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Mental rotation impairs attention shifting and short-term memory encoding: Neurophysiological evidence against the response-selection bottleneck model of dual-task performance

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ABSTRACT

Dual tasks and their associated delays have often been used to examine the boundaries of processing in the brain. We used the dual-task procedure and recorded event-related potentials (ERPs) to investigate how mental rotation of a first stimulus (S1) influences the shifting of visual-spatial attention to a second stimulus (S2). Visual-spatial attention was monitored by using the N2pc component of the ERP. In addition, we examined the sustained posterior contralateral negativity (SPCN) believed to index the retention of information in visual short-term memory. We found modulations of both the N2pc and the SPCN, suggesting that engaging mechanisms of mental rotation impairs the deployment of visual-spatial attention and delays the passage of a representation of S2 into visual short-term memory. Both results suggest interactions between mental rotation and visual-spatial attention in capacity-limited processing mechanisms indicating that response selection is not pivotal in dual-task delays and all three processes are likely to share a common resource like executive control.

1. Introduction

Performing two tasks at the same time can overload the capacity of the brain in such a way that performance is delayed or impaired. And yet, some combinations of tasks seem to be easier to perform than others, suggesting that the costs of multitasking depend on the types of cognitive processes that overlap in time. A particularly helpful tool in telling apart processes that do and do not produce dual-task costs is the so-called psychological refractory period (PRP) paradigm (Telford, 1931). This paradigm commonly involves a dual task (Task 1 and Task 2) in which two stimuli (S1, S2) are presented, and each requires a speeded response (R1, R2). The two stimuli are separated in time by a stimulus onset asynchrony (SOA), so as to manipulate the temporal overlap of the two tasks. Results typically show an increased reaction time (RT) to S2 (RT2) with decreasing SOA, suggesting that some processes necessary to carry out the second response need to wait (or slow down) until some other processes in the first task have been completed-this slowing of R2 is called the PRP effect (Welford, 1967).

Under the assumption of a single capacity limitation, the combined effect on RT2 of SOA and a Task 2 variable can clarify which processes are deferred in the PRP paradigm. Capacity-limited processes of Task 1 and Task 2 cannot run simultaneously, while processes occurring before or after the capacity-limited process of one task can be performed concurrently with any other process of the other task (capacity limited or not). If the effect of a Task 2 variable onto RT2 is equal for short and long SOAs (i.e., additive with the SOA effect), this implies that the Task 2 effect is related to a capacity-limited Task 2 process or some other process following this capacity-limited process. If instead the effect of the Task 2 variable is smaller for short than for long SOAs (i.e., combines underadditively with the SOA effect, as SOA is reduced), this implies that at least some of the Task 2 effect arises before capacity-limited processes. Underadditive effects are thought to occur because at short SOAs capacity-limited processes are deferred, and this causes a state of slack for Task 2 processes. This slack in a sense "swallows" at least part of the Task 2 effect, so that a Task 2 variable that affects processes preceding the capacity limitation in Task 2 delays RT2 for a shorter time with short than with long SOAs (Pashler & Johnston, 1989). Additional clues about which processes are capacity limited

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can come from the effect of Task 1 variables onto RT2. Effects of Task 1 variables on capacity-limited processes or earlier will defer Task 2 processes and affect RT2, whereas Task 1 variables that take effect after capacity-limited processes will not affect RT2.

Several PRP studies employing the logic described in the above have yielded support for a response-selection bottleneck model (Pashler, 1994; Smith, 1967; Welford, 1952, 1980), which assumes that response selection – a process of translating stimulus codes to response codes (Pashler & Johnston, 1989) – is the major bottleneck in multitasking, in the sense that only one response can be selected at a time. Even though the response-selection bottleneck model has been very successful in explaining a wide variety of observations (see Pashler, 1994, for an overview), there is increasing evidence that response selection is not the only cognitive process with bottleneck characteristics. In the present study, we focused on two processes that based on previous observations can be suspected to have such characteristics: mental rotation and the shifting of visual-spatial attention. In contrast to previous studies that investigated the interaction between these processes and response selection, we were interested in the direct interaction between mental rotation and attentional shifting. Before we describe the rationale of our study in more detail, we first review the available evidence suggesting that mental rotation and attentional shifting might indeed possess bottleneck characteristics.

1.1. *Mental rotation*

In a mental-rotation task, participants categorize asymmetric visual stimuli, such as (most) letters, as normally oriented vs. mirror-reversed. Importantly, the stimuli are rotated to some angle from their usual upright orientation, which makes the task more difficult. Results show that RT increases monotonically with increasing angle from normal orientation (Cooper, 1975, 1976; Cooper & Shepard, 1973; Shepard & Metzler, 1971). Although the mechanisms underlying this observation are still largely unknown, the empirical findings are very robust and replicable (see Shepard & Cooper, 1982, for a review). As suggested by the study of Corballis (1986), the mirror/normal discrimination can only be made if participants have actually carried out something like a mental rotation of the stimulus representation into the normal upright position. This process is assumed to have analog characteristics, so that stimuli that deviate more strongly from their normal position have to be "mentally rotated" for a longer time-which is taken to explain the monotonic, and often linear, relationship between RT and rotation angle.

