

Mental Rotation Requires Visual Short-term Memory: Evidence from Human Electric Cortical Activity

David J. Prime and Pierre Jolicoeur

Abstract

■ The purpose of the present study was to seek evidence that mental rotation is accomplished by transforming a representation held in visual short-term memory (VSTM). In order to accomplish this goal, we utilized the sustained posterior contralateral negativity (SPCN), an electrophysiological index of the maintenance of information in VSTM. We hypothesized that if mental rotation is accomplished by transforming a representation held in VSTM, then the duration that this representation is maintained in VSTM should be related to the degree to which the representation must be rotated to reach the desired orientation. Therefore, the SPCN should offset at progressively longer latencies as the degree of rotation required increases. We tested this prediction in two experiments utilizing rotated alphanumeric characters. Experiment 1 utilized a nor-

mal versus mirror discrimination task that is known to require mental rotation. Experiment 2 utilized a letter versus digit discrimination, a task that does not require mental rotation. In Experiment 1, the offset latency of the SPCN wave increased with increases in the angle of rotation of the target. This effect indicates that targets were maintained in VSTM for longer durations as the angle of rotation increased. Experiment 2 revealed that target orientation did not affect SPCN offset latency when subjects did not adopt a mental rotation strategy, confirming that the effects on the SPCN latency effects observed in Experiment 1 were not due to the mere presentation of rotated patterns. Thus, these two experiments provide clear evidence that mental rotation involves representations maintained in VSTM. ■

INTRODUCTION

In the natural environment, observers are frequently required to make perceptual judgments about objects or shapes viewed from a variety of viewpoints. It has long been known that the effect of target orientation is dependent on the nature of the perceptual judgment being performed (Jolicoeur, 1985, 1990; McMullen & Jolicoeur, 1990; Corballis, 1988; Jolicoeur & Kosslyn, 1983). Target orientation has a particularly dramatic effect on performance when observers are required to distinguish between a shape and its mirror image. Shepard and colleagues demonstrated that the time required to make such a mirror-normal parity judgment increases with the angle of rotation between two shapes (Shepard & Metzler, 1971) or between a shape and its normal upright orientation (Cooper & Shepard, 1973). This effect of target orientation is now known as the *mental rotation* effect (for a general review, see Shepard & Cooper, 1982).

At the present time, the neurocognitive mechanisms underlying mental rotation have not been precisely specified. The term mental rotation is derived from the initial account provided by Shepard and colleagues. According to this account, before attempting to make the parity judgment, observers form an internal visual representation of the perceived form and then transform the

internal image by rotating it in an analogue manner through intermediate positions until it reaches the usual upright orientation (see Shepard & Cooper, 1982). More recently, it has been proposed that there are at least two distinct mechanisms that can be used to rotate mentally the internal representation of objects, and these strategies can be adopted voluntarily (Kosslyn, Thompson, Wraga, & Alpert, 2001; Kosslyn, DiGirolamo, Thompson, & Alpert, 1998). One strategy is visual and can be evoked by imagining the object rotating in response to an unseen force. The second strategy is associated with motor cortex activity and can be evoked by imagining grasping and manually rotating the object.

Although analogue accounts of mental rotation that involve mental imagery have been very influential, they are not universally accepted. In contrast to analogue accounts, it has been proposed that mental rotation may rely on propositional data structures (e.g., Pylyshyn, 1979; Anderson, 1978). According to propositional accounts, the processes underlying mental rotation are cognitively penetrable and operate by performing computational transformations on abstract representations of the stimulus. Unlike analogue accounts, intermediate stages of the transformation need not have a one-to-one correspondence to the intermediate stages of the external rotation of an object.

For over three decades, research on mental rotation has played an influential role in theoretical development and debate in visual cognition and imagery. During this

Université de Montréal, Montreal, Canada

time, researchers have applied a wide variety of experimental methodologies to the study of mental rotation, including behavioral measures, ERPs, and neuroimaging techniques.

The initial studies to use ERPs to investigate mental rotation found that the amplitude of the parietal P3 evoked by rotated characters was inversely related to the angle of rotation of the target character from the normal upright orientation (Perronet & Farah, 1989; Wijers, Otten, Feenstra, Mulder, & Mulder, 1989). Both Perronet and Farah (1989) and Wijers et al. (1989) proposed that the P3 amplitude differences arose from a superposition of the P3 with a negative slow wave that increased in amplitude with the angle of rotation of the target. Subsequent research has provided strong evidence that the parietal amplitude effect is an electrophysiological correlate of brain processes underlying mental rotation (for a review, see Heil, 2002). The parietal amplitude effect has proven to be useful in chronometric studies of mental rotation (e.g., Heil, 2002; Heil & Rolke, 2002). However, the exact processes indexed by this effect and their neural origin have not yet been identified.

Numerous studies have utilized fMRI and PET to study the neural mechanisms underlying mental rotation. Although there are several foci of brain activity that have been repeatedly associated with mental rotation, there is considerable variability between the results of the available neuroimaging studies. Because these studies have utilized a wide range of experimental and control tasks, the exact causes of the cross-study variation in results have yet to be identified. Recently, Zacks (2008) performed a review and meta-analysis of 32 fMRI and PET neuroimaging studies. This analysis revealed that mental rotation is reliably associated with activity in parietal, occipital, and frontal areas, as well as primary motor cortex and the supplementary motor area of the precentral sulcus. The involvement of parietal cortex in mental rotation tasks is further supported by both TMS (Feredoes & Sachdev, 2006; Harris & Miniussi, 2003), and neuropsychological (Dittunno & Mann, 1990) evidence. The involvement of motor cortex in mental rotation is also supported by evidence from studies utilizing TMS (Eisenegger, Herwig, & Jäncke, 2007; Tomasino, Borroni, Isaja, & Rumiati, 2005; Ganis, Keenan, Kosslyn, & Pascual-Leone, 2000). However, the involvement of motor cortex in mental rotation may be dependent on the individual adopting a motor strategy (Kosslyn et al., 1998, 2001).

