 ms until ~700 to 800 ms, reducing an overlapping late positive complex (LPC). In most of these ERP studies, an alphanumeric character in the canonical image (e.g., “R”) or a mirror-reversed version was shown in the standard upright or one of several 2D rotated orientations. Participants judged whether the character was the canonical image or mirror-reversed, regardless of rotation. Behavioral results show the typical linear increase in RT with greater angular disparity (Shepard and Cooper, 1982; Heil, Bajric, Rosler, and Hennighausen, 1996). However, as all past ERP studies used 2D rotations of alphanumeric characters (e.g., Peronnet and Farah, 1989; Rieckensky and Jagla, 2008) or meaningless stick figures (e.g., Ruchkin, Johnson, Canoune, and Ritter, 1991), but never the Shepard–Metzler task and 3D rotations, it remains unknown whether this time course applies also to mental rotation during this classic object mental rotation task and for 3D rotations, not just 2D. For example, the timing may have been underestimated because identifying alphanumeric characters misoriented in 2D produces shorter RTs than the classic Shepard–Metzler version.

The present experiment compared the time course of cortical activity recruited for the task of mental rotation using the classic pairs of Shepard–Metzler cube objects and depth rotations. Participants decided whether two objects, which are simultaneously presented, are identical (i.e., the same) or mirror images of each other (i.e., different), regardless of angular displacement, called a *parity judgment* task. RTs were predicted to increase linearly with greater angular displacement, the classic effect. Further, because ERP studies of

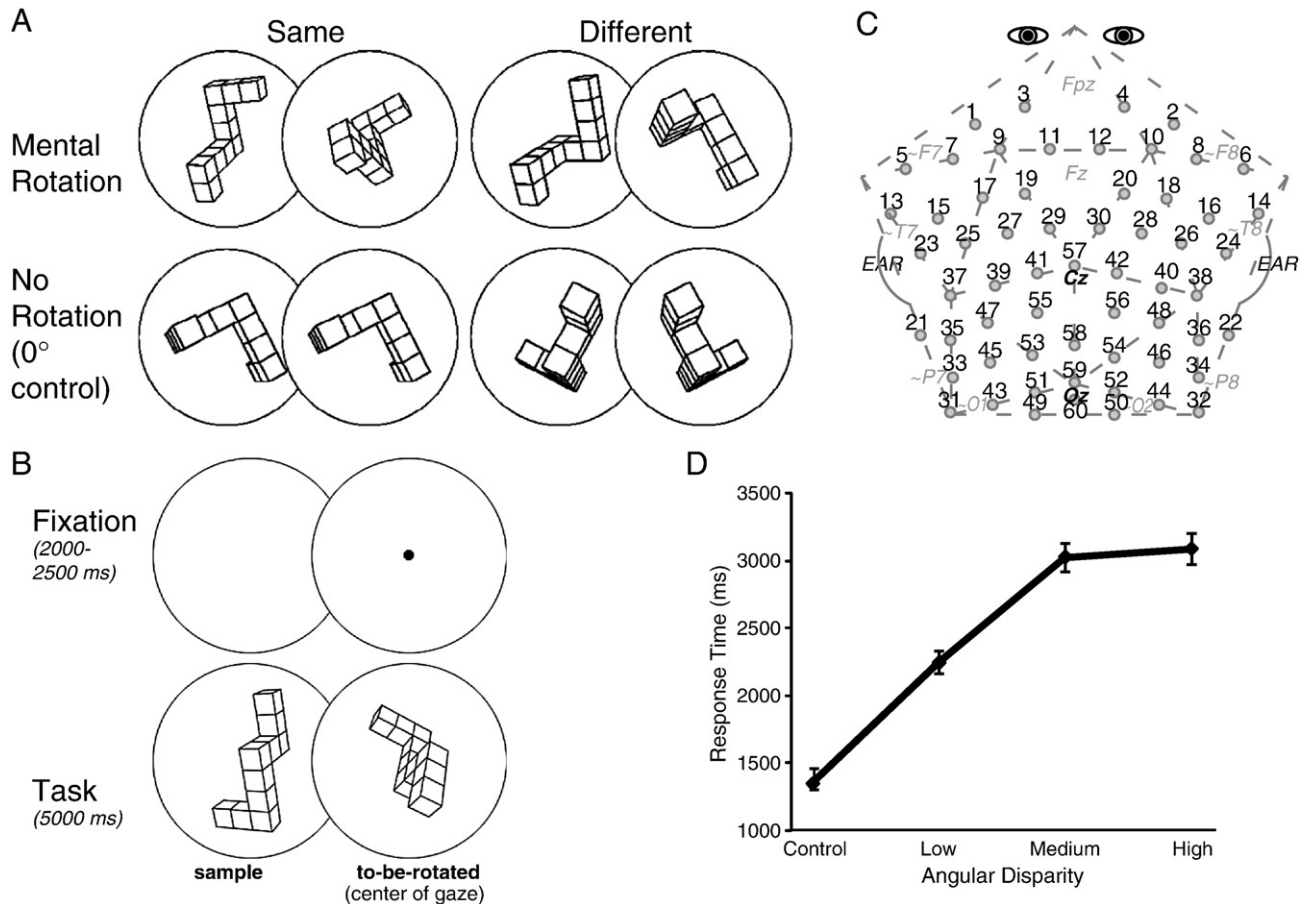
unusual views of objects suggests that a spatial transformation process may be recruited earlier than the parietal negativity, specifically during the N350 complex (Schendan and Kutas, 2003; Schendan and Lucia, submitted for publication-a), we expected that, as orientation disparity in depth increases between pairs of 3D Shepard–Metzler cube objects, there will be corresponding linear increases in negativity for both the N350 from 200 to 500 ms and the parietal negativity from 500 to 900 ms. This object mental rotation task provides a crucial link between behavioral studies of object mental rotation in normal and neurological patients (e.g., Amick et al., 2006; Olesen et al., 2007; Shepard and Cooper, 1982), and fMRI and ERP studies of mental rotation, visual object categorization, and recognition (Heil, 2002; Schendan and Kutas, 2003; Schendan and Stern, 2007; Schendan and Stern, 2008; Schendan and Lucia, submitted for publication-b).

## 2. Results

### 2.1. Performance

The characteristic increase in mean RTs with higher rotation (Fig. 1D) was significant ( $F[3, 69]=226.60, p<.001$ ). The planned linear contrast demonstrated that the typical linear mental rotation curve was obtained ( $F=393.79, p<.001$ ). Planned pairwise comparisons showed significant increases with rotation angle for control ( $M=1343$ ) versus low ( $M=2237$ ;  $F=174.75, p<.001$ ), and low versus medium ( $M=3018$ ;  $F=178.20, p<.001$ ), but not medium versus high ( $M=3080$ ;  $F=1.83, p=.189$ ). Performance data were re-analyzed without the 180° condition, which can differ from other high rotations (Metzler and Shepard, 1982): 140° and 160° rotations for the high level ( $M=3111$  ms). Rotation was still significant ( $F[3, 69]=216.26, p<.001$ ) as was the planned contrast for a linear mental rotation curve ( $F=356.12, p<.001$ ). The planned pairwise comparison still did not show a difference between medium and this high condition ( $F=.91, p=.351$ ). As the pattern of results was the same as when the high condition included 180°, levels in the Rotation factor from this point on will include 180° to have the most trials.

As prior research suggested that mental rotation processes differ between genders (Gootjes et al., 2008; Heil and Jansen-Osmann, 2008; Masters and Sanders, 1993), RTs were compared between females ( $n=22$ ) and males ( $n=9$ ). Separately, both the male and female group exhibited the same pattern of behavioral effects. Results showed significant main effects of Rotation ( $F_s>91.57, p_s<.001$ ) that also showed significant linear trends ( $F_s>101.21, p_s<.001$ ). Pairwise comparisons among these subgroups also yielded the same results as the entire group; separately, both groups showed significant effects for comparisons of control versus low and low versus medium such that RTs were longer with larger rotation conditions. There were no significant differences between medium and high rotation conditions. T-tests that compared mean RTs for each rotation condition (control, low, medium, high) between males and females were non-significant. This is consistent with a report by Peters and Battista (2008) finding either small or no gender differences in Shepard–Metzler mental rotation tasks when stimuli are presented in pairs, as