From a response-selection bottleneck model, one would not expect that mental rotation as indexed in such a comparison task shares resources with response selection. And yet, there is evidence suggesting this possibility. A number of studies have looked into the interactions between mental rotation and response selection in a PRP paradigm. With a mental-rotation task as Task 2, Ruthruff, Miller, and Lachmann (1995) observed that a large proportion of the Task 2 orientation effect was still present at very short SOAs and concluded that mental rotation shares limited capacity with response selection in Task 1. Comparable findings were reported by Van Selst and Jolicœur (1994), Heil, Wahl, and Herbst (1999), and others; and Band and Miller (1997) observed that mental rotation interferes with concurrent response preparation. Taken together, these studies provide strong evidence that mental rotation has bottleneck properties similar to response selection.

1.2. *Visual-spatial attention shifting*

Considering their different computational functions, the observed similarities between mental rotation and response selection may seem rather surprising. Probably less surprising are commonalities between deployment of visual attention (involving disengagement, shifting and engagement of visual attention) and response selection. The main function of a response-selection process should be the identification and activation of the cognitive representation of an action that meets the current situational requirements and task goals. Visual attention often serves comparable purposes by identifying and activating the cognitive representation of a relevant stimulus or target, and by optimizing the collection of information about this stimulus by directing attention to its location in space. Accordingly, if response selection draws on cognitive resources to a degree that renders it an effective processing bottleneck, it makes sense to assume that stimulus selection does the same. Investigations of the possible bottleneck characteristics of visual attention shifting turned out to be rather varied however.

A first study addressing this issue was reported by Pashler (1991), who investigated the potential bottleneck properties of visual-spatial attention in a dual task. In his PRP study, Task 1 was a tone identification task and Task 2 was an unspeeded masked-letter identification task. If spatial attention has bottleneck properties and spatial attention is required to perform Task 2, then accuracy on Task 2 should be impaired at short SOAs, that is, if response selection in Task 1 would temporally overlap, and slow or postpone, directing attention in Task 2. In view of a small interaction of Task 2 performance and SOA (although the effect was statistically significant), Pashler concluded that visual-spatial attention does not have bottleneck properties. But note that Dell'Acqua and Jolicœur (2000) arrived at a different conclusion when they used a more complex first task.

Along the same lines, Johnston, McCann, and Remington (1995) asked whether attention is one unitary process comprising of both input selection and output selection or rather a set of separate and dissociable selection processes by measuring both input selection and output selection in two separate experiments. Based on the results, Johnston et al. (1995) argued that input and output attention can be seen as a set of related but separate selection processes, in which response selection-conceived of as "central," capacity-limited process-prevents the simultaneous execution of other capacity-limited processes, whereas the deployment of visual-spatial attention can overlap other capacity-limited or unlimited processes. But note that this conclusion was drawn from a comparison across two separate experiments, without directly looking into the interaction between response selection and attentional shifting.

Even though these first studies did not seem to provide strong evidence for the idea that shifting visual attention might possess bottleneck properties, more recent studies that used event-related brain potentials (ERP) have changed the picture considerably. Brisson and Jolicœur (2007a, 2007b) showed how the N2pc component (a negative posterior contralateral component that peaks usually after 200–300 ms) can be used to monitor task relevant visual-spatial attentional processes on a moment-to-moment basis in the context of dual-task situations (Brisson & Jolicœur, 2007a, 2007b) and others showed how the N2pc can also reflect attentional suppression of nontargets (Woodman & Luck, 1999, 2003). The N2pc is defined as activity measured over the contralateral electrode positions compared to activity over the ipsilateral electrode positions in the range of the N2 in the regular ERP, relative to the visual hemifield of the target (Eimer, 1996; Luck & Hillyard, 1994; Woodman & Luck, 2003). A difference wave is created when ERPs over ipsilateral are subtracted from ERPs over contralateral electrode positions. These difference waves are referred to as event-related lateralizations (ERL; Wascher & Wauschkuhn, 1996). The N2pc is generally observed on the lateral posterior sides of the head, usually with a maximum amplitude at electrode-pair PO7/PO8. Other nearby electrode-pairs are sometimes also measured and included in pooled waveforms, together with the waveforms observed at PO7/PO8 (e.g., Brisson & Jolicœur, 2007a; Eimer, 1996; Woodman & Luck, 2003). The neural generators of the N2pc are likely in extrastriate visual cortex (Hopf et al., 2000; Hopf & Mangun, 2000).