Although the neuroimaging evidence that mental rotation is associated with brain activity in spatially mapped visual areas of occipital and parietal cortex is informative, the exact nature of the representation of the visual object utilized by the processes responsible for mental rotation remains unknown. The purpose of the present study is to seek evidence that mental rotation is accomplished by utilizing representations stored in visual short-term memory (VSTM). In order to accomplish this goal, we utilized an ERP component, which we refer to as the sustained posterior contralateral negativity (SPCN; Jolicoeur, Sessa,

Dell'Acqua, & Robitaille, 2006a, 2006b). A growing body of evidence, reviewed below, supports the hypothesis that the SPCN reflects neural activity specifically related to the maintenance of information stored in VSTM. The SPCN is observed following the encoding of laterally presented visual stimuli. In order to avoid confounding effects from low-level stimulus differences, the target stimuli in one visual field are presented with an equivalent set of distractor stimuli in the other visual field. The SPCN is observed as a relatively more negative ERP at posterior electrodes contralateral to the encoded visual field (e.g., the voltage is more negative at electrode PO8 than at PO7 for stimuli encoded from the left visual field).

The SPCN was first proposed to be an index of brain activity related to the storage of information in VSTM by Klaver, Talsma, Wijers, Heinze, and Mulder (1999), which they described as a contralateral negative slow wave. This view has received strong support by the work of McCollough, Machizawa, and Vogel (2000) and Vogel and Machizawa (2004). In these studies, a central visual cue directed participants to encode the stimuli appearing in either the left or right visual field. A target display consisting of simple stimulus shapes was then presented for 100 msec. After a retention interval of 900 msec, another set of stimuli was presented and participants decided whether or not the second set was the same as the first in the encoded hemifield. During the retention interval, beginning at about 300 msec from the onset of the memory array, an SPCN effect was observed. Importantly, the amplitude of the voltage difference between contralateral and ipsilateral electrodes increased as the number of target items increased, reaching a maximum when the number of stimuli to be encoded equaled or exceeded the estimated capacity of VSTM (on a subject-by-subject basis; Vogel & Machizawa, 2004; see also Perron et al., 2009). Furthermore, the voltage difference was smaller on incorrect response trials relative to correct trials, suggesting that this activity contributes to accurate performance. In variants of the attentional blink task requiring the processing of lateralized visual targets, one also observes an SPCN that covaries with accuracy in the task (e.g., Dell'Acqua, Sessa, Jolicoeur, & Robitaille, 2006; Jolicoeur et al., 2006a, 2006b).

The SPCN is also observed in tasks that do not require the maintenance of visual information over a prolonged retention interval, including tasks that require a speeded response. Consistent with the proposal that VSTM is used as an intermediate processing buffer when fine analysis of briefly presented stimuli is required (e.g., Bravo & Nakayama, 1992), the SPCN is observed in discrimination tasks (Jolicoeur, Brisson, & Robitaille, 2008; Brisson & Jolicoeur, 2007a, 2007b; Mazza, Turatto, Umiltà, & Eimer, 2007), but not in localization tasks (McDonald, Hickey, Green, & Whitman, 2009; Mazza et al., 2007). Furthermore, to-be-ignored irrelevant distractors that involuntarily capture attention elicit an N2pc but not an SPCN (Leblanc, Prime, & Jolicoeur, 2008), indicating that the SPCN is only observed when stimuli are actively encoded.

Recently, Jolicoeur et al. (2008) demonstrated that the amplitude of the SPCN observed in a task requiring an immediate response was sensitive to memory load. In this study, identical stimuli were used across conditions, and memory load was manipulated by instructions to encode and respond to either one or two stimuli. Consistent with previous studies that utilized conventional VSTM memory tasks (e.g., Vogel & Machizawa, 2004), SPCN amplitude increased as memory load increased. The fact that SPCN amplitude is sensitive to memory load in both traditional memory tasks and tasks without a retention interval, combined with the fact that the SPCN scalp distributions observed in these two types of tasks closely match (e.g., Jolicoeur et al., 2008; McCollough et al., 2007), indicate that the SPCN indexes the same processes in both types of tasks.

In the context of a dual-task paradigm requiring two speeded responses, Brisson and Jolicoeur (2007a, 2007b) found that the onset of the SPCN could be delayed by concurrent dual-task interference (the so-called psychological refractory period effect). These results suggest that studies examining the detailed time course of the SPCN could reveal when information enters VSTM (by measuring onset times) and when information is no longer maintained in VSTM (by measuring offset times). Indeed, Perron et al. (2009) showed that the SPCN returns to baseline later when the memory probe is presented later, suggesting that representations held in VSTM are discarded some time after task-critical information is no longer required.

Because of the high temporal resolution of ERPs, we should be able to use the SPCN to determine how long information is held in VSTM. If mental rotation is accomplished by transforming a representation held in VSTM, the length of time for which the representation is maintained in VSTM should be related directly to the degree to which the representation must be rotated to reach the desired orientation. Therefore, the SPCN should offset at progressively longer latencies as the degree of rotation required increases. We tested this prediction in two experiments utilizing rotated alphanumeric characters. In the first experiment, the subjects were required to determine if a laterally presented target character was presented in its normal or mirror-reversed form. This task is known to produce the typical mental rotation effect on reaction time (RT; e.g., Cooper & Shepard, 1973), and we expected that target orientation would have a corresponding effect on the offset of the SPCN. A second experiment was conducted to ensure that any effect of target orientation on SPCN offset latency was not due to processes sensitive to target orientation per se, but unrelated to mental rotation. In this experiment, subjects were required to determine if the target character was a letter or a digit, a task that does not produce the mental rotation effect (Corballis & Nagourney, 1978) for stimuli presented multiple times in the same session (Jolicoeur & Milliken, 1989; Jolicoeur, Snow, & Murray, 1987; Jolicoeur, 1985). No effect of target orientation on SPCN offset was expected for this task, confirming that the effects

on the SPCN observed when mental rotation was thought to be required were not due to the mere presentation of rotated patterns.

EXPERIMENT 1

Methods

Subjects

Eighteen undergraduate volunteers (9 men, age = 19–35 years, mean age = 23.9 years) were paid \$20 (Canadian) dollars for participating in a single 2-hr session. All subjects reported normal or corrected-to-normal vision.