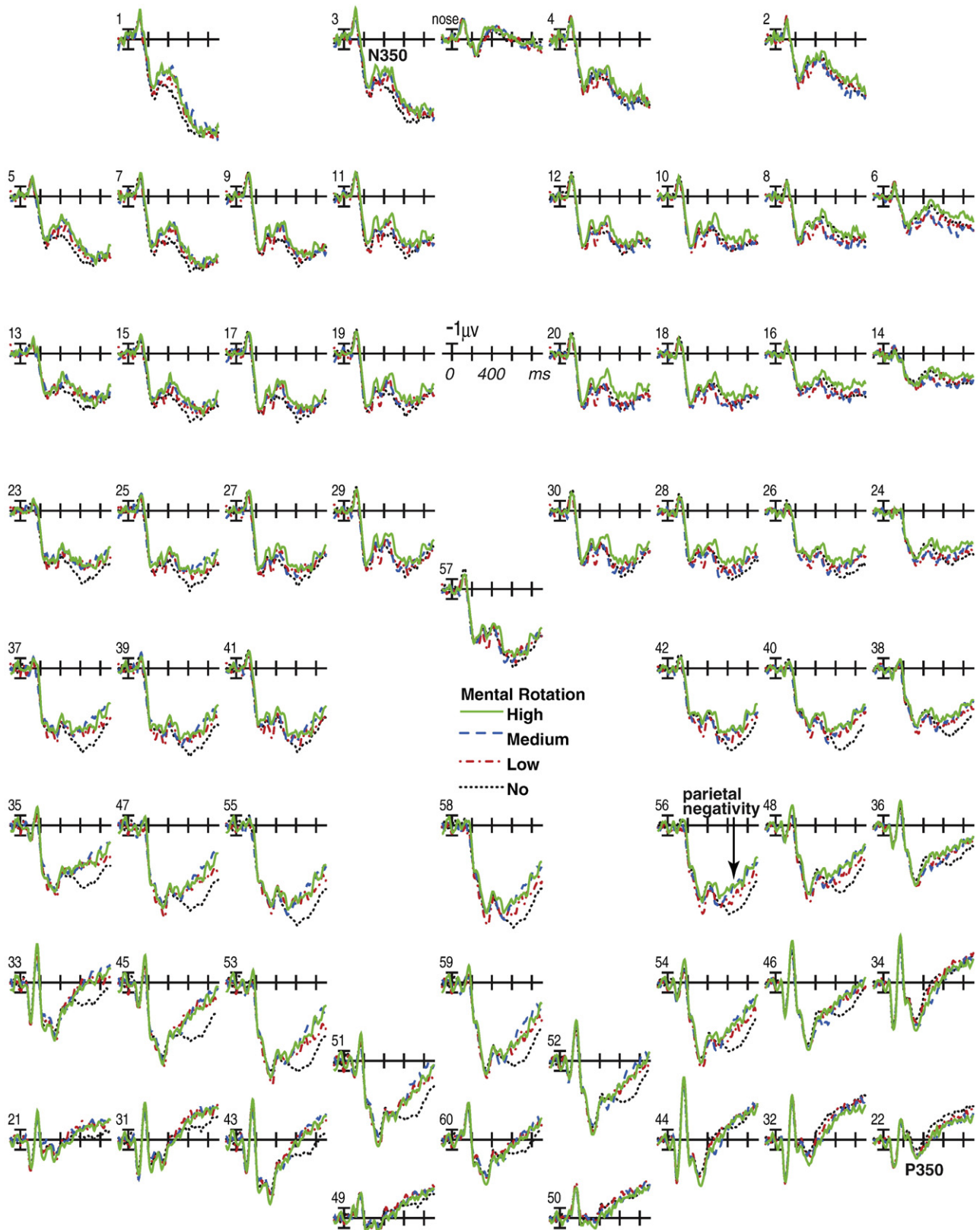
**Fig. 1 – Methods and performance.** (A) Design: Each quadrant shows each one of the four types of 3D objects. For the Mental Rotation conditions, angular disparity in-depth between the two objects was 20°–180° (in 20° increments), and examples show Same objects rotated 60° from each other (top left) and Different objects (mirror images) rotated 60° from each other (top right). For the No Rotation control condition, disparity was 0° between the two objects, and examples show Same control objects (bottom left) and Different control objects which are mirror images (bottom right); both pairs are at 60° from the target 0° angle used in the corresponding Mental Rotation conditions. (B) Trial Sample: Subjects fixated the center of the screen where the dot appeared in the Fixation stimulus followed by the Task stimulus in either a no rotation control or a mental rotation condition (shown for a 120° rotation). During the intertrial interval, participants fixated the dot at the center of the right circle. At this location, the to-be-rotated stimulus appeared (i.e., at the center of gaze). The sample stimulus, which was always the same for each object type, was to the left of fixation. Participants decided whether the object on the right side was exactly the same as or different from (i.e., the mirror image of) the object on the left. Duration is shown in parentheses. (C) 60 channel geodesic montage: Circles and numbers label each electrode location. Pairs 31–32 and 49–50 are 1 cm below theinion. Site 57 is Cz and site 60 is Oz of the 10–20 system; other approximate 10–20 sites are shown in gray italics. (D) Performance: Response times on control (0° no rotation) trials were compared to the mental rotation trials for which the nine rotation angles were collapsed into three levels of depth rotation: low (20°, 40°, 60°), medium (80°, 100°, 120°), and high (140°, 160°, 180°). Mean response times showed the typical linear increase with higher rotation angles.

opposed to a different test of mental rotation, the [Vandenberg and Kuse test \(1978\)](#), which involves identifying which two of four objects match a target object. However, in the present study, males were a small subgroup so null effects of Gender have little statistical power.

## 2.2. ERPs

We first report omnibus results from lateral and midline ANOVAs followed by focal site results for each time period. For lateral ANOVAs, the design was Rotation (4: Control [0°], Low [20°, 40°, 60°], Medium [80°, 100°, 120°], High [140°, 160°, 180°])

by Electrode (28) by Hemisphere (2: left, right). For midline ANOVAs, the design was Rotation (4) by Lobe (2: parietal, occipital) by Electrode (2: dorsal, ventral). Results reported below are from lateral sites unless otherwise labeled (as midline results). Only significant main effects of or interactions with the factor of interest, Rotation, will be reported. For brevity, we report here that degrees of freedom are (1, 23) for linear trends and paired comparisons between Rotation conditions, and report degrees of freedom for other effects only the first time each is significant. As performance results showed no difference between medium versus high, for ERPs, this planned pairwise comparison was replaced with planned



**Fig. 2 – Rotation effects at all sites.** Grand average ERPs to control (0° no rotation), low (20°, 40°, 60°), medium (80°, 100°, 120°), and high (140°, 160°, 180°) conditions during the mental rotation task from –100 until 900 ms after stimulus onset at all sites referenced to the average of left and right mastoids, filtered at low pass 30 Hz, and plotted negative up. Tics mark 200 ms intervals. The plot shows two times when ERPs differ between mental rotation and no rotation control conditions: (1) frontocentral and occipitotemporal sites between 200 and 700 ms, and (2) parietal sites between 500 and 900 ms.

comparisons of no versus medium and no versus high (full ERP set: control vs. low, no vs. medium, no vs. high, low vs. medium). As there were no Gender effects behaviorally, this factor was not assessed for ERPs.

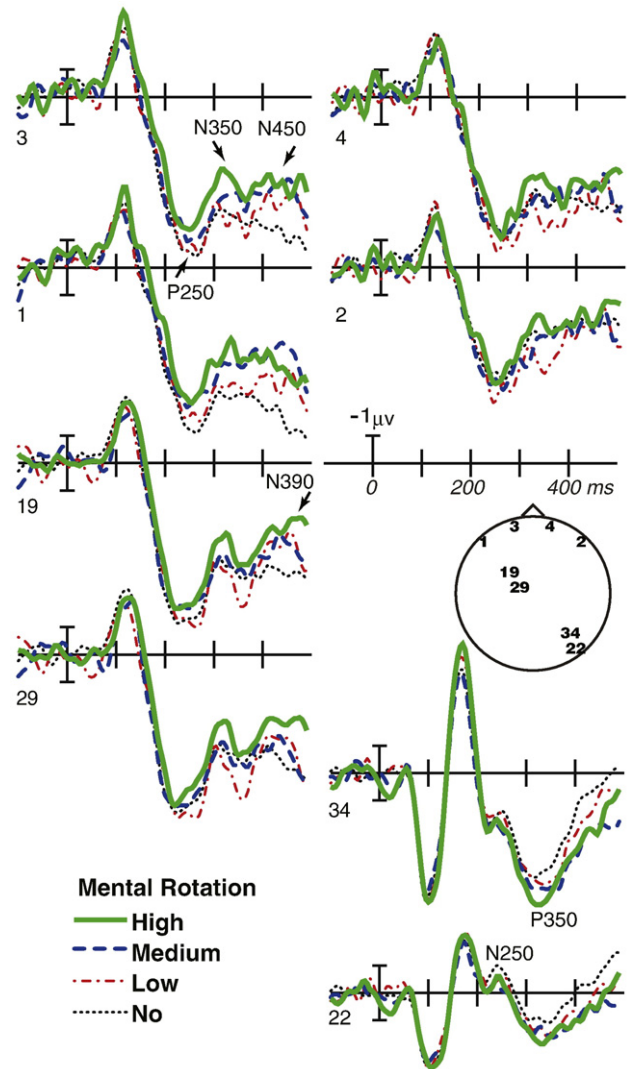
### 2.2.1. 55–199 ms

No linear rotation effects were found until after 200 ms (Fig. 2). The earlier time periods of the C1, P1, and the VPP/N170 showed only scalp location effects, as did focal spatiotemporal results, and so are not reported further; note, 165 to 195 ms, midline results showed a small interaction, Rotation×Lobe×Electrode ( $F[3, 69]=2.87, p=.046, \epsilon=.948$ ), but not a linear pattern predicted for mental rotation, and focal spatiotemporal results revealed no VPP rotation effects.

### 2.2.2. 200–499 ms

Negativity was greater for rotation than control conditions at frontopolar sites from 200 to 499 ms, and at centrofrontal sites from 300 to 499 ms when occipitotemporal sites showed a similar effect but with inverted polarity (Fig. 3). Posterior rotation effects did not yet show the expected linear modulation, consistent with prior results indicating a later onset of parietal negativity effects of rotation. Omnibus lateral results from 300–399 and 400–499 ms showed marginal or significant Rotation by Electrode effects ( $F[81, 1863]=1.88, p=.059, \epsilon=.107$  and  $F=2.96, p=.001, \epsilon=.135$ , respectively) and linear trends for both Rotation by Electrode ( $F=3.15, p=.089$  and  $F=4.93, p=.037$ , respectively) and Rotation by Hemisphere ( $F=6.69, p=.016$  and  $F=14.63, p=.001$ , respectively). From 400–499 ms also showed a significant Rotation by Hemisphere effect ( $F[3, 69]=4.53, p=.006$ ) and a significant linear trend for Rotation by Electrode by Hemisphere ( $F=5.38, p=.030$ ). Omnibus midline results from 200–299 ms showed a significant Rotation by Lobe by Electrode effect ( $F=4.79, p=.004$ ) that also showed a significant linear trend ( $F=7.18, p=.013$ ). From 300–399 and 400–499 ms, Rotation by Lobe was significant ( $F_s[3, 69]>2.93, p<.04$ ), and, from 400–499 ms, Rotation by Electrode was significant ( $F[3, 69]=3.00, p=.036$ ) and linear trends for Rotation by Electrode ( $F=9.83, p=.005$ ) and Rotation by Lobe by Electrode were significant ( $F=4.31, p=.049$ ).