Brisson and Jolicœur (2007a) used a PRP paradigm in which they presented a tone discrimination task for the first task that was either easy (the highest or the lowest tone) or difficult (the middle two tones) to distinguish. In the second task, subjects had to shift covert attention to a specified colored square presented in the left or right visual field and the N2pc was measured. S2 was presented at different SOAs (300, 650, or 1000 ms), after S1, or in different conditions of central load, in different variants of the PRP paradigm. The general finding was that the amplitude of the N2pc was reduced when central load at the time of presentation of S2 was increased (e.g., by decreasing SOA). But note that Kiss, Van Velzen, and Eimer (2008) suggested that the N2pc waveform reflects selective attention processes triggered after the attentional shift. Such results suggest that the deployment of visual-spatial attention is impaired by PRP interference, which in turn suggests that shifting visual-spatial attention does require capacity-limited processing mechanisms that overlap with those that lead to the PRP effect-such as response selection.

Following the N2pc, the contralateral minus ipsilateral waveform often has a sustained posterior contralateral negativity (SPCN). A growing body of work provides strong arguments for a functional interpretation of the SPCN as a reflection of stimulus encoding in visual short-term memory (VSTM; Jolicœur, Brisson, & Robitaille, 2008; McCollough, Machizawa, & Vogel, 2006; Perron et al., 2009; Predovan et al., 2009; Robitaille & Jolicœur, 2006; Vogel & Machizawa, 2004). Like the N2pc, the SPCN is a greater negativity at posterior electrodes contralateral to the side from which visual information was encoded. The onset latency of the SPCN is around 300 ms and the component often has a lengthy sustained period. Interestingly, the amplitude of the SPCN increases as the amount of information held in VSTM increases (Jolicœur et al., 2008; McCollough et al., 2006; Perron et al., 2009; Vogel & Machizawa, 2004) with a plateau reached when the number of stored items equals the capacity of VSTM (Vogel & Machizawa, 2004). Additionally, if the process that requires VSTM takes longer, then the onset latency of the SPCN wave will have increased. Prime and Jolicoeur (2009) showed in their experiment that longer mental rotation of an alphanumerical character is related to a prolonged SPCN in a normal-mirror discrimination task but not a letter-digit discrimination task and argued that VSTM is used in mental rotation. In Brisson and Jolicœur (2007a) PRP experiment with an easy vs. difficult response selection for Task 1 and a covert visual-spatial attention shifting task for Task 2, SPCN onset was delayed when Task 1 response selection was more difficult. Brisson and Jolicœur (2007a) argued that the encoding of information into VSTM was postponed by Task 1 response selection. These results are in line with the results obtained for the N2pc.

1.3. *The present experiment*

The increasing evidence that processes other than response selection proper possess bottleneck characteristics challenges the traditional response-selection bottleneck model. Apparently, it is not just rather “late” operations that draw heavily on sparse cognitive resources, but also operations that select stimulus information and/or reprocess and prepare it for further processing. However, in previous studies researchers providing such evidence have always tried to validate their conclusions by demonstrating interactions with response selection or at least with PRP effects related to response selection. Accordingly, the available findings are still consistent with the possibility that response selection plays a pivotal role-so that one may argue that the response-selection bottleneck model could simply be extended by assuming that some limited capacity can be shared between response selection proper and other (still to be defined) processes. To rule out this possibility we aimed at demonstrating that PRP-type interference can be observed between processes that do not involve response selection at all.

Given the strong evidence that both mental rotation and the shifting of visual-spatial attention interact with response selection, we sought to pit these two processes against each other directly. We thereby took advantage from the fact that mental rotation is a rather well-defined process and that its duration can be systematically manipulated by varying the orientation of the target stimulus to normal upright. In particular, we carried out a PRP experiment, in which Task 1 was a mental-rotation task and Task 2 required a covert shift of the focus of visual-spatial attention. In the mental-rotation task stimuli were presented either in their upright position or rotated from this position by 140°. The latter condition can be estimated to keep the mental-rotation operation active for approximately 250 ms, so that dual-task interference from mental rotation on attention can be reliably measured. The SOA variation across the levels of 300 and 650 ms provided a different way to diagnose dual-task interference, because this manipulation affects the timing of response selection independent of mental rotation. In Task 2, participants responded to a colored square in a set of four visual stimuli, two on either side of the screen center. Just as in recent studies by Brisson and Jolicœur (2007a, 2007b), the N2pc and SPCN were measured as indicators of the deployment of visual-spatial attention to, and VSTM storage of, stimuli shown in Task 2.

According to the traditional response-selection bottleneck model the deployment of attention does not have bottleneck properties (Pashler, 1991), suggesting that neither N2pc nor SPCN would be affected by either SOA or the concurrent mental rotation required in the rotation condition. If instead the deployment of attention is subject to the same capacity limitations as response selection, as argued by Brisson and Jolicœur (2007a, 2007b), an SOA effect is predicted on behavior, the N2pc amplitude and the SPCN onset latency. Moreover, if response selection, mental rotation, and the deployment of attention are all subject to shared capacity limitations, then the N2pc and SPCN should be affected by both S1 orientation and SOA.