Stimuli and Procedure

Subjects viewed a computer monitor from a distance of 57 cm and a chin rest was used to stabilize the head. Trials were self-paced and subjects initiated each trial by pressing the spacebar. Each trial began with the presentation of a centrally located fixation cross ($0.75^\circ \times 0.75^\circ$) that remained visible throughout the trial. Subjects were instructed to maintain eye fixation on the fixation cross during the trials and to blink between trials. After a 500-msec delay the target display was presented for 200 msec. The target display consisted of pair of alphanumeric characters presented 2.5° from fixation, one on the left side and the other on the right. The alphanumeric characters were selected from the set of 2, 5, 7, G, J, and R. The characters were 1° in height and were presented either in their normal form or left–right mirror reversed. Furthermore, the characters were presented in either their normal upright position or rotated 180° or 120° in either the clockwise or counterclockwise direction. One of the characters was colored red and the other green. The luminance of all stimuli was 12.8 cd/m^2 , as measured by a Minolta CS-100 chroma and luminance meter. One of the two colors was designated as the target color for each subject, with the target color counterbalanced across subjects. The task was to determine if the target character was presented in its normal or mirror-reversed form. Responses were made on a standard computer keyboard by pressing the “F” key with the left index finger for normal form targets and the “J” key with their right index finger for mirror-reversed targets. Both speed and accuracy were stressed in the instructions. The fixation point remained on screen for 1000 msec after the response, and the trial was terminated if a response was not made within 2500 msec.

Each experimental session consisted of 60 practice trials followed by five experimental blocks of 144 trials each. During the practice trials, the maximum response latency was increased to 3500 msec and response accuracy feedback for the previous trial was presented between trials. Each experimental block consisted of an equal number of trials for each combination of visual field

of target (left or right), target orientation (0° , $\pm 120^\circ$, 180°), target version (normal or mirror), and target identity. A minimum 30-sec rest break was required between blocks.

Electrophysiological Recording and Processing

The electroencephalogram (EEG) was recorded from the left and right mastoids and 64 standard 10–10 scalp sites with active Ag/AgCl electrodes (BioSemi Active Two System; BioSemi, Amsterdam, Netherlands) mounted on an elastic cap. Eye position was monitored by both the horizontal and vertical electrooculograms (EOG). EEG and EOG channels were low-pass filtered at 67 Hz and digitized at 256 Hz. After acquisition, the EEG channels were referenced to the average of the left and right mastoids and high-pass filtered at 0.05 Hz (half power cutoff). Trials containing blinks, eye movements, or EEG artifacts were removed prior to ERP averaging by applying automated artifact detection routines.

ERP averages were calculated from EEG epochs time-locked to the presentation of the target display. Only trials with correct responses were included in the ERP analysis. Separate ERPs were calculated for each combination of visual field and target orientation. The resulting ERP waves were then low-pass filtered at 8 Hz and baseline corrected by subtracting the mean voltage during the 100-msec pre-stimulus period from observations at all time points. In order to isolate the lateralized SPCN activity, ERP waveforms from electrodes ipsilateral to the target were subtracted from those contralateral electrodes, and the resulting difference waves for each visual field were averaged.

Three ERP effects were analyzed: the mental rotation parietal amplitude effect, the amplitude of the SPCN peak, and the offset latency of the SPCN. The mental rotation parietal amplitude effect was measured as the mean amplitude of the ERP waveform at Pz between 450 and 700 msec. Amplitude and offset latency measurements of the SPCN were performed on the difference waves calculated from electrodes PO7 and PO8. The amplitude of the SPCN peak was measured as the mean amplitude between 400 and 450 msec. The offset latencies of the SPCN waves were analyzed with the threshold technique commonly used in analyzing lateralized readiness potential onset latencies (Miller, Patterson, & Ulrich, 1998). The threshold was set to 50% of the peak amplitude of the SPCN for each condition. Although this threshold technique does not allow absolute onset and offset latencies to be determined, simulations have shown that the technique provides a powerful and unbiased estimate of relative differences in latencies between conditions for a variety of ERP components (Kiesel, Miller, Jolicoeur, & Brisson, 2008). The offset latencies were measured and statistically assessed with a jackknifing procedure (Ulrich & Miller, 2001; Miller et al., 1998). This jackknifing procedure involves determining the SPCN offset latency for n different subsample grand averages, with each partici-

pant omitted from one of the subsamples. The values of these offset latencies across subsamples are then used to calculate jackknife standard errors for comparisons between conditions.

Statistical Analyses

The effect of target orientation on all behavioral and ERP measurements was assessed by separate repeated measures ANOVAs. The Greenhouse–Geisser (1959) procedure was used to mitigate violations of the sphericity assumption where appropriate.

Results

Behavioral Results

Mean RTs and mean error rates are presented in Table 1. As expected, the typical mental rotation effect was observed. As the angle of rotation increased, the mean RT also increased [$F(2, 34) = 104.3, p < .0001, \epsilon = 0.80, \eta_p^2 = .856$]. Pairwise comparisons between the target orientation conditions revealed significant differences between each pair of conditions [0° vs. $\pm 120^\circ, F(1, 17) = 105.0, p < .0001, \eta_p^2 = .861$; 0° vs. $180^\circ, F(1, 17) = 151.6, p < .0001, \eta_p^2 = .899$; and $\pm 120^\circ$ vs. $180^\circ, F(1, 17) = 44.9, p < .0001, \eta_p^2 = .725$]. The analysis of error rates revealed a pattern of performance that was consistent with the RT results. As the angle of rotation increased, the percentage of errors also increased [$F(2, 34) = 10.3, p < .01, \epsilon = 0.78, \eta_p^2 = .377$]. This pattern of error rates indicates that the RT results do not arise from speed–accuracy tradeoffs.