Focal spatiotemporal results indicated that the direction of effects was as expected (i.e., more negative with more rotation) after 400 ms but not uniformly so earlier. During the N350 from 200 to 499 ms, high was more negative than control on the left, but from 200–399 ms, positivity was instead greater for low than control on the right, and only later from 400 to 499 ms, negativity was greater in all mental rotation conditions relative to control trials on the left. Results for pairs 1–2 and 3–4 together from 200–299, 300–399, and 400–499 ms showed significant linear trends for Rotation by Hemisphere ( $F=5.63, p=.026$ ;  $F=6.02, p=.022$ ; and  $F=10.17, p=.004$ , respectively), and paired comparisons showed low and control differed marginally or significantly (Rotation×Hemisphere,  $F=3.83, p=.063$ ,  $F=5.42, p=.029$ , and  $F=7.06, p=.014$ , respectively; 300–399 ms, Rotation×Electrode×Hemisphere,  $F=4.02, p=.057$ ), and high was significantly more negative than control (Rotation×Hemisphere,  $F=5.39, p=.029$ ;  $F=10.02, p=.004$ ; and  $F=14.19, p=.001$ , respectively). From 300–399 ms, the linear trend of Rotation by Electrode by Hemisphere was significant ( $F=4.70, p=.041$ ). From 400–499 ms, there were significant interactions of Rotation by Hemisphere ( $F[3, 69]=3.29, p=.026$



**Fig. 3 – Rotation effects on frontopolar, centrofrontal, and occipitotemporal ERPs. Grand average ERPs to control (0° no rotation), low (20°, 40°, 60°), medium (80°, 100°, 120°), and high (140°, 160°, 180°) conditions during the mental rotation task from –100 until 500 ms after stimulus onset at sites where components are maximal and overlap least with other components (frontopolar 1–4 and centrofrontal 19 and 29, right occipitotemporal 22 and 34), referenced to the average of left and right mastoids, filtered at low pass 30 Hz, and plotted negative up. Tics mark 100 ms intervals. Schematic head with nose at top shows relative electrode locations. The plot shows clearly the modulation of ERPs by mental rotation conditions at frontal sites (mainly on the left) and occipitotemporal sites (mainly on the right) where ERPs invert polarity.**

and Rotation by Electrode by Hemisphere ( $F[3, 69]=3.75, p=.017, \epsilon=.940$ ) and a linear trend for Rotation ( $F=4.28, p=.050$ ), and paired comparisons showed that negativity was greater for medium than control (Rotation×Hemisphere,  $F=6.54, p=.018$ ; Rotation×Electrode×Hemisphere,  $F=6.33, p=.019$ ) and greater for high than medium (Rotation×Electrode×Hemisphere,  $F=4.37, p=.048$ ).

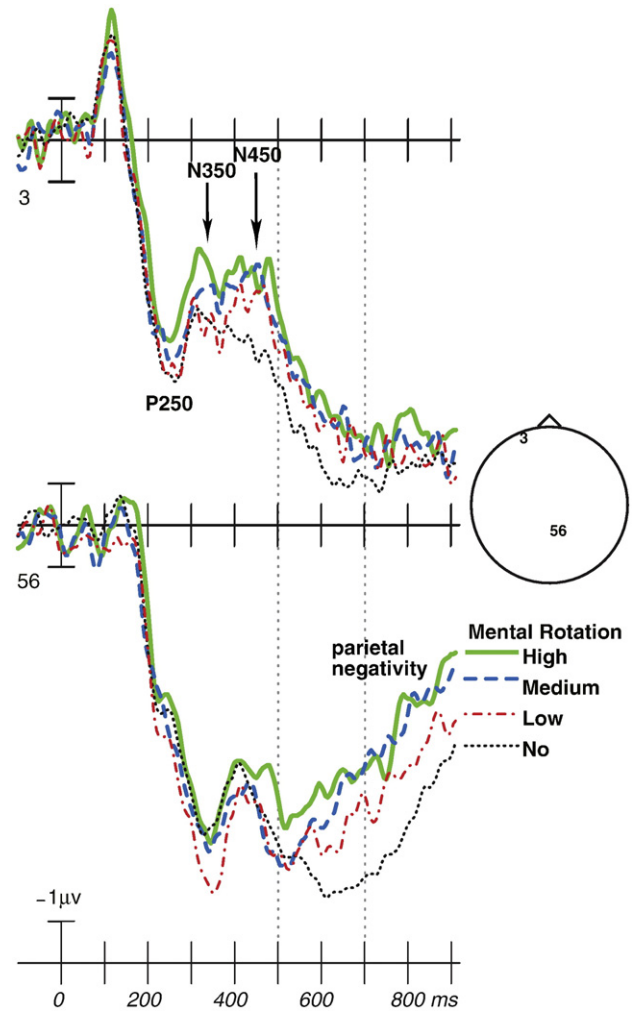
Similarly but with a later time course, centrofrontal N390 pairs 19–20 and 29–30 together from 400–499 ms showed a significant effect of Rotation ( $F[3, 69]=3.28, p=.026$ ), and linear trends of Rotation ( $F=7.57, p=.011$ ) and Rotation by Hemisphere ( $F=5.51, p=.028$ ), and paired comparisons showed high, medium, and low were significantly more negative than control on the left (Rotation×Hemisphere,  $F=5.36, p=.030$ ;  $F=8.05, p=.009$ ; and  $F=7.03, p=.014$ , respectively), and high was significantly more negative than medium (Rotation,  $F=4.48, p=.045$ ). Occipitotemporal sites showed frontal effects inverted polarity: from 200–299 ms, Rotation by Hemisphere was significant (pair 21–22,  $F[3,69]=3.09, p=.033$ ), and paired comparisons showed medium was more negative than high (Rotation×Hemisphere,  $F=9.08, p=.006$ ), and, from 300–399 ms, pair 33–34 showed significant linear trends for Rotation ( $F=4.43, p=.046$ ) and Rotation by Hemisphere ( $F=4.52, p=.045$ ), and paired comparisons showed control was more negative than both medium (Rotation×Hemisphere,  $F=3.10, p=.092$ ) and high (Rotation,  $F=3.45, p=.076$ ).

Finally, parietal pair 55–56 of the mental rotation negativity showed Rotation by Hemisphere was significant from 200–299 and 400–499 ms ( $F[3, 69]=3.34, p=.036, \epsilon=.780$  and  $F=4.38, p=.008, \epsilon=.960$ , respectively), and, from 200–299 ms, the linear trend for Rotation by Hemisphere was significant ( $F=7.09, p=.014$ ). Paired comparisons showed that, from 200–299 ms, high was more negative than both medium and control on the right (Rotation×Hemisphere,  $F=9.55, p=.005$ , and  $F=11.61, p=.002$ , respectively), and, from 400–499 ms, low was more negative than control on the left (Rotation×Hemisphere,  $F=8.42, p=.008$ ), low rotation was paradoxically more negative than medium on the left (Rotation×Hemisphere,  $F=5.26, p=.031$ ), and high was more negative than control (Rotation,  $F=5.00, p=.035$ ). These deviations from the expected linear direction indicate these earlier posterior rotation effects are not related to a linear mental rotation process.

### 2.2.3. 500–699 ms

After 500 ms, as predicted, the parietal negativity, overlapping the LPC, especially over right parietal sites, showed mental rotation effects, becoming more negative with increasing rotation angles in a linear manner (Figs. 2 and 4), and, mimicking the pattern of RTs, which increased linearly with greater rotation angles. Specifically, ERPs for medium and high rotations were similar, as for RTs. ERPs were more negative for both medium and high than low rotations, which, in turn, were more negative than for control. Lateral results showed a significant Rotation by Hemisphere effect ( $F=3.98, p=.011$ ), and significant linear trends for Rotation ( $F=6.52, p=.018$ ) and Rotation by Hemisphere ( $F=10.84, p=.003$ ). Midline results showed a significant Rotation by Lobe by Electrode effect ( $F=6.15, p=.001$ ), and significant linear trends for Rotation ( $F=5.27, p=.031$ ) and Rotation by Lobe by Electrode ( $F=28.83, p<.001$ ).

Focal spatiotemporal analyses confirmed a Rotation effect at posterior sites. Parietal pair 55–56 showed significant effects of Rotation ( $F[3, 69]=3.83, p=.013$ ) and Rotation by Hemisphere ( $F=3.17, p=.030, \epsilon=.977$ ), and Rotation showed a significant linear trend ( $F=9.61, p=.005$ ). Paired comparisons showed that



**Fig. 4 – Late rotation effects on frontopolar ERPs and parietal negativity.** Grand average ERPs to control ( $0^\circ$  no rotation), low ( $20^\circ, 40^\circ, 60^\circ$ ), medium ( $80^\circ, 100^\circ, 120^\circ$ ), and high ( $140^\circ, 160^\circ, 180^\circ$ ) conditions during the mental rotation task from  $-100$  until  $900$  ms after stimulus onset at sites where components are maximal and overlap least with other components (left frontopolar 3, right parietal 56), referenced to the average of left and right mastoids, filtered at low pass  $30$  Hz, and plotted negative up. Tics mark  $100$  ms intervals. Schematic head with nose at top shows relative electrode locations. Vertical gray dashed lines are plotted at  $500$  ms and  $700$  ms. The plot shows clearly the modulation of ERPs by mental rotation conditions at parietal sites between  $500$  and  $900$  ms, largest on the right, while effects at frontocentral sites are significant between  $200$  and  $700$  ms.

control was significantly more positive than low (Rotation,  $F=11.40, p=.003$ ; Rotation×Hemisphere,  $F=5.15, p=.033$ ), medium (Rotation,  $F=5.15, p=.033$ ), and high (Rotation,  $F=11.01, p=.003$ ).