2. Methods

2.1. *Participants*

Thirty right-handed students of Leiden University between 18 and 30 years old participated in the experiment. The experiment was conducted in accordance with relevant laws and institutional guidelines and was approved by the local ethics committee from the Faculty of Social Sciences. All students had normal or corrected to normal eyesight. They received either fourteen euros or course credits or a comparable combination of both. Data from 11 participants did not comply with the electrophysiological criteria (described below) and were therefore discarded from analysis. Data from another four participants were excluded from analysis because behavioral performance was below a 74% threshold. This left 15 participants (four male) in the sample (mean age: 22 years). The dual task was very difficult, as is shown by the long RTs and the fact that four participants that responded incorrectly to one or both of the stimuli more than a quarter of the time. The task being difficult in its own right, participants had difficulty keeping their eyes in the center of the screen, presumably related to the overall difficulty of the task. Additionally, we displayed stimulus 2 on the screen until the response was given, which was longer than display times from earlier experiments (up to 3 s vs. 133 ms.) (i.e., Brisson & Jolicœur, 2007a). This has probably made it much harder for participants to keep their eyes fixated on the center of the screen, and we had to discard more trials because of it. All in all we were left with 15 participants in our sample on which we could run all analyses.

2.2. *Apparatus*

Participants were tested individually, in a dimly lit shielded room. They sat in front of a 17 in. computer screen at a viewing distance of approximately 75 cm. Responses were made with key-presses with the left and right foot for Task 1

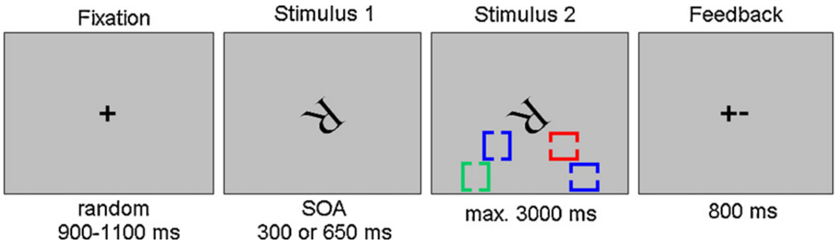

Fig. 1. Sequence of events within one trial in the PRP paradigm: the '+' served as a fixation symbol. S1 (the first stimulus) appeared in the center of the screen, and after an SOA of 300 ms or 650 ms, S2 (second stimulus) and distractors appeared on both sides, below the center of the screen. Accuracy feedback was presented at the end of each trial. The actual colors of the squares were blue (one on each side), red, and green (and they were isoluminant to each other). The sizes of the letters (and digits) in S1, and squares in S2, and their distances to each other and to the fixation symbol are not to scale.

responses and the left and right index finger for Task 2 responses. The pedals (Psychological Software Tools, Inc.) were embedded in a sloping footboard that was put in front of the participants in such a way that, at rest, the feet and ankles were relaxed. The pedals needed a light press to give a detectable response and an adequate response was marked by an audible click. Of the two response boxes for the fingers (one for each hand) with four keys (no key for the thumb) only the keys for the index fingers were used (situated closest to the middle).

2.3. Stimuli

The stimuli used in Task 1 were presented on the screen and were the alphanumeric characters 2, 4, 5, 7, f, G, k, Q, R, and t. These stimuli were selected because their asymmetry allowed the creation of unambiguous rotation and mirroring conditions (hence the mixture of uppercase and lowercase letters). They were oriented either normally or left-right mirror-imaged and their orientation was 0° or 140°. Clockwise (CW) and counter-clockwise (CCW) tilted stimuli occurred equally often in case of the 140° condition. The characters were presented at the center of the screen, in black on a grey screen, at a visual angle of approximately 3° in height. Because S1 was always presented in the middle of the screen, possible spatial capture by the onset of S1 was the same for both orientation conditions. Participants made a speeded mirror/normal classification of the rotated stimulus.

For Task 2, four squares were presented in the bottom half of the screen, two on each side of the center. The squares had two gaps, always on opposite sides such that an imaginary line could be drawn through the gaps, either vertically or horizontally. All squares in the visual display subtended a visual angle of 1° × 1° and the gaps were 0.33°. The center of the squares nearest to fixation was 1.5° below and 3.5° to the left or right of fixation. The center of the far squares was 3° below and 5° to the left or right of fixation (see also: Brisson & Jolicœur, 2007a). To balance the physical properties of the display, there was always a blue colored square on each side of the center, while of the two remaining squares one was green and one red (one on each side), and the colors were isoluminant. The stimulus intensity was 76 cd/m^2 and the RGB color definitions were for green: 0:128:0; for red: 255:0:0; and for blue: 0:90:205. The grey background had a luminosity of 192 cd/m^2 and the RGB color definitions were 128:128:128. Half of the subjects responded to the red square and half to the green square. Any residual nonattentional unilateral electrophysiological activation due to low-level factors would cancel out when the N2pc and SPCN difference waves were calculated (and grand averaged). The task was to indicate the orientation of the imaginary line (vertical vs. horizontal) that could be drawn through the gaps of the green or the red square, and the color of the target square was constant for a given participant and counterbalanced across participants.