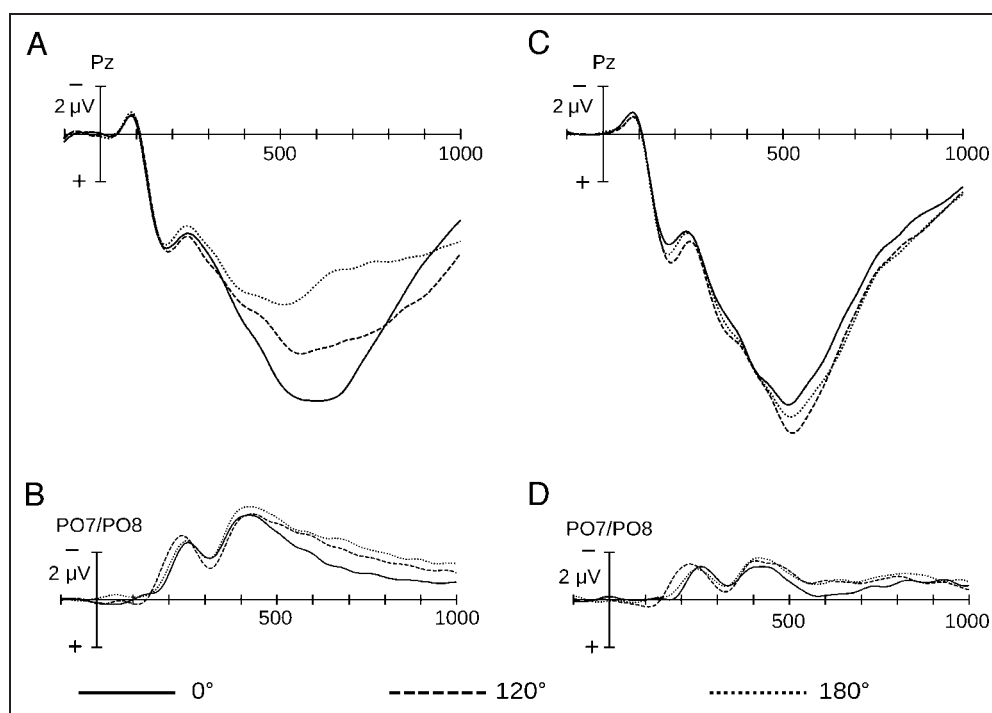
Electrophysiological Results

Parietal ERPs are shown in Figure 1A and occipital ipsilateral minus contralateral difference waves are shown in Figure 1B. When target stimuli are selected on the basis of a simple stimulus feature (e.g., color), the attention-

Table 1. Mean RTs (msec) and Mean Percent Errors (%E) as a Function of Target Orientation

Orientation	RT	%E
<i>Experiment 1</i>		
0°	762	5.1
$\pm 120^\circ$	918	9.7
180°	1065	14.8
<i>Experiment 2</i>		
0°	641	3.4
$\pm 120^\circ$	659	5.4
180°	657	3.8

Figure 1. ERPs at Pz and SPCN waves from PO7 and PO8 for each of the three orientation conditions. ERPs at Pz from Experiments 1 and 2 are shown in A and C, respectively. SPCN waves from Experiments 1 and 2 are shown in B and D, respectively.



related N2pc component (e.g., Eimer, 1996) is typically observed at latency between about 200 and 300 msec. When the experimental task requires the processing and/or remembering of the target item(s), the SPCN follows the N2pc. Inspection of Figure 1B reveals that the anticipated N2pc/SPCN ERP morphology was observed. In addition, the scalp topography of the SPCN peak (Figure 2) closely matches previously reported SPCN topographies (e.g., Jolicoeur et al., 2008; McCollough et al., 2007). Thus, the ERP morphology and scalp topography indicate that the SPCN observed here is the same component observed in previous studies.

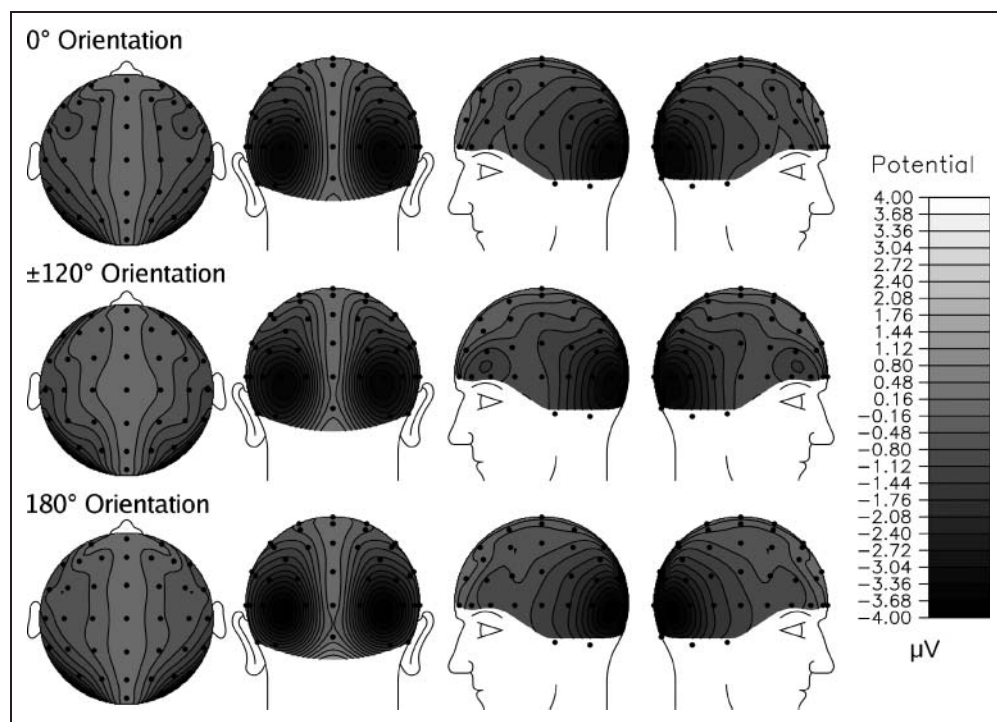
Amplitude and latency measures are presented in Table 2. Consistent with the behavioral data, the typical mental rotation parietal amplitude effect was observed (Figure 1A). As the angle of rotation increased, the amplitude at Pz decreased [$F(2, 34) = 56.1, p < .0001, \epsilon = 0.94, \eta_p^2 = .768$]. As anticipated, an SPCN wave was observed during the response interval and the amplitude of this wave did not differ between conditions [$F(2, 34) = 1.8, p > .18, \epsilon = 0.96, \eta_p^2 = .095$].

An inspection of the scalp topography time series (Figure 3) reveals that, at the peak of the SPCN wave (400–500 msec), the typical SPCN scalp topography was observed for all orientations. Furthermore, as the latency increased, the SPCN amplitude decreased (Figure 1B) and the locus of voltage maximum gradually became more inferior. In accordance with our predictions, as the angle of rotation increased, the rate of voltage decrease was slower and the scalp topography maintained the typical SPCN distribution longer. These observations are supported by the SPCN offset measurements. As the angle of rotation increased, the offset latency of the SPCN also increased

[$F(2, 34) = 5.6, p < .02, \epsilon = 0.86$]. Subsequent paired comparisons were performed between all combinations of orientation. A significant offset latency difference was obtained between the 0° orientation and the 180° orientation [$F(1, 17) = 17.6, p < .0001$]. The latency difference between the 0° and $\pm 120^\circ$ orientations approached significance [$F(1, 17) = 4.1, p < .06$], but the difference between the $\pm 120^\circ$ and 180° conditions did not ($F < 1$).