At left frontopolar sites, higher rotation continued to be more negative than low and control, conditions demonstrating that frontal and posterior effects were temporally overlapping. Frontopolar pairs 1–4 showed a significant Rotation by Electrode by Hemisphere effect ( $F=2.95, p=.045, \epsilon=.904$ ),

and a linear trend for Rotation by Hemisphere ( $F=4.71$ ,  $p=.041$ ). Paired comparisons showed that high was significantly (Rotation  $\times$  Electrode,  $F=4.60$ ,  $p=.043$ ) and medium was marginally (Rotation  $\times$  Hemisphere,  $F=4.16$ ,  $p=.053$ ) more negative than control on the left, medium was marginally more negative than low rotation on the left (Rotation  $\times$  Electrode  $\times$  Hemisphere,  $F=3.13$ ,  $p=.09$ ), and high was more negative than medium only on the right (Rotation  $\times$  Electrode  $\times$  Hemisphere,  $F=4.13$ ,  $p=.054$ ). At centrofrontal pairs 19–20 and 29–30, high was significantly more negative than control (Rotation,  $F=4.91$ ,  $p=.037$ ).

#### 2.2.4. 700–899 ms

The right parietal negativity effect continued (Figs. 2 and 4). Lateral results showed a significant Rotation by Electrode by Hemisphere effect ( $F[81, 1863]=1.82$ ,  $p=.021$ ,  $\epsilon=.230$ ) and a linear trend for Rotation ( $F=5.73$ ,  $p=.025$ ). Midline results showed significant effects of Rotation ( $F=3.53$ ,  $p=.019$ ) and Rotation by Lobe by Electrode ( $F[3, 69]=11.63$ ,  $p<.001$ ), and significant linear trends for Rotation ( $F=7.02$ ,  $p=.014$ ) and Rotation by Lobe by Electrode ( $F=38.77$ ,  $p<.001$ ).

Focal spatiotemporal results at parietal pair 55–56 showed significant effects of Rotation ( $F=4.70$ ,  $p=.005$ ) and Rotation by Hemisphere ( $F=1.16$ ,  $p=.048$ ), and a significant linear trend for Rotation ( $F=11.61$ ,  $p=.002$ ). Paired comparisons showed high, medium, and low were all significantly more negative than control (Rotation,  $F=11.57$ ,  $p=.002$ ;  $F=11.10$ ,  $p=.003$ ; and  $F=8.15$ ,  $p=.009$ ), respectively. Visual inspection indicated that the parietal negativity was greater for high and medium than low, which was more negative than control. In contrast, at frontopolar pairs 1–2 and 3–4 together and centrofrontal pairs 19–20 and 29–30 together, there were no significant effects of Rotation, linear trends, or paired comparisons. Thus, while posterior mental rotation effects continued, frontal effects had ended by this late time.

### 3. Discussion

Findings not only replicate linear mental rotation effects on performance and parietal negativity but also reveal that the frontocentral N350 complex, which indexes visual object cognition processes, shows a linear trend and is more negative for mental rotation than control between 200 and 700 ms, especially at frontopolar sites. The pattern of linear increases in parietal negativity and performance with greater mental rotation have been discussed in detail elsewhere (Bajric et al., 1999; Desrocher et al., 1995; Gootjes et al., 2008; Heil, 2002; Inoue et al., 1998; Johnson et al., 2002; Milivojevic et al., 2003; Muthukumaraswamy et al., 2003; Peronnet and Farah, 1989; Rieckensky and Jagla, 2008; Ruchkin et al., 1991; Schendan and Stern, 2007; Thayer and Johnson, 2006), but we note that not only performance, as found in prior studies (Shepard and Cooper, 1982), but also ERP measures in the present study show linearity primarily at lower rotations and deviate from linearity at the highest rotation, consistent with a relationship between performance and ERPs. This discussion focuses on the new finding of a frontopolar N350 effect, and its implications for understanding the relation between object cognition, spatial transformation, and mental rotation.

#### 3.1. Functional significance of N350 rotation effects

The time course of rotation effects on the frontocentral N350 complex, which indexes visual object cognition processes, is consistent with the two-state interactive account. Our results indicate that control images and rotation images differentially recruit the visual object cognition processes underlying the N350; note, it is not that control images do not recruit these cognitive processes, but they do so to a different degree than mental rotation images. The present findings demonstrate that object mental rotation effects start before the parietal negativity and during the frontocentral N350 between 200 and 700 ms, and the frontopolar and centrofrontal subcomponents dissociate, consistent with evidence that each indexes distinct processes. The frontopolar N350 subcomponent shows a linear modulation with angular disparity from 200 to 700 ms, though the pattern varies somewhat over time. Frontopolar ERPs are generally more negative in all rotation conditions (high, medium, low) than control, especially over the left hemisphere. This left frontopolar negativity is greater for high and low rotation than control from 200 to 400 ms, high than medium rotation than control from 400 to 700 ms, and medium than low rotation from 500 to 700 ms. In contrast to frontopolar ERPs, centrofrontal negativity shows rotation effects that start later and modulate linearly only between 400 and 500 ms over the left hemisphere when negativity is greater in all rotation conditions than control, and high is more negative than medium. Later, centrofrontal negativity from 500 to 700 ms is only greater for high rotation than control. However, it is important to emphasize that these object cognition processes start earlier but later on overlap temporally with rotation effects on parietal negativity between 500 and 700 ms. While parietal negativity shows the typical linear modulation with increasing angular disparity that parallels the RTs, the frontocentral N350 complex shows a different linear pattern. Processes underlying the frontocentral N350 complex thus seem to contribute to but are independent of the imagery process of mental rotation per se (i.e., effortful mental visualization).

We propose that these findings can be explained by incorporating *object model verification* theory into the two-state interactive account of visual object cognition. Model verification theory is a type of perceptual hypothesis testing account (Enns and Lleras, 2008; Fazl et al., 2009; Grossberg, 1999; Lee and Mumford, 2003; Lowe, 1985; Lowe, 2000) that aims to explain the visual constancy of object cognition, as when viewing conditions are more visually impoverished, but perhaps also more generally, as when viewpoints differ between representations of a pair of objects on a mental rotation task (Ganis et al., 2007; Kosslyn et al., 1994; Schendan and Stern, 2008). According to this theory, top-down processes in prefrontal and parietal cortex drive iterative processes of model verification that determine the stored model, which represents the perceptual form of an object, in occipitotemporal cortex that best accounts for the visual percept (Ganis et al., 2007; Kosslyn et al., 1994; Schendan and Stern, 2008). When viewing conditions are optimal, the bottom-up pass through the ventral visual stream is largely sufficient to match the percept to the correct model for a cognitive decision with minimal or no additional processing. However, when visual

input is relatively perceptually impoverished, such as when an object is obscured by fog, viewed under poor lighting, or in an unusual orientation, the bottom-up pass may find only an initial weak match to object representations. Consequently, top-down processes of model verification are recruited, which involve cognitive control, selective attention, and working memory functions in ventrolateral prefrontal cortex (VLPFC; BA 45, BA 47/12), PMv, and vcIPS (Courtney, 2004; Enns and Lleras, 2008; Kastner and Pinsk, 2004; Postle, 2006). Model verification involves iterative cycles of model prediction and model testing in two prefrontal–posterior networks. (1) The *model prediction* network, indexed by the centrofrontal N390, “predicts” the visual object representation that best matches the perceived input. This process involves VLPFC processes of retrieval, disambiguation, and active maintenance of information about visual object structure from the LOS until a cognitive decision is made. (2) The *model testing* network in vcIPS, PMv, and ITS regions, indexed by the frontopolar N350, tests the similarity of the spatial configuration of features between the perceived object and the predicted model or another perceived object, as on mental rotation.

Most important, evidence for this explanation comes from similar patterns of effects in ERP and fMRI studies. More than less impoverished visual images of objects (e.g., unusual views rotated in-depth relative to canonical views, more than less fragmented drawings of known objects) show greater negativity on the frontopolar N350 and the parietal negativity and greater fMRI activation in the model testing network of the vcIPS region, PMv, and ITS on categorization and recognition tasks, indicating that model testing is a task-general process. In addition, more than less impoverished objects show greater negativity on the centrofrontal ERPs and fMRI activation in VLPFC and LOS on categorization more than recognition, indicating that model prediction is a task-specific process (Ganis et al., 2007; Schendan and Kutas, 2003; Schendan and Stern, 2008; Schendan and Lucia, submitted for publication-b).

The present findings indicate that the model prediction network, indexed by centrofrontal negativity, has a smaller role that starts later relative to the contribution of model testing to mental rotation. Consistent with the centrofrontal N390 rotation finding from 400 to 700 ms, the VLPFC and LOS regions implicated in model prediction are activated during object mental rotation in the parallel fMRI version of the present ERP study (Schendan and Stern, 2007). With the unknown Shepard–Metzler cube objects, a small role of long-term memory for visual object structure is possible because there were 4 distinct cube objects that could become increasingly well-known across the experiment, and they were shown twice prior to ERP recording. Such acquisition of object memory could result in processes of object model selection for stimulus categorization underlying part of the 400 to 500 ms linear effects on the centrofrontal N390. Such categorization would be expected to become less successful with increasing rotation. Accordingly, the N390 is larger for higher than lower rotations, and this negativity has been found to be greater for less than more successful categorization (Schendan and Kutas, 2002; Schendan and Maher, 2009). Rotation effects on the centrofrontal negativity could reflect retrieval, disambiguation, and active maintenance of object information in working memory in the VLPFC and object

shape processing in LOS (Kourtzi and Kanwisher, 2001; Soldan et al., 2008), consistent with the two-state interactive account (Schendan and Kutas, 2007; Schendan and Stern, 2008; Schendan and Maher, 2009). Indeed, maintaining nonsense visual shapes in working memory interferes with model verification effects on categorization (Ganis et al., 2007).