The two presented stimuli were separated by a SOA of 300 ms or 650 ms. SOA, mirror/normal presentation, rotation direction (CW/CCW), target orientation (0° or 140°), position of the squares and horizontal/vertical orientation of the gaps in the squares were all varied randomly within each block with the constraint that all possible combinations of the levels of these factors occurred equally often in each block. An illustration of the stimuli in a trial is shown in Fig. 1.

Left foot and right foot presses were used for Task 1 responses and their mapping onto normally presented or mirror image stimuli was counterbalanced across participants. Left and right index finger presses were used for Task 2 responses and their mapping onto horizontal or vertical line gaps was also counterbalanced across participants, as was the color of the target square (red or green).

2.4. Procedure

Before the start of the experiment, participants received written instructions. They were asked to respond as quickly as possible, and not to be too cautious in their response. To avoid response grouping, participants were told not to withhold the response to S1 until S2 was presented, but rather to initiate a response as soon as possible. Lastly, they were told to keep their eyes fixated in the center of the screen (and not to make an eye movement to the sides [except for the eye movement calibration task described below]) and to limit eye blinks to the time between the trials.

Next, the computer experiment was started. First, eye movements were measured during a 5 min calibration test in which participants needed to follow a target that moved from the center to the left or the right side of the screen to measure horizontal eye movements and calibrate the eye movement recordings. Second, the first task was practiced by itself, as a single-task (16 trials). Two dual-task blocks followed to practice the full dual-task paradigm (32 trials per block).

Experimental trials were presented in 12 blocks of 74 trials. Pauses separated the blocks and participants were encouraged to use them. Within the experimental blocks, the trial started with the presentation of a fixation point in the center of the screen replaced after 500 ms by S1. After a variable SOA S2 appeared while S1 remained in view. As soon as S2 appeared, participants had 3000 ms to respond before feedback appeared. Responding to S2 also caused feedback to appear. Feedback consisted of a '+' or '–' sign left of the middle for S1 and right of the middle for S2 shown for 800 ms, and marking the end of the trial. After a randomly jittered inter-trial interval of 900–1100 ms the fixation point appeared in the center of the screen to indicate the beginning of the next trial. At the end of each block, an average reaction time (RT) and a percentage correct (PC) for each task up to then was presented to give participants insight in their progress, and to motivate them to keep trying to respond faster on every block.

2.5. Electrophysiological measurements

The electroencephalogram was recorded continuously while the task was performed with 29 Ag/AgCl electrodes at the following sites: Fz, F3, F4, FC3, FC4, C5, C3, C1, Cz, C2, C4, C6, T7, T8, CP3, CP4, P7, P3, Pz, P4, P8, PO7, PO3, POz, PO4, PO8, O1, Oz, and O2 in the extended international 10/20 system (Sharbrough et al., 1991). The signals were digitized at 256 Hz with an input antialiasing low-pass filter set at 67 Hz using a BioSemi Active Two system. Eye movements and blinks were recorded by electro-oculogram (EOG). Horizontal EOG (hEOG) was the bipolar signal of the left vs. right outer canthus and vertical EOG (vEOG) was the bipolar signal of above vs. below the left eye. The EEG was high-pass filtered at 0.01 Hz (24 dB/octave) and low-pass filtered at 8 Hz (48 dB/octave) (Hanslmayr et al., 2005; Wascher, Hoffmann, Sänger, & Grosjean, 2009) during post-recording analyses.

Electrodes of interest were P7/P8, PO7/PO8, P3/P4, PO3/PO4, and O1/O2, for the N2pc and SPCN. Artifacts at any of these electrode sites led to the exclusion of that particular trial as did eye blinks (vEOG > 100 μV). For the N2pc it was important to keep the eyes fixated at the center of the screen: any trials containing large eye movement (hEOG > 35 μV) were therefore excluded. Comparable to Woodman and Luck (2003) and Brisson and Jolicœur (2007a), after ocular artifact rejection a 3.2 μV cut off was used for residual eye movements towards the targets (squares) in the average hEOG waveforms computed for trials with a target in the left visual field and for trials with a target in the right visual field. Ten participants exceeded this criterion in one or more of the conditions and they were excluded from further analysis. This way, the remaining subjects did not move their eyes in the direction of the target by more than .2° of visual angle (see Luck, 2005). The number of trials that contributed to the ERP waveforms was 97 for the condition 0°/300 ms; 96 for the condition 140°/300 ms; 95 for the condition 0°/650 ms; and 93 for the condition 140°/650 ms.