The present experiment produced two important results. First, a large SPCN wave ($\geq 3.5 \mu\text{V}$) was elicited by the target characters. This indicates that VSTM was utilized during target processing. Second, the SPCN offset latency increased as the angle of rotation increased. To our knowledge, the only factor that has been shown to affect SPCN offset latency is the duration of the retention interval. Within the context of a VSTM memory task, Perron et al. (2009) found that the SPCN returns to baseline later when the memory probe is presented later. Importantly, the measured difference in SPCN offset latency between probe onset conditions (204 msec) closely matched the difference in probe onset time (200 msec). These results demonstrated that SPCN offset latency is sensitive to the duration that information is held in VSTM. Furthermore, SPCN offset latency does not appear to be sensitive to general task difficulty or RT differences. For example, in the context of a psychological refractory period paradigm, Brisson and Jolicoeur (2007a, 2007b) found that RT was related to changes in SPCN onset, not offset. In addition, the SPCN offset effects obtained by Perron et al. were observed in the absence of a difference in RT or accuracy between probe onset conditions. Thus, the offset latency effects observed here indicate that targets were maintained in VSTM for longer durations as the angle of

Figure 2. Topographic voltage maps of the SPCN difference waves for each of the three orientation conditions. The maps represent the topography of the mean voltage of the SPCN in the latency range of the peak (400–450 msec). Symmetric scalp topographies were formed by calculating contralateral minus ipsilateral differences waves for each electrode pair and mirroring the resulting SPCN waves across the midline.



rotation increased. This latter finding is consistent with the proposition that mental rotation relies on the transformation of representations maintained in VSTM.

EXPERIMENT 2

The later offset of the SPCN for characters rotated further from upright, in Experiment 1, suggests that mental rotation through a larger angle of rotation required the active maintenance of a representation in VSTM for a longer period of time. Before we accept this conclusion, however, we need to eliminate the possibility that the observed effect of target orientation on SPCN offset was not specific to mental rotation and may arise whenever disoriented characters are processed. We tested this possibility in Experiment 2 by utilizing a letter–digit character classification task that did not produce the mental rotation effect (Corballis & Nagourney, 1978).

Methods

Subjects

Eighteen subjects participated in Experiment 2 (4 men, age = 20–31 years, mean age = 22.2 years).

Stimuli, Procedure, and Analysis

All aspects of this experiment were identical to Experiment 1 with the exception of the experimental task. The task was to determine if the target character was a letter or a digit. Subjects were required to press the “F”

key with their left index finger for letter targets and to press the “J” key with their right index finger for digit targets. The behavioral and electrophysiological data were analyzed with the same procedures used in Experiment 1. In addition, cross-experiment analyses were also performed on all measures.

Results

Behavioral Results

Mean RTs and error rates are presented in Table 1. As in Experiment 1, RTs for targets in the 0° condition were shorter than RTs for rotated targets [$F(2, 34) = 13.9$,

Table 2. Event-related Potential Measurements

	Component	Orientation		
		0°	±120°	180°
<i>A. Mean Amplitude (µV) of P300 and SPCN Components</i>				
Experiment 1	P300	10.7	8.8	6.5
	SPCN	−3.5	−3.6	−3.9
Experiment 2	P300	10.4	9.2	11.3
	SPCN	−1.4	−1.6	−1.7
<i>B. Offset Latency of SPCN Component (msec) as a Function of Orientation</i>				
Experiment 1	SPCN	615	749	806
	SPCN	509	536	525

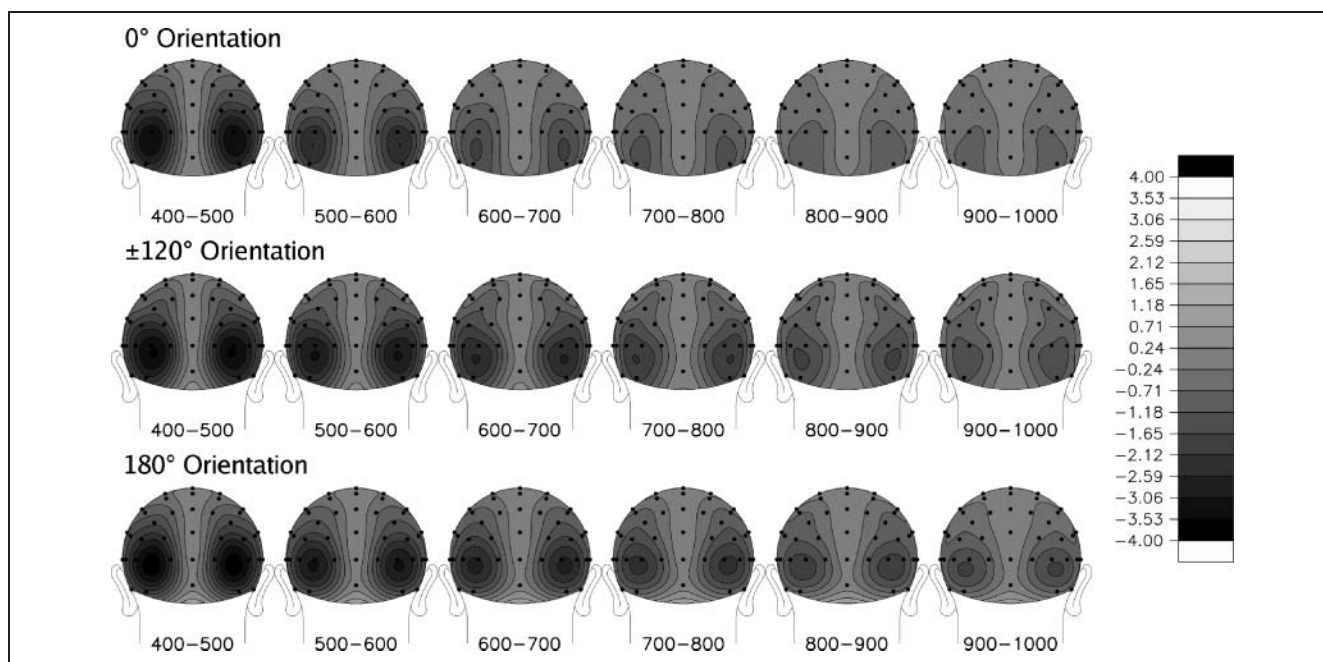


Figure 3. Time series of topographic voltage maps of the SPCN difference waves. The individual scalp maps represent the topography of the mean voltage of the SPCN in the indicated latency windows.