The model testing network is the most task-general, showing similar effects on categorization, recognition, and mental rotation. We thus propose that the model testing network facilitates visual constancy on most, if not all, object cognition tasks, resolving visual differences between distinct representations of objects to enable an accurate cognitive decision about them. This network, especially the vcIPS region and ITS, could include processes that determine the global orientation of each object, which has long been thought to precede the mental imagery process on a mental rotation task (Goodale and Milner, 1992; Shepard and Cooper, 1982) and is automatically associated with object categorization (Boucart and Humphreys, 1992; Boucart et al., 1995; Boucart et al., 2000). The present findings demonstrate that this process contributes to mental rotation of objects between 200 and 700 ms after stimulus onset, and overlaps in time with the first 200 to 300 ms of mental imagery of rotation, indexed by parietal negativity.

Accordingly, overall, the present findings on the N350 complex indicate that visual object cognition processes in networks of interactive prefrontal and posterior regions between 200 and 700 ms can contribute to mental imagery of object rotation between 500 and 900 ms. During the N350, the visual perceptual structure of the pair of visual objects is analyzed. After all, the mental rotation processes need to manipulate representations of the visual structures of the pair of objects. The present findings indicate that, during object mental rotation, the structural analyses of the objects underlying the N350 from 200 to 700 ms start well before and end during the early phase of the mental imagery of mental rotation processes underlying the parietal negativity between 500 and 700 ms. This time course is consistent with that from prior ERP studies suggesting that, during categorization, object model selection processes for visual cognition precede but also overlap temporally with mental imagery of object rotation (Schendan and Kutas, 2003; Schendan et al., submitted; Schendan and Lucia, submitted for publication-b).

### 3.2. Prior ERP mental rotation findings

To relate the N350 and parietal negativity findings more fully, relevant prior ERP mental rotation studies are reviewed next, some of which reported a frontocentral negativity that was larger with greater rotation but only in studies that did not use alphanumeric characters, consistent with an object cognition interpretation. Most studies used alphanumeric stimuli and assessed parietal negativity, which most often shows rotation effects. In the first study, same versus mirror-image judgment of pairs of nonsense geometric shapes at 2D angular disparities of 135° relative to 45° generated greater parietal negativity than object naming (Stuss et al., 1983). An early study with letters showed greater parietal negativity with increasing rotation starting from 350–400 ms onward but recorded from only 4 midline sites (Fz to Oz) and not

frontopolar ones (Wijers et al., 1989). The first validated mental rotation task (i.e., normal vs. mirror-reversed decision) used letters rotated in 2D between 0° and 180° in 45° increments, and found greater parietal negativity with increasing rotation away from 0° (Peronnet and Farah, 1989). Using a similar paradigm, when a valid orientation cue precedes mental rotation of alphanumeric characters at 0° to 360° in 45° increments, greater parietal negativity, especially over the right hemisphere, is still found with increasing rotation away from the upright (Bajric et al., 1999). Also, 135° and 180° ERPs resembled each other and were more negative than 0° and 45° ERPs, which resembled each other, and ERPs for 90° were in between these higher and lower rotations, similar to the present findings. Recent high-density ERP studies found the parietal negativity effect of mental rotation for single letters at 0° to 300° in 60° increments and suggest right lateralization in most cases (Johnson et al., 2002; Milivojevic et al., 2003). Also, greater parietal negativity is found to letters with and without flankers with increasing rotation (60° steps) from 500 to 700 ms, but earlier parietal ERPs from 130 to 400 ms were instead more positive for rotated than control conditions (Gootjes et al., 2008).

A review by Heil (2002) concluded that mental rotation of single alphanumeric characters consistently shows increasing parietal negativity with angular disparity from the normal upright, and the mental rotation process is independent of earlier processes of perceptual encoding and categorization of the stimulus and its orientation, and later processes of parity judgment (same vs. mirror-image), response selection, and response execution. Also, manipulations of perceptual encoding, stimulus categorization, orientation determination, and stimulus onset asynchrony, delay the onset of parietal negativity effects, suggesting serial processing. However, the late parietal negativity may not be responsible for the RT effect. A recent study (Rieccansky and Jagla, 2008) found greater parietal negativity for 120° than 60° than 0° rotations from the upright orientation of alphanumeric characters, but the RT rotation effect did not correlate with this stimulus-locked ERP rotation effect but rather the response-locked ERPs, suggesting parietal negativity (350–700 ms) reflects mental rotation effort but not necessarily a process that directly supports the final correct decision.

Crucially, a few other studies have reported 2D rotation effects on an N350-like component. An early study assessed a mental rotation task (same vs. mirror image) with pairs of asymmetric stick figures and found that frontopolar and centrofrontal negativity from 200 to 500 ms (N380 peak) and parietal negativity were greater for high (150–180°) than low (10–20°) rotations (Ruchkin et al., 1991). As the N380 was not seen in an arithmetic task in the same study, and was similar for object naming and shape parity judgment in a previous study (Stuss et al., 1983), it was considered to be related to stimulus evaluation. This is consistent with the idea that the frontocentral N350 complex reflects visual object cognition processes, including object model selection (Schendan and Maher, 2009; Schendan and Lucia, submitted for publication-b). Another study of 2D mental rotation (0–180° in 45° increments) found a greater N350-like component with pairs of shapes than letters (with a noncephalic reference), consistent with a shape-processing interpretation; even so, a latency

effect was found but no rotation effect on amplitude for either stimulus type (Desrocher et al., 1995). A study of sequential matching of decagons at 0° to 324° in 36° increments found the parietal negativity effect with mental rotation and found that occipitotemporal ERPs (with an Fpz reference) from 265 to 665 ms were more positive for rotated than upright conditions, similar to the polarity-inverted P350 rotation effect here (Pierret et al., 1994); note, with a frontal (Fpz, nose) or common average reference, frontocentral N350 complex effects instead largely appear as occipitotemporal P350 effects (Supplemental Figure S1) (Schendan and Maher, 2009). Finally, while not all studies with object-like stimuli report mental rotation effects on frontal negativity, this could be due to methodological differences. High-density ERPs during sequential matching of well-learned complex geometric shapes using a scalp effect strength measure supported only the parietal negativity as an index of mental rotation (Muthukumaraswamy et al., 2003), but conventional ERP analysis was not applied, so a frontal effect may have been missed. Sequential matching of stick figures at 0° to 180° in 60° increments showed only that parietal negativity was greater for a rotation and mirror image than an identical figure condition (Inoue et al., 1998), but this could have reflected sequential recognition processes, as ERPs are more positive for repeated than novel stimuli (Rugg and Curran, 2007), instead of mental rotation processes. In sum, these and the present findings are consistent with a partially serial account in which prefrontal and posterior processes for visual object cognition (e.g., analysis of shape and the spatial configuration of features, stimulus categorization, orientation determination), indexed by the frontocentral N350 complex, largely precede (200–500 ms) but also overlap for a substantial period (500–700 ms) the mental rotation process proper, indexed by parietal negativity.

### 3.3. Time course of distinct contributions to mental rotation of visual objects

Altogether, the parietal negativity and frontopolar N350 findings demonstrate the time course of contributions of visual object cognition processes to object mental rotation. The frontopolar N350 has previously been shown to be larger for unusual views, which entail spatial transformation, than canonical views, which do not, and shows a pattern of view and memory effects similar to a network of vCIPS, PMv, and ITS cortices in neuroimaging studies of object cognition, which are also recruited as a critical network during object mental rotation (Schendan and Kutas, 2003; Schendan and Kutas, 2007; Schendan and Stern, 2007; Schendan and Stern, 2008; Schendan and Lucia, submitted for publication-b). This network appears to compute the spatial relations among parts of the objects prior to and during the initial phase (500–700 ms) of the later mental rotation processes indexed by the parietal negativity. The present results show that from 200 to 700 ms, frontopolar negativity shows a linear effect and is overall more negative for any mental rotation than the no rotation control condition, whereas later, from 500 to 900 ms, parietal negativity shows the typical monotonic linear increase with angular disparity, and prior ERP studies have demonstrated the full parametric effect on parietal negativity (Heil, 2002). Frontopolar negativity clearly started (onset

~200 ms) well before parietal negativity (onset ~500 ms). We obtained clear evidence for temporal overlap between visual object cognition and mental rotation processes between 500 and 700 ms, consistent with psychological models of mental rotation positing overlap between a late phase of object cognition and an early phase of mental rotation (Ruthruff et al., 1995). The present findings indicate that, once visual object cognition processes, indexed by the N350, are well underway, they continue for about 200 ms longer during the initial phase of visualized object mental rotation from 500 to 700 ms. However, mental rotation effects on parietal negativity were largest after 700 ms. This suggests that the 500 to 700 ms time of overlap between object cognition and mental rotation processes may reflect a time when information about object structure is perceptually encoded into the system for imagined mental rotation. From 500 to 700 ms, information about the spatial configuration of parts in the vcIPS (and PMv and ITS) network, indexed by frontopolar negativity, is maintained and transferred to the network involving the SPL to carry out later processes of visualized object mental rotation. Convergent neuroimaging and the present ERP evidence suggests that both the vcIPS network and the SPL network show linear mental rotation effects similar to those found behaviorally, though with some deviation from perfect linearity in both cases, consistent with some behavioral deviations from linearity (Gauthier et al., 2002; Schendan and Stern, 2008; Zacks, 2008). We suggest that both the vcIPS and SPL networks contribute critical spatial processes to mental rotation, but the vcIPS network contributes to analyzing the spatial configuration of features of an object, and spatial transformation, as needed, not only on object mental rotation but also diverse object cognition tasks, like categorization and recognition. In contrast, the SPL network may be involved in mental imagery of object rotation.