For N2pc and SPCN, segments of 200 ms prior to S2 presentation to 900 ms after S2 presentation were used, baseline corrected on the 200 ms period before S2 presentation. We quantified the N2pc as the mean amplitude of the pooled difference (mean contralateral minus mean ipsilateral) waveform for the five posterior lateralized electrode pairs in our montage, in the time window of 190–260 ms from S2 onset. This time window best captures the outer limits of the negative N2pc component for all electrode-pairs across the four conditions.

SPCN onset latency was analyzed to test for deferment of the processes underlying SPCN by S1 orientation and SOA. This was done using a jackknife analysis (Kiesel, Miller, Jolicœur, & Brisson, 2008; Miller, Patterson, & Ulrich, 1998; Ulrich & Miller, 2001) over the pooled difference waveform for the five posterior lateralized electrode pairs in our montage. With the jackknife method, *N* grand average waveforms are computed, each one with *N* – 1 participants (a different participant is removed for each waveform). Onset-latency measures are obtained for each of these *N* grand average waveforms, and the values are submitted to a conventional

Table 1
Mean reaction time (ms) and percentage correct for Task 1 and Task 2, in each condition, with the standard error of the mean in parenthesis.

SOA (ms)	RT1		PC1		RT2		PC2	
	300	650	300	650	300	650	300	650
S1 upright (0°)	845 (36)	863 (39)	94 (0.5)	94 (0.6)	921 (44)	719 (33)	94 (0.9)	91 (1.3)
S1 rotation (140°)	1109 (38)	1117 (34)	86 (1.3)	86 (1.3)	1174 (50)	865 (38)	92 (1.0)	92 (1.0)

analysis of variance (ANOVA). In order to compensate for the smaller variance of the jackknife waveforms, the F value in the ANOVA is adjusted using the following formula (Ulrich & Miller, 2001):

$$F_{\text{adjusted}} = \frac{F}{(N-1)^2}.$$

The onset latency of the SPCN was defined as the latency at which the filtered pooled difference wave became more negative than −0.4 μV, starting 300 ms after stimulus presentation.

3. Results

3.1. Behavioral results

RTs longer than 3000 ms or shorter than 150 ms and trials in which R2 preceded R1 were excluded from the analysis of RT and accuracy data. The percentages of trials eliminated based on these restrictions were 0.94% for the S1 upright orientation/short SOA condition, 1.29% for the S1 rotated orientation/short SOA condition, 0.74% for the S1 upright orientation/long SOA condition and 1.06% for the S1 rotated orientation/long SOA condition. Mean RTs were based on trials with a correct response to both stimuli. We excluded all trials from the data in which R2 preceded R1, which happened in a total of 2.5% of the trials. Analyses of Variance (ANOVAs) were conducted using a 2 × 2 design with the within-subjects factors S1 orientation and SOA and an alpha of 0.05. Table 1 shows the mean behavioral performance data.

RT1 was 259 ms shorter in the upright condition compared to the tilted condition (854 ms vs. 1113 ms), $F(1, 14) = 421.1$, $MSE = 2392.9$, $p < .001$. The mean RT1 did not vary significantly over SOA, $F(1, 14) < 1.5$. There was no interaction effect between SOA and orientation for S1 accuracy or RT, $Fs < 1$.

S1 orientation did affect the accuracy of responses to S1 with an 8.5% higher accuracy with an upright S1 (94.4%) than a rotated (140°) S1 (85.9%), $F(1, 14) = 52.5$, $MSE = 20.5$, $p < .001$. Mean S1 accuracy did not change over SOA, $F < 1$ and no interaction was found, $F < 1$.

RT2 for the rotated and upright orientation for each SOA are shown in Fig. 2. RT2 was 200 ms shorter at 0° than at 140° (820 ms vs. 1020 ms), $F(1, 14) = 234.2$, $MSE = 2552.7$, $p < .001$. Mean RT2 increased by 256 ms with decreasing SOA (from 792 ms to 1048 ms), $F(1, 14) = 358.6$, $MSE = 2736.4$, $p < .001$, showing the expected PRP effect. Additionally, the interaction effect of S1 orientation and SOA on RT2 indicated that the orientation effect was 107 ms larger at short than at longer SOAs (253 ms vs. 146 ms), $F(1, 14) = 104.7$, $MSE = 408.6$, $p < .001$. We looked at this interaction effect further to see whether the orientation effect existed on both SOA levels and whether the SOA effect existed on both orientation levels. We first examined the effect of SOA for trials with an upright S1 for which no mental rotation was required. RT2 was 202 ms longer for the short relative to the long SOA, $F(1, 14) = 185.0$, $MSE = 1660.5$, $p < .001$. Second, we examined the effect for trials with a tilted S1 (thus requiring mental rotation). Here, RT2 was 309 ms longer for the short relative to the long SOA, $F(1, 14) = 483.0$, $MSE = 1484.4$, $p < .001$. Next, we examined the effect of S1 orientation in the long and short SOA condition separately. At SOA = 300 ms, the effect of orientation was 253 ms shorter for the S1 in upright position, $F(1, 14) = 291.5$, $MSE = 1647.4$, $p < .001$. At SOA = 650 ms, an S1 of 0° showed a 146 ms shorter RT2 compared to an S1 in tilted position, $F(1, 14) = 122.0$, $MSE = 1313.9$, $p < .001$.