$p < .0001$, $\epsilon = 0.96$, $\eta_p^2 = .45$]. Pairwise comparisons between the target orientation conditions revealed significant differences between the 0° orientation and the two other orientations [0° vs. $\pm 120^\circ$, $F(1, 17) = 19.6$, $p < .001$, $\eta_p^2 = .535$; 0° vs. 180° , $F(1, 17) = 19.8$, $p < .001$, $\eta_p^2 = .538$]. However, the RT to targets in the 180° condition did not differ significantly from the RT to targets in the $\pm 120^\circ$ condition ($F < 1$). Furthermore, the effect of target orientation was much smaller in the present experiment than in Experiment 1 and a significant Experiment \times Orientation interaction was obtained [$F(2, 68) = 90.5$, $p < .0001$, $\epsilon = 0.81$, $\eta_p^2 = .727$]. In addition, RTs were significantly shorter in the present experiment than in Experiment 1 [$F(1, 34) = 55.7$, $p < .0001$, $\eta_p^2 = .621$]. Unsurprisingly, the main effect of orientation in the cross-experiment analysis was also significant [$F(2, 68) = 112.1$, $p < .0001$, $\epsilon = 0.81$, $\eta_p^2 = .767$]. The analysis of error rates also revealed a significant effect of orientation in the present experiment [$F(2, 34) = 6.8$, $p < .01$, $\epsilon = 0.82$, $\eta_p^2 = .286$]. The pattern of error rates indicate that the RT results do not arise from speed-accuracy tradeoffs. The cross-experiment analysis revealed that significantly fewer errors were made in the present experiment than in Experiment 1 [$F(1, 34) = 14.2$, $p < .001$, $\eta_p^2 = .295$]. Furthermore, both the main effect of orientation [$F(2, 68) = 10.9$, $p < .001$, $\epsilon = 0.74$, $\eta_p^2 = .242$] and the Experiment \times Orientation interaction [$F(2, 68) = 9.2$, $p < .01$, $\epsilon = 0.74$, $\eta_p^2 = .214$] were significant.

Electrophysiological Results

Parietal ERPs are shown in Figure 1C and occipital SPCN waves are shown in Figure 1D. Amplitude and latency

measures are presented in Table 2. Unlike Experiment 1, the typical mental rotation parietal amplitude effect was not observed in this experiment (Figure 1C). Although a significant effect of orientation on P3 amplitude was observed at Pz [$F(2, 34) = 9.2$, $p < .001$, $\epsilon = 0.96$, $\eta_p^2 = .352$], P3 amplitude did not decrease in accordance with the angle of target rotation. This difference between experiments is supported by a significant Experiment \times Orientation interaction [$F(2, 68) = 38.9$, $p < .0001$, $\epsilon = 0.99$, $\eta_p^2 = .533$].

As was the case in Experiment 1, target orientation had no effect on SPCN amplitude ($F < 1$). However, the SPCN wave elicited in the present experiment was significantly smaller than the SPCN wave observed in Experiment 1 [$F(1, 34) = 15.0$, $p < .001$, $\eta_p^2 = .306$]. Furthermore, target orientation had no effect on the offset latency of the SPCN ($F < 1$). This difference between experiments is supported by a significant Experiment \times Orientation interaction [$F(2, 68) = 3.9$, $p < .03$, $\epsilon = 0.99$, $\eta_p^2 = .970$]. Consistent with the RT results, the SPCN offset at a shorter latency in the present experiment than in Experiment 1 [$F(1, 34) = 18.5$, $p < .001$, $\eta_p^2 = .994$].

Although the present experiment used identical stimuli and experimental parameters as Experiment 1, modifying the task had a dramatic effect on both the behavioral and ERP effects. Target orientation had very little effect on RT in the present experiment and the typical mental rotation effect of progressive increases in RT with orientation was not observed (Table 1). Moreover, the mental rotation parietal amplitude effect was not observed. Thus, in accordance with previous results (Corballis & Nagourney, 1978), the present results indicate that the subjects did not use a mental rotation strategy to perform the letter-digit classification

task given that the same stimuli were used repeatedly during the experimental session (Jolicoeur et al., 1987). This change in cognitive strategy was accompanied by changes in the SPCN. The SPCN peak amplitude observed in the current experiment was less than half that observed in Experiment 1 (Table 2). This indicates that subjects relied on VSTM representations to a greater degree in Experiment 1 than in Experiment 2. Critically, no differences in SPCN offset were observed in the present experiment. This demonstrates that the effect of target orientation on SPCN offset latency does not arise from stimulus differences or from the need to process disoriented character forms.

GENERAL DISCUSSION

The purpose of the present study was to determine if mental rotation is accomplished by transforming a representation held in VSTM. We hypothesized that, if mental rotation is accomplished by transforming a representation held in VSTM, then the duration for which this representation is maintained in VSTM should be related to the degree to which the representation must be rotated to reach the desired orientation. The current results provide strong support for this hypothesis. Experiment 1 demonstrated that the offset latency of the VSTM-related SPCN wave increased with increases in the angle of rotation of the target. This effect indicates that targets were maintained in VSTM for longer durations as the angle of rotation increased. Experiment 2 revealed that target orientation did not affect SPCN offset latency when subjects did not adopt a mental rotation strategy to perform the experimental task. Thus, these two experiments provide clear evidence that mental rotation involves representations maintained in VSTM.

The current results converge with the results of a recent behavioral study that also found a relationship between mental rotation and VSTM. Hyun and Luck (2007) required subjects to perform a mirror-normal judgment task on rotated alphabetic characters during the retention interval of a visual working memory task. When the memory task required the storage of object features, there was mutual interference between the two tasks. In addition, the degree of interference increased as the angle of target rotation increased. In contrast, when the memory task required the storage of spatial location, only a minor amount of interference was observed and the amount of interference was independent of the angle of target rotation. These results are consistent with the view that mental rotation involves a VSTM system that stores object features. Thus, the present results and the results of Hyun and Luck provide converging behavioral and electrophysiological evidence that the processes underlying mental rotation utilize representations held in VSTM. The current results also indicate that the duration information is stored in VSTM is related to target orientation. The longer duration of the SPCN with a longer period of mental rotation also suggests that the

VSTM memory system supporting mental rotation is the same system as the one used to maintain simple object features in memory, such as color (Perron et al., 2009; Vogel & Machizawa, 2004) or rectangle orientation (McCollough et al., 2007).