Consistent with this, behavioral evidence suggests that the later parietal negativity and SPL processes might be more related to post-spatial transformation processes that verify the initial spatial analysis, indexed by the frontopolar N350 and related to activity in the model testing (vcIPS, PMv, ITS) network. A series of studies tested a *rotate-before-cognition* hypothesis that mental rotation is required to match an object to stored view representations (i.e., the multiple-views-plus-transformation account) and a *double-checking* hypothesis in which matching occurs but is only weakly successful and so requires later verification (De Caro and Reeves, 2000). Studies of 2D rotation of common objects suggests a *rotate-to-orient* version of double-checking wherein object cognition occurs (e.g., an object is categorized say as a dog) and then its orientation is checked. Later related studies, in which checking of object category versus object orientation were compared, further support the idea that processes of mental rotation in the SPL network, indexed by parietal negativity, reflect post-object cognition processes of checking (DeCaro and Reeves, 2002). These double-checking ideas are similar to model verification accounts of object cognition. We propose that the model testing network that includes the vcIPS region supports object model verification that facilitates matching between representations in object working memory (e.g., on mental rotation tasks) or between a percept and stored visual object knowledge (e.g., on categorization tasks) or episodic

memory (e.g., on recognition tasks). In contrast, the SPL network is activated only during mental rotation, suggesting that this network is not required for spatial transformation during object cognition processes that support tasks, like categorization and recognition.

#### 4. Conclusion

We conclude that the frontopolar N350 mental rotation processes observed here reflect the critical spatial transformation processes in the model testing (vcIPS, PMv, ITS) network, whereas the later parietal negativity reflects post-object cognition processes of spatial working memory in the SPL network that are engaged to check the prior spatial analysis and to visualize mentally the rotation of the object before response selection and execution. This later evaluation process is time-consuming and requires more resources for larger than smaller rotation and so scales with angular disparity. The present ERP time course shows that during the classic Shepard–Metzler task of in-depth object mental rotation, critical object and spatial cognitive processes are both parallel and serial. During object mental rotation in-depth, the visual and spatial structure of objects is analyzed between 200 and 700 ms. Once these visual analysis processes are well underway, between 500 and 900 ms, mental rotation processes involving frontal and parietal interactions act on these object representations during imagined object mental rotation. Thus between 500 and 700 ms, visual object cognitive processes indexed by effects on the frontocentral N350 complex operate in parallel with mental imagery of rotation effects indexed by parietal negativity. After 700 ms, however, visual analysis appears to be complete, and mental rotation processes continue. These findings provide the first evidence for the time course of visual structural analysis of objects during mental rotation (200–700 ms), and demonstrate that these visual analyses start well before the ~500 ms start of mental rotation processes indexed by the parietal negativity. Findings from this ERP study using the classic object Shepard–Metzler mental rotation task are important because this is the classic and most-established spatial cognition task (Shepard and Cooper, 1982), fMRI work has used this task, revealing the critical brain areas, and multiple-views-plus-transformation accounts of visual object cognition (Tarr and Pinker, 1989) predict that dorsal stream areas necessary for mental rotation are recruited also to facilitate object constancy during ventral stream tasks of categorization and recognition (Schendan and Stern, 2008).

#### 5. Experimental procedures

Methods will be brief, as they were the same as for the fMRI version (Schendan and Stern, 2007), except as needed for this ERP study.

##### 5.1. Materials

In each stimulus image, two cube objects inside circles were presented side-by-side (Fig. 1A). The two objects were either

identical (i.e., the same) or mirror images of each other (i.e., different). For the mental rotation condition, the right object was rotated in-depth relative to the left object. Rotations were made in 20° increments from 20° to 180° in-depth around an axis passing through the object's center horizontally, perpendicular to the axis extending through the center of the object and the observer's eyes. For the control (0°) condition, pictures were constructed from the objects in the mental rotation condition (Amick et al., 2006), but the object on the right was not rotated relative to the one on the left. A fixation stimulus had a central fixation dot and two circles but no objects (Fig. 1B). Of 144 trials total, in the 72 control and 72 mental rotation conditions, there were 4 trials (1 for each of 4 types of objects) at each of 9 rotation levels (20°, 40°, 60°, 80°, 100°, 120°, 140°, 160°, 180°) for both identical and mirror-image trial types. The stimuli were modified from line drawings constructed from four types of Shepard–Metzler cube objects in black on a white background. Unlike for fMRI, to minimize eye movements for ERPs, the two objects in a pair were placed as close together as possible, surrounding circles overlapped, the to-be-rotated stimulus on the right was at central fixation, designated by a centered dot in the preceding fixation image, and images subtended 9° of visual angle horizontally and 5° vertically at a distance of ~86 cm (Fig. 1B).

## 5.2. Design and procedure

A one-way repeated measures design was used. The Rotation factor had 4 levels: Control (0° no rotation), Low (20°, 40°, 60°), Medium (80°, 100°, 120°), and High (140°, 160°, 180°). The paradigm was blocked or mixed, counterbalanced across participants. In the blocked paradigm, 7 blocks of mental rotation alternated with 7 blocks of the control condition. Each block had 10–12 trials. In the mixed paradigm, mental rotation and control trials alternated (in an order used in Amick et al., 2006). Each paradigm presented stimuli in forward or reversed order, counterbalanced across participants. There were thus 4 lists: 2 paradigms (blocked, mixed) each of which had 2 orders (forward, reversed). Each trial began with a fixation stimulus for 2000 to 2500 ms followed by the test stimulus with an object pair for 5000 ms. Prior to testing, participants received detailed task instructions that emphasized speed and accuracy and extensive practice with the mental rotation task using a practice object and angular disparities not included in the test (20° increments from 10° to 170°). Participants were then shown each of the four cube objects twice to minimize repetition effects during the experiment. Instructions were to press one button if both objects were the same or another if they were different (mirror images of each other), regardless of angular disparity. Subjects were instructed to refrain from blinks, eye and other movements, and to maintain fixation on the center of the screen as long as the pair of objects was on the screen.

## 5.3. Dependent measures

RTs assessed performance. The ERP System software suite (Holcomb, 2003) was used for stimulus presentation, data recording, and analysis on PCs running Windows XP with a Belkin Nostromo game pad for responses. Electroencephalo-

graphic (EEG) activity was sampled at 200 Hz (bandpass 0.01–100 Hz) from 60 Ag/AgCl electrodes on a plastic cap in a geodesic arrangement, including Cz and Oz of the 10–20 system (Fig. 1C). Cap and right mastoid electrodes and an electrode below the right eye were referenced to the left mastoid; bilateral eye electrodes placed lateral to the outer canthi of each eye were referenced to each other. ERPs were calculated by averaging EEG in each condition between –100 and 900 ms relative to stimulus onset, excluding trials with above threshold muscle activity, eye-blinks, horizontal eye movements, or other movement artifacts, re-referencing to the mean of both mastoids, and time-locking to image onset with a 100 ms pre-stimulus baseline. It is noteworthy that, by rejecting trials with above threshold saccades in the analysis time periods, ERPs reflect minimal or no contribution of eye movements (Luck, 2005) and so such artifacts could not explain the results. Also Supplemental Fig. S1 shows the frontopolar N350 effect with the common average reference (Nunez and Srinivasan, 2006), which shifts the maxima of this ERP to occipitotemporal sites, where eye artifacts could not affect the ERPs, and polarity inverts to a P350 (Schendan and Maher, 2009).

## 5.4. Analyses

For all analyses, rotation trials were collapsed across three levels of rotation: low (20–60°), medium (80–120°), and high (140–180°), as in our prior work (Amick et al., 2006; Schendan and Stern, 2007), and between-subjects factors of Gender and List were included as nuisance variables of no interest. Since the 180° rotation might involve different processes (e.g., mental flipping as opposed to mental rotation), all data were also re-assessed without this condition, and any results differing from results with 180° are reported. As prior mental rotation studies indicate that effort of rotation (as opposed to accuracy) is critical for effects (Shepard and Cooper, 1982), data from all trials, regardless of accuracy, were analyzed; note, analysis of results on correct trials indicated a similar pattern of effects. RTs and mean amplitudes were subjected to repeated measures analyses of variance (ANOVAs) with a within-subject factor of Rotation (no rotation [control], low, medium, high) and between-subjects factors of Gender and List. List was a nuisance variable of no interest used to control between-subject variability and so not reported. Huynh–Feldt adjustment to degrees of freedom corrected for violation of the sphericity assumption; epsilon ( $\epsilon$ ) values <1.0 are reported. To demonstrate when the typical linear mental rotation curve was obtained, planned linear trend contrasts are reported. For significant rotation effects, planned pairwise comparisons (Fisher's least significant difference [LSD] test) of RT and ERP amplitude differences between successive rotation conditions (control vs. low, low vs. medium, medium vs. high) are reported.

For RTs, to remove outliers, a cut-off of the mean  $\pm$  2.5 SDs was applied to each condition separately. For ERPs, factorial ANOVAs on mean amplitudes were first carried out across the whole head on lateral and midline sites separately, and then focused on specific sites and time frames to explore each component separately. Sites 1–56 were included in the lateral ANOVAs such that odd numbered sites were positioned across

the left side while the even numbered sites were on the right side of each individual's head. Within-subjects factors of hemisphere (2: left, right) and electrode (28 levels, one for each electrode pair) were included in all lateral ANOVAs. Midline ANOVAs included sites 57–60, and within-subjects factors of lobe (2: parietal [57, 58], occipital [59, 60]) and electrode (2: dorsal [57, 59], ventral [58, 60]).

Omnibus ANOVAs examined visual, object cognition, and mental rotation-related ERP components and time periods based on prior research. (i) The first visual evoked component, C1, was assessed from 55 to 90 ms. (ii) The early and late parts of the P1 were assessed from 95 to 115 ms and 120 to 140 ms, respectively (Di Russo et al., 2001). (iii) Early object perception and perceptual categorization processes indexed by a vertex positive peak (VPP) and its polarity-inverted occipitotemporal N170 were assessed from 145 to 160 and 165 to 195 ms (Ganis and Schendan, 2008; Joyce and Rossion, 2005; Schendan et al., 1998; Schendan and Lucia, submitted for publication-a). (iv) The frontocentral N350 index of object model selection was assessed from 200 to 299 ms, 300 to 399 ms, and 400 to 499 ms (Schendan and Kutas, 2002; Schendan and Kutas, 2003; Schendan and Kutas, 2007; Schendan and Maher, 2009). (v) Parietal negativity indexing mental rotation was assessed from 500 to 699 ms (Peronnet and Farah, 1989; Riechansky and Jagla, 2008; Ruchkin et al., 1991). (vi) Continuing parietal negativity and a late frontocentral slow wave that differs between same and different views of objects were assessed from 700 to 899 ms (Schendan and Kutas, 2003; Schendan and Maher, 2009).