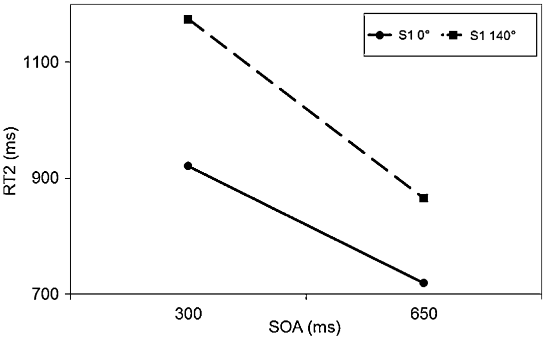

Fig. 2. Mean response times in Task 2 (RT2) for each orientation of S1 (upright vs. rotated) and each SOA between S1 and S2.

For Task 2, there was no significant difference in percentage correct as a function of S1 orientation, $F < 1$. We found a significant effect of SOA, $F(1, 14) = 5.4$, $MSE = 4.7$, $p < .05$, for Task 2 accuracy. Responses were 1.3% more accurate at a SOA of 300 as compared to 650 ms (92.9% vs. 91.6%). There was a marginally significant interaction effect for the percentage correct of Task 2, $F(1, 14) = 4.0$, $MSE = 5.1$, $p < .10$.

3.2. Electrophysiological results

3.2.1. N2pc

The mean N2pc amplitudes from the pooled difference waveform for the five posterior lateralized electrode pairs were submitted to an ANOVA with S1 orientation and SOA as

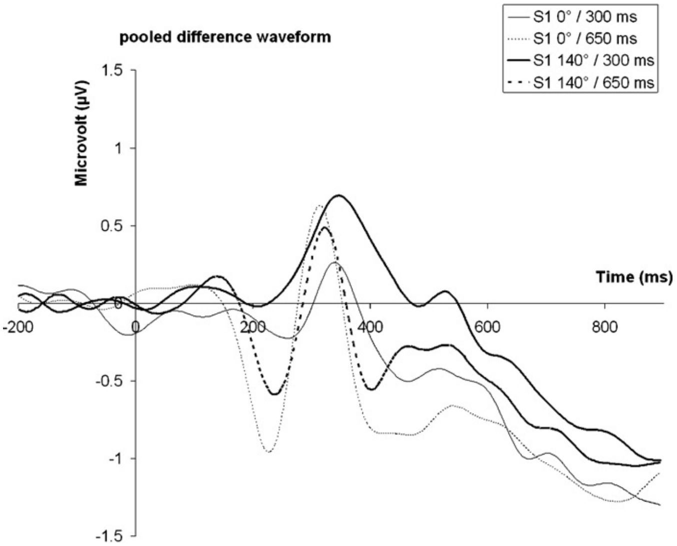

Fig. 3. N2pc and SPCN difference waves (contralateral minus ipsilateral) locked to the onset of S2 (time = 0), for the four different conditions: S1 0°/300 ms SOA; S1 0°/650 ms SOA; S1 140°/300 ms SOA; S1 140°/650 ms SOA at the pooled difference waves over the five electrode pairs. Thin lines represent S1 at 0° orientation, bold lines represent S1 at 140° orientation, continuous lines represent short SOA conditions and dotted lines represent long SOA conditions.