Converging evidence, such as that provided by the present results and those of Hyun and Luck (2007), is extremely important in scientific research. Our interpretation of the present results is based on prior evidence that the SPCN indexes the maintenance of information in VSTM (e.g., Robitaille, Grimault, & Jolicoeur, 2009; Jolicoeur et al., 2008; Vogel & Machizawa, 2004) and that SPCN offset latency is related to the duration that information is held in VSTM (Perron et al., 2009). However, it is not possible to be completely certain that no other factors could be responsible for the SPCN offset effects observed here. Similarly, it is not possible to be completely certain that the interference effects observed by Hyun and Luck are due to VSTM being used to store the target object during rotation. Both our conclusions and those of Hyun and Luck are based on “reverse inferences” (Poldrack, 2006), in which the engagement of a covert cognitive process is inferred from variations in dependent variables (e.g., SPCN offset latency) that have previously been shown to be sensitive to the engagement of the cognitive process in question. Such inferences are commonly used when seeking evidence for the involvement of a cognitive process in a task that does not directly manipulate the cognitive process. Reverse inferences could only be made with complete certainty by demonstrating that only changes in the inferred cognitive process could produce the observed variations in the dependent variables. Nevertheless, the fact that two studies using completely different methodologies both found evidence of VSTM involvement during mental rotation provides converging evidence that is far stronger than the results of either study taken in isolation.

Results from mental rotation tasks have been at the center of the debate concerning the nature of underlying representations of visual stimuli (e.g., Kosslyn, 1981; Pylyshyn, 1981). The present work helps to narrow the debate by providing strong support for the involvement of a distinctly visual level of representation (Perron et al., 2009; Jolicoeur et al., 2008; McCollough et al., 2007; Vogel & Machizawa, 2004) likely maintained in extrastriate visual cortex and dorsal parietal regions during the mental rotation of alphanumeric characters (Robitaille et al., 2009; Xu & Chun, 2006; Todd & Marois, 2004, 2005). The fine temporal resolution of the ERP method demonstrates that VSTM is involved during the mental transformation process, allowing us to rule out posttransformation feedback from regions processing more abstract (amodal) forms of representation. The possibility of such posttransformation feedback from nonvisual to visual brain regions complicates the interpretation of results from methods with lower temporal resolution. Given that the exact nature of representations held in VSTM (as indexed by the SPCN) remains largely unknown, however, further research

will be required to provide a definitive resolution to the imagery debate.

Acknowledgments

This work was made possible by research grants from the Natural Sciences and Engineering Research Council of Canada (NSERC) and the Canadian Institutes of Health Research (CIHR), by infrastructure support from the Canada Fund for Innovation (DFI) and the Fonds pour la Recherche en Santé du Québec (FRSQ), and by the Canada Research Chairs program awarded to P. J., and by postdoctoral fellowship funding from NSERC awarded to D. P. We thank Kristelle Alumni-Menichini and Hugo Chénier for technical assistance.

Reprint requests should be sent to David J. Prime, Département de Psychologie, Université de Montréal, Montréal, QC, Canada, or via e-mail: david_john_prime@yahoo.com.