Focal ANOVAs were done to isolate spatiotemporally overlapping ERP effects at selected sites where effects were maximum and overlap least with other components based on prior work. Times are the same as for omnibus analyses. (i) The C1 was assessed at occipital pairs 45–46 and 53–54, and its polarity-inverted negativity at frontal pairs 17–20 and 29–30. (ii) The early P1 was assessed at 33–34 and 43–44, and the late P1 at pairs 45–46 and 51–52. (iii) The VPP was assessed at vertex site 57 and centropolar pair 29–30, separately, and, its polarity-inverted N170 was assessed at occipitotemporal pairs 31–34. (iv) For the frontocentral N350 complex, the subcomponents of the frontopolar P250, N350, and N450 were assessed at pairs 1–4 together, and their polarity-inverted counterparts at occipitotemporal pairs 21–22 and 33–34, separately, and the centropolar N350 and N390 were assessed at pairs 19–20 and 29–30, together (Schendan and Maher, 2009; Scott et al., 2006). (v) Late parietal negativity was assessed at pair 55–56 (Heil, 2002). In addition, to determine the relative time course of object cognition versus mental rotation effects, frontocentral N350 complex sites (pairs 1–4; 19–20; 29–30) were assessed at parietal negativity times (500–699 and 700–899 ms), and sites associated with parietal negativity (pair 55–56) were assessed at object cognition times (200–299, 300–399, 400–499 ms).

### 5.5. Participants

Right-handed Tufts University undergraduates in psychology and members of the local community responding to advertisements ( $M=21.74$ ,  $SD=3.99$ , Range: 18–34 years) volunteered for course credit or cash. Data from 4 people (11%) were

excluded for excessive movement artifacts leaving 31 participants (22 females) for analyses.

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.brainres.2009.07.036](https://doi.org/10.1016/j.brainres.2009.07.036).

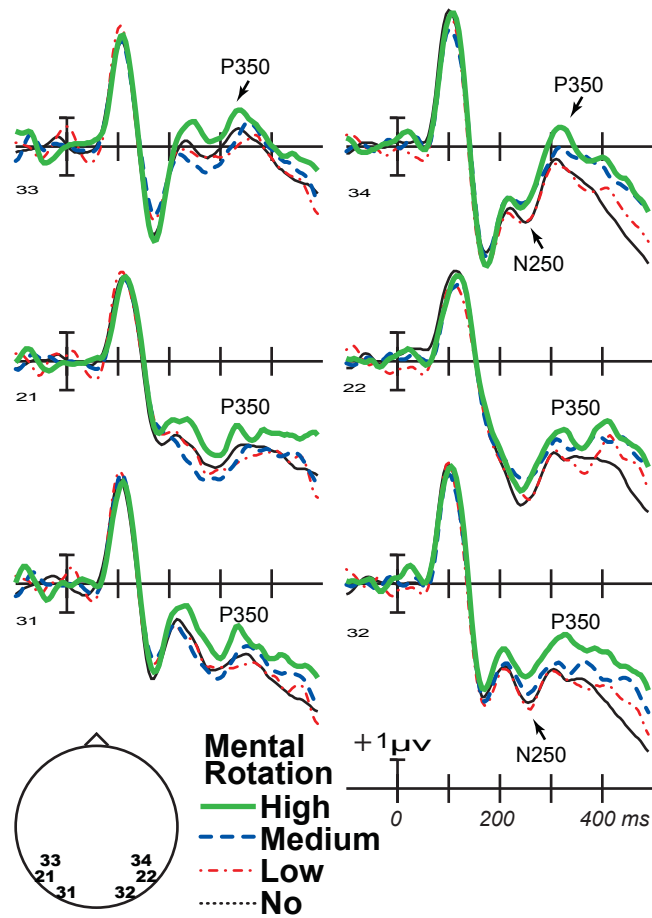
## REFERENCES

- Amick, M.M., Schendan, H.E., Ganis, G., Cronin-Golomb, A., 2006. Frontostriatal circuits are necessary for visuomotor transformation: mental rotation in Parkinson's disease. *Neuropsychologia* 44, 339–349.
- Bajric, J., Rosler, F., Heil, M., Hennighausen, E., 1999. On separating processes of event categorization, task preparation, and mental rotation proper in a handedness recognition task. *Psychophysiology* 36, 399–408.
- Boucart, M., Humphreys, G.W., 1992. Global shape cannot be attended without object identification. *J. Exp. Psychol. Hum. Percept. Perform.* 18, 783–806.
- Boucart, M., Humphreys, G.W., Lorenceau, J., 1995. Automatic access to object identity: attention to global information, not to particular physical dimensions, is important. *J. Exp. Psychol. Hum. Percept. Perform.* 21, 584–601.
- Boucart, M., Meyer, M.E., Pins, D., Humphreys, G.W., Scheiber, C., Gounod, D., Foucher, J., 2000. Automatic object identification: an fMRI study. *Neuroreport* 11, 2379–2383.
- Carpenter, G.A., Grossberg, S., Markuzon, N., Reynolds, J.H., Rosen, D.B., 1992. Fuzzy ARTMAP: a neural network architecture for incremental supervised learning of analog multidimensional maps. *IEEE Trans. Neural. Netw.* 3, 698–713.
- Carpenter, P.A., Just, M.A., Keller, T.A., Eddy, W., Thulborn, K., 1999. Graded functional activation in the visuospatial system with the amount of task demand. *J. Cogn. Neurosci.* 11, 9–24.
- Corballis, M.C., 1988. Recognition of disoriented shapes. *Psychol. Rev.* 95, 115–123.
- Courtney, S.M., 2004. Attention and cognitive control as emergent properties of information representation in working memory. *Cogn. Affect Behav. Neurosci.* 4, 501–516.
- Courtney, S.M., Petit, L., Maisog, J.M., Ungerleider, L.G., Haxby, J.V., 1998. An area specialized for spatial working memory in human frontal cortex. *Science* 279, 1347–1351.
- David, O., Harrison, L., Friston, K.J., 2005. Modeling event-related responses in the brain. *Neuroimage* 25, 756–770.
- De Caro, S.A., Reeves, A., 2000. Rotating objects to determine orientation, not identity: evidence from a backward-masking/dual-task procedure. *Percept. Psychophys.* 62, 1356–1366.
- DeCaro, S.A., Reeves, A., 2002. The use of word–picture verification to study entry-level object recognition: further support for view-invariant mechanisms. *Mem. Cognit.* 30, 811–821.
- 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 Cogn.* 28, 14–38.
- Di Russo, F., Martinez, A., Sereno, M.I., Pitzalis, S., Hillyard, S.A., 2001. Cortical sources of the early components of the visual evoked potential. *Hum. Brain Mapp.* 15, 95–111.
- Enns, J.T., Lleras, A., 2008. What's next? New evidence for prediction in human vision. *Trends Cogn. Sci.* 12, 327–333.
- Fazl, A., Grossberg, S., Mingolla, E., 2009. View-invariant object category learning, recognition, and search: how spatial and object attention are coordinated using surface-based attentional shrouds. *Cogn. Psychol.* 58, 1–48.

- Folstein, J.R., Van Petten, C., 2004. Multidimensional rule, unidimensional rule, and similarity strategies in categorization: event-related brain potential correlates. *J. Exp. Psychol. Learn. Mem. Cogn.* 30, 1026–1044.
- Ganis, G., Kutas, M., Sereno, M.I., 1996. The search for common sense: an electrophysiological study of the comprehension of words and pictures in reading. *J. Cogn. Neurosci.* 8, 89–106.
- Ganis, G., Kutas, M., 2003. An electrophysiological study of scene effects on object identification. *Brain Res. Cogn. Brain Res.* 16, 123–144.
- Ganis, G., Schendan, H.E., Kosslyn, S.M., 2007. Neuroimaging evidence for object model verification theory: role of prefrontal control in visual object categorization. *Neuroimage* 34, 384–398.
- Ganis, G., Schendan, H.E., 2008. Visual mental imagery and perception produce opposite adaptation effects on early brain potentials. *Neuroimage* 42, 1714–1727.
- Gauthier, I., Hayward, W.G., Tarr, M.J., Anderson, A.W., Skudlarski, P., Gore, J.C., 2002. BOLD activity during mental rotation and viewpoint-dependent object recognition. *Neuron* 34, 161–171.
- Goodale, M.A., Milner, A.D., 1992. Separate visual pathways for perception and action. *Trends Neurosci.* 15, 20–25.
- 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.
- Gratton, C., Evans, K.M., Federmeier, K.D., 2009. See what I mean? An ERP study of the effect of background knowledge on novel object processing. *Mem. Cognit.* 37, 277–291.
- Grossberg, S., 1999. The link between brain learning, attention, and consciousness. *Conscious Cogn.* 8, 1–44.
- Harris, I.M., Egan, G.F., Sonkila, C., Tochon-Danguy, H.J., Paxinos, G., Watson, J.D.G., 2000. Selective right parietal lobe activation during mental rotation: a parametric PET study. *Brain* 123, 65–73.
- Heil, M., 2002. The functional significance of ERP effects during mental rotation. *Psychophysiology* 39, 535–545.
- Heil, M., Bajric, J., Rösler, F., Hennighausen, E., 1996. Event-related potentials during mental rotation: Disentangling the contributions of character classification and image transformation. *J. Psychophysiol.* 10, 326–335.
- Heil, M., Jansen-Osmann, P., 2008. Sex differences in mental rotation with polygons of different complexity: do men utilize holistic processes whereas women prefer piecemeal ones? *Q. J. Exp. Psychol. (Colchester)* 61, 683–689.
- Inoue, M., Yoshino, A., Suzuki, A., Ogasawara, T., Nomura, S., 1998. Topographic study of human event-related potentials using a task requiring mental rotation. *Neurosci. Lett.* 253, 107–110.
- 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.
- Jordan, K., Wustenberg, T., Heinze, H.J., Peters, M., Jancke, L., 2002. Women and men exhibit different cortical activation patterns during mental rotation tasks. *Neuropsychologia* 40, 2397–2408.
- Joyce, C., Rossion, B., 2005. The face-sensitive N170 and VPP components manifest the same brain processes: the effect of reference electrode site. *Clin. Neurophysiol.* 116, 2613–2631.
- Kastner, S., Pinsk, M.A., 2004. Visual attention as a multilevel selection process. *Cogn. Affect. Behav. Neurosci.* 4, 483–500.
- Kosslyn, S.M., Alpert, N.M., Thompson, W.L., Chabris, C.F., Rauch, S.L., Anderson, A.K., 1994. Identifying objects seen from different viewpoints. A PET investigation. *Brain* 117, 1055–1071.
- 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.
- Kourtzi, Z., Kanwisher, N., 2001. Representation of perceived object shape by the human lateral occipital complex. *Science* 293, 1506–1509.
- Lamme, V.A., Roelfsema, P.R., 2000. The distinct modes of vision offered by feedforward and recurrent processing. *Trends Neurosci.* 23, 571–579.
- Lee, T.S., Mumford, D., 2003. Hierarchical Bayesian inference in the visual cortex. *J. Opt. Soc. Am. A. Opt. Image Sci. Vis.* 20, 1434–1448.
- Lowe, D.G., 1985. *Perceptual Organisation and Visual Recognition*, Vol. Kluwer Academic, Boston.
- Lowe, D.G., 2000. Towards a computational model for object recognition in IT cortex. In: *First IEEE International Workshop on Biologically Motivated Computer Vision*. Seoul, Korea. pp. 20–31.
- Luck, S.J., 2005. *An Introduction to the Event-Related Potential Technique*, Vol. MIT Press, Cambridge, MA.
- Masters, M.S., Sanders, B., 1993. Is the gender difference in mental rotation disappearing? *Behav. Genet.* 23, 337–341.
- McPherson, W.B., Holcomb, P.J., 1999. An electrophysiological investigation of semantic priming with pictures of real objects. *Psychophysiology* 36, 53–65.
- Milivojevic, B., Johnson, B.W., Hamm, J.P., Corballis, M.C., 2003. Non-identical neural mechanisms for two types of mental transformation: event-related potentials during mental rotation and mental paper folding. *Neuropsychologia* 41, 1345–1356.
- Muthukumaraswamy, S.D., Johnson, B.W., Hamm, J.P., 2003. A high density ERP comparison of mental rotation and mental size transformation. *Brain Cogn.* 52, 271–280.
- Nunez, P.L., Srinivasan, R., 2006. *Electric Fields of the Brain: The Neurophysics of EEG*, Vol. Oxford University Press, New York.
- Olesen, P.J., Schendan, H.E., Amick, M.M., Cronin-Golomb, A., 2007. HIV infection affects parietal-dependent spatial cognition: evidence from mental rotation and hierarchical pattern perception. *Behav. Neurosci.* 121, 1163–1173.
- Peronnet, F., Farah, M.J., 1989. Mental rotation: an event-related potential study with a validated mental rotation task. *Brain Cogn.* 9, 279–288.
- Peters, M., Battista, C., 2008. Applications of mental rotation figures of the Shepard and Metzler type and description of a mental rotation stimulus library. *Brain Cogn.* 66, 260–264.
- Pierret, A., Peronnet, F., Thevenet, M., 1994. An electrophysiological study of the mental rotation of polygons. *Neuroreport* 5, 1153–1156.
- Podzebenko, K., Egan, G.F., Watson, J.D., 2002. Widespread dorsal stream activation during a parametric mental rotation task, revealed with functional magnetic resonance imaging. *Neuroimage* 15, 547–558.
- Podzebenko, K., Egan, G.F., Watson, J.D., 2005. Real and imaginary rotary motion processing: functional parcellation of the human parietal lobe revealed by fMRI. *J. Cogn. Neurosci.* 17, 24–36.
- Postle, B.R., 2006. Working memory as an emergent property of the mind and brain. *Neuroscience* 139, 23–38.
- Rieckens, I., Jagla, F., 2008. Linking performance with brain potentials: mental rotation-related negativity revisited. *Neuropsychologia* 46, 3069–3073.
- Ruchkin, D.S., Johnson Jr., R., Canoune, H., Ritter, W., 1991. Event-related potentials during arithmetic and mental rotation. *Electroencephalogr. Clin. Neurophysiol.* 79, 473–487.
- Rugg, M.D., Curran, T., 2007. Event-related potentials and recognition memory. *Trends Cogn. Sci.* 11, 251–257.
- Ruthruff, E., Miller, J., 1995. Can mental rotation begin before perception finishes? *Mem. Cognit.* 23, 408–424.
- Ruthruff, E., Miller, J., Lachmann, T., 1995. Does mental rotation require central mechanisms? *J. Exp. Psychol. Hum. Percept. Perform.* 21, 552–570.
- Sayala, S., Sala, J.B., Courtney, S.M., 2006. Increased neural efficiency with repeated performance of a working memory task is information-type dependent. *Cereb. Cortex* 16, 609–617.
- Schendan, H.E., Ganis, G., Kutas, M., 1998. Neurophysiological evidence for visual perceptual categorization of words and faces within 150 ms. *Psychophysiology* 35, 240–251.
- Schendan, H.E., Kutas, M., 2002. Neurophysiological evidence for two processing times for visual object identification. *Neuropsychologia* 40, 931–945.

- Schendan, H.E., Kutas, M., 2003. Time course of processes and representations supporting visual object identification and memory. *J. Cogn. Neurosci.* 15, 111–135.
- Schendan, H.E., Kutas, M., 2007. Neurophysiological evidence for the time course of activation of global shape, part, and local contour representations during visual object categorization and memory. *J. Cogn. Neurosci.* 19, 734–749.
- Schendan, H.E., Stern, C.E., 2007. Mental rotation and object categorization share a common network of prefrontal and dorsal and ventral regions of posterior cortex. *Neuroimage* 35, 1264–1277.
- Schendan, H.E., Stern, C.E., 2008. Where vision meets memory: prefrontal–posterior networks for visual object constancy during categorization and recognition. *Cerebral Cortex* 18, 1695–1711.
- Schendan, H.E., Maher, S.M., 2009. Object knowledge during entry-level categorization is activated and modified by implicit memory after 200 ms. *Neuroimage* 44, 1423–1438.
- Schendan, H.E., Lucia, L.C., submitted for publication-a. Neurophysiological evidence that extrastriate occipital and ventral temporal cortex is object-sensitive before and after 200 ms.
- Schendan, H.E., Lucia, L.C., submitted for publication-b. ERP view atypicality effects reveal common and distinct cortical processes for visual object categorization and recognition after 200 ms.
- Scott, L.S., Tanaka, J.W., Sheinberg, D.L., Curran, T., 2006. A reevaluation of the electrophysiological correlates of expert object processing. *J. Cogn. Neurosci.* 18, 1453–1465.
- Shepard, R.N., Metzler, J., 1971. Mental rotation of three-dimensional objects. *Science* 171, 701–703.
- Shepard, R.N., Cooper, L.A., 1982. *Mental Images and Their Transformations*, Vol. MIT Press, Cambridge, MA.
- Soldan, A., Zarah, E., Hilton, H.J., Stern, Y., 2008. Global familiarity of visual stimuli affects repetition-related neural plasticity but not repetition priming. *Neuroimage* 39, 515–526.
- Stuss, D.T., Sarazin, F.F., Leech, E.E., Picton, T.W., 1983. Event-related potentials during naming and mental rotation. *Electroencephalogr. Clin. Neurophysiol.* 56, 133–146.
- Tagaris, G.A., Kim, S.-G., Strupp, J.P., Andersen, P., Ugurbil, K., Georgopoulos, A.P., 1997. Mental rotation studied by functional magnetic resonance imaging at high field (4 Tesla): performance and cortical activation. *J. Cogn. Neurosci.* 9, 419–432.
- Tarr, M.J., Pinker, S., 1989. Mental rotation and orientation-dependence in shape recognition. *Cogn. Psychol.* 21, 233–282.
- Thayer, Z.C., Johnson, B.W., 2006. Cerebral processes during visuo-motor imagery of hands. *Psychophysiology* 43, 401–412.
- Vandenberg, S.G., Kuse, A.R., 1978. Mental rotations, a group test of three-dimensional spatial visualization. *Percept. Mot. Skills* 47, 599–604.
- Wijers, A.A., Otten, L.J., Feenstra, S., Mulder, G., Mulder, L.J.M., 1989. Brain potentials during selective attention, memory search, and mental rotation. *Psychophysiology* 26, 452–467.
- Zacks, J.M., 2008. Neuroimaging studies of mental rotation: a meta-analysis and review. *J. Cogn. Neurosci.* 20, 1–19.

Figure S1



Supplemental Figure S1. Rotation Effects on Frontopolar, Centrofrontal, and Occipitotemporal ERPs with the Common Average Reference. This figure is the same as Figure 3, except for the following. Grand average ERPs are plotted relative to the common average reference of all channels, except eye channels, positive voltage is up, and filtered at low pass 20 Hz. ERPs are shown at lateral occipitotemporal pairs where the frontopolar N350 effects appear with inverted polarity, that is, as a P350; the occipitotemporal N250 is also labeled, which is how the frontopolar P250 looks with the common average reference.