REFERENCES

- Anderson, J. R. (1978). Arguments concerning representations for mental imagery. *Psychological Review*, *85*, 249–277.
- Bravo, M. J., & Nakayama, K. (1992). The role of attention in different visual-search tasks. *Perception & Psychophysics*, *51*, 465–472.
- Brisson, B., & Jolicoeur, P. (2007a). Electrophysiological evidence of central interference on the control of visual-spatial attention. *Psychonomic Bulletin & Review*, *14*, 126–132.
- Brisson, B., & Jolicoeur, P. (2007b). A psychological refractory period in access to visual short-term memory and the deployment of visual-spatial attention: Multitasking processing deficits revealed by event-related potentials. *Psychophysiology*, *44*, 323–333.
- Cooper, L. A., & Shepard, R. N. (1973). Chronometric studies of the rotation of mental images. In W. G. Chase (Ed.), *Visual information processing* (pp. 75–176). New York: Academic Press.
- Corballis, M. C. (1988). Recognition of disoriented shapes. *Psychological Review*, *95*, 115–123.
- Corballis, M. C., & Nagourney, B. A. (1978). Latency to categorize disoriented alphanumeric characters as letters or digits. *Canadian Journal of Psychology*, *23*, 186–188.
- Dell'Acqua, R., Sessa, P., Jolicoeur, P., & Robitaille, N. (2006). Spatial attention freezes during the attentional blink. *Psychophysiology*, *43*, 394–400.
- Dittunno, P. L., & Mann, V. A. (1990). Right hemisphere specialization for mental rotation in normals and brain damaged subjects. *Cortex*, *26*, 177–188.
- Eimer, M. (1996). The N2pc component as an indicator of attentional selectivity. *Electroencephalography and Clinical Neurophysiology*, *99*, 225–234.
- Eisenegger, C., Herwig, U., & Jäncke, L. (2007). The involvement of primary motor cortex in mental rotation revealed by transcranial magnetic stimulation. *European Journal of Neuroscience*, *25*, 1240–1244.
- Feredoes, E. A., & Sachdev, P. S. (2006). Differential effects of transcranial magnetic stimulation of left and right posterior parietal cortex on mental rotation tasks. *Cortex*, *42*, 750–754.
- Ganis, G., Keenan, J. P., Kosslyn, S. M., & Pascual-Leone, A. (2000). Transcranial magnetic stimulation of primary motor cortex affects mental rotation. *Cerebral Cortex*, *10*, 175–180.
- Greenhouse, W. W., & Geisser, S. (1959). On methods in the analysis of profile data. *Psychometrika*, *24*, 95–112.
- Harris, I. M., & Miniussi, C. (2003). Parietal lobe contribution to mental rotation demonstrated with rTMS. *Journal of Cognitive Neuroscience*, *15*, 315–323.
- Heil, M. (2002). The functional significance of ERP effects during mental rotation. *Psychophysiology*, *39*, 535–545.
- Heil, M., & Rolke, B. (2002). Toward a chronopsychophysiological of mental rotation. *Psychophysiology*, *39*, 414–422.
- Hyun, J., & Luck, S. J. (2007). Visual working memory as the substrate for mental rotation. *Psychonomic Bulletin & Review*, *14*, 154–158.
- Jolicoeur, P. (1985). The time to name disoriented natural objects. *Memory & Cognition*, *13*, 289–303.
- Jolicoeur, P. (1990). On the role of mental rotation and feature extraction in the identification of disoriented objects: A dual-systems theory. *Mind and Language*, *5*, 387–410.
- Jolicoeur, P., Brisson, B., & Robitaille, N. (2008). Dissociation of the N2pc and sustained posterior contralateral negativity in a choice response task. *Brain Research*, *1215*, 160–172.
- Jolicoeur, P., & Kosslyn, S. M. (1983). Coordinate systems in the long-term memory representation of three-dimensional shapes. *Cognitive Psychology*, *15*, 301–345.
- Jolicoeur, P., & Milliken, B. (1989). Identification of disoriented objects: Effects of context of prior presentation. *Journal of Experimental Psychology: Memory, Learning, and Cognition*, *15*, 200–210.
- Jolicoeur, P., Sessa, P., Dell'Acqua, R., & Robitaille, N. (2006a). Attentional control and capture in the attentional blink paradigm: Evidence from human electrophysiology. *Psychological Research*, *19*, 560–578.
- Jolicoeur, P., Sessa, P., Dell'Acqua, R., & Robitaille, N. (2006b). On the control of visual spatial attention: Evidence from human electrophysiology. *Psychological Research*, *70*, 414–424.
- Jolicoeur, P., Snow, D., & Murray, J. (1987). The time to identify disoriented letters: Effects of practice and font. *Canadian Journal of Psychology*, *41*, 303–316.
- Kiesel, A., Miller, J., Jolicoeur, P., & Brisson, B. (2008). Measurement of ERP latency differences: A comparison of single-participant and jackknife-based scoring methods. *Psychophysiology*, *45*, 250–274.
- Klaver, P., Talsma, D., Wijers, A. A., Heinze, H.-J., & Mulder, G. (1999). An event-related brain potential correlate of visual short-term memory. *NeuroReport*, *10*, 2001–2005.
- Kosslyn, S. M. (1981). The medium and the message in mental imagery: A theory. *Psychological Review*, *88*, 46–66.
- 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.
- Kosslyn, S. M., Thompson, W. L., Wraga, M., & Alpert, N. M. (2001). Imaging rotation by endogenous versus exogenous forces: Distinct neural mechanisms. *NeuroReport*, *12*, 2519–2525.
- Leblanc, É., Prime, D. J., & Jolicoeur, P. (2008). Tracking the location of visuospatial attention in a contingent capture paradigm. *Journal of Cognitive Neuroscience*, *20*, 657–671.
- Mazza, V., Turatto, M., Umiltà, C., & Eimer, M. (2007). Attentional selection and identification of visual objects are reflected by distinct electrophysiological responses. *Experimental Brain Research*, *181*, 531–536.
- McCollough, A. W., Machizawa, M. G., & Vogel, E. K. (2007). Electrophysiological measures of maintaining representations in visual working memory. *Cortex*, *43*, 77–94.
- McDonald, J. J., Hickey, C., Green, J. J., & Whitman, J. C. (2009). Attention is biased against returning to recently attended locations. *Journal of Cognitive Neuroscience*, *21*, 725–733.

- McMullen, P. A., & Jolicoeur, P. (1990). The spatial frame of reference in object naming and discrimination of left–right reflections. *Memory & Cognition*, *18*, 99–115.
- Miller, J., Patterson, T., & Ulrich, R. (1998). Jackknife-based method for measuring LRP onset latency differences. *Psychophysiology*, *35*, 99–115.
- Perron, R., Lefebvre, C., Robitaille, N., Brisson, B., Gosselin, F., Arguin, M., et al. (2009). Attentional and anatomical considerations for the representation of simple stimuli in visual short-term memory: Evidence from human electrophysiology. *Psychological Research*, *73*, 222–232.
- Perronet, F., & Farah, M. J. (1989). Mental rotation: An event-related potential study with a validated mental rotation task. *Brain and Cognition*, *9*, 279–288.
- Poldrack, R. A. (2006). Can cognitive processes be inferred from neuroimaging data? *Trends in Cognitive Sciences*, *10*, 59–63.
- Pylyshyn, Z. W. (1979). The rate of “mental rotation” of images: A test of a holistic analogue hypothesis. *Memory & Cognition*, *7*, 19–28.
- Pylyshyn, Z. W. (1981). The imagery debate: Analogue media versus tacit knowledge. *Psychological Review*, *87*, 16–45.
- Robitaille, N., Grimault, S., & Jolicoeur, P. (2009). Bilateral parietal and contralateral responses during maintenance of unilaterally encoded objects in visual short-term memory: Evidence from magnetoencephalography. *Psychophysiology*, *46*, 1090–1099.
- Shepard, R. N., & Cooper, L. A. (1982). *Mental images and their transformations*. Cambridge, MA: MIT Press.
- Shepard, R. N., & Metzler, J. (1971). Mental rotation of three-dimensional objects. *Science*, *171*, 701–703.
- Todd, J. J., & Marois, R. (2004). Capacity limit of visual short-term memory in human posterior parietal cortex. *Nature*, *428*, 751–754.
- Todd, J. J., & Marois, R. (2005). Posterior parietal cortex activity predicts individual differences in visual short-term memory capacity. *Cognitive, Affective, and Behavioral Neuroscience*, *5*, 144–155.
- Tomasino, B., Borroni, P., Isaja, A., & Rumiati, R. I. (2005). The role of the primary motor cortex in mental rotation: A TMS study. *Cognitive Neuropsychology*, *22*, 348–363.
- Ulrich, R., & Miller, J. (2001). Using the jackknife-based scoring method for measuring LRP onset effects in factorial designs. *Psychophysiology*, *38*, 816–827.
- Vogel, E. K., & Machizawa, M. G. (2004). Neural activity predicts individual differences in visual working memory capacity. *Nature*, *428*, 748–751.
- 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.
- Xu, Y., & Chun, M. M. (2006). Dissociable neural mechanisms supporting visual short-term memory for objects. *Nature*, *440*, 91–95.
- Zacks, J. M. (2008). Neuroimaging studies of mental rotation: A meta-analysis and review. *Journal of Cognitive Neuroscience*, *20*, 1–9.