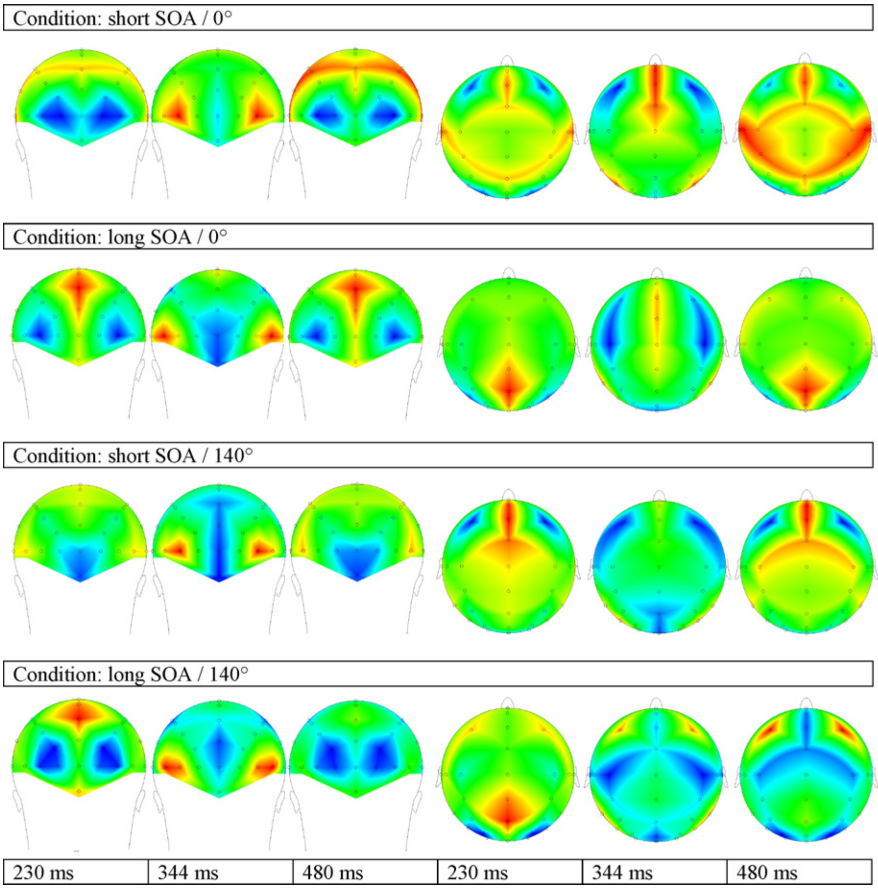

Fig. 4. Topographical maps (back and top) of the difference wave forms[2] for the 4 different conditions (short SOA/0°; long SOA/0°; short SOA/140°; long SOA/140°) at the peak of the N2pc (230 ms), the positive-going deflection separating N2pc and SPCN (344 ms) and the onset of the SPCN (480 ms).

within-subjects factors. We used the Greenhouse–Geisser Epsilon (Jennings & Wood, 1976) to correct the p and MSE where appropriate (but original *df*'s are reported). The difference waveforms are shown in Fig. 3 for the pooled electrodes. Scalp distributions for the N2pc, SPCN and the positive-going deflection that often separates the N2pc and SPCN are shown in Fig. 4. The effect for S1 orientation was significant, $F(1, 14) = 5.7$, $MSE = 0.1$, $p < .05$, due to less negative amplitude of the N2pc when S1 was rotated (i.e., a reduction of the N2pc). There was also a significant main effect of SOA, $F(1, 14) = 11.2$, $MSE = 0.1$, $p < .01$, indicating that the amplitude of the N2pc was attenuated at short SOA relative to long SOA. The interaction between S1 orientation and SOA was not significant, $F(1, 14) = .81$, $MSE = 0.04$, $p = .383$.

3.2.1.1. Planned comparisons. Although the interaction between S1 orientation and SOA was not significant, planned comparisons were conducted to test specific predictions deriving from models attributing bottleneck properties only to response selection (Pashler, 1994; Smith, 1967; Welford, 1952, 1980), or independently to mental rotation. To test dual-task interference due to response selection, the effect of SOA on N2pc was restricted to trials with an upright S1, where no mental rotation was required. There was a significant attenuation of N2pc for the short relative to the long SOA, $F(1, 14) = 5.0$, $MSE = .05$, $p < .05$. A comparable SOA effect was found with tilted stimuli, SOA, $F(1, 14) = 5.7$, $MSE = .07$, $p < .05$. The reduction of the N2pc amplitude with decreasing SOA confirms that response selection in itself diminishes the deployment of visual-spatial attention in a following task, as observed by Brisson and Jolicœur (2007a, 2007b).

A mental rotation bottleneck model would predict orientation effects for short SOAs. Indeed, at SOA = 300 ms, the N2pc was smaller with S1 at 140° than with upright stimuli, $F(1, 14) = 5.8$, $MSE = .1$, $p < .05$. The orientation effect did not occur on long SOAs, $F(1, 14) = 2.7$, $MSE = .1$, $p > .1$. The result at a SOA of 300 ms shows that mental rotation, per se, interferes with visual-spatial attention, independent of response selection.

3.2.2. SPCN onset latency

To test whether the SPCN onset latency was affected by S1 orientation and SOA, we used a jackknife analysis (Kiesel et al., 2008; Miller et al., 1998; Ulrich & Miller, 2001). The onset latencies of the pooled difference waveform for the five posterior lateralized electrode pairs were submitted to an ANOVA with SOA and S1 orientation as within-subjects factors. The jackknife analysis confirmed what can be seen in Fig. 3, namely that the SPCN onset was earliest for the S1 0°/650 ms SOA condition, succeeded by the S1 140°/650 ms SOA condition, then the S1 0°/300 ms SOA condition, followed later by the most centrally taxing condition, the S1 140°/300 ms SOA condition. This was reflected in the ANOVA by significant effects of S1 orientation, $F_{\text{adjusted}}(1, 14) = 5.7$, $MSE_{\text{adjusted}} = 34{,}949$, $p < .05$, and SOA, $F_{\text{adjusted}}(1, 14) = 7.5$, $MSE_{\text{adjusted}} = 46{,}639$, $p < .05$. There was a marginally significant interaction between S1 orientation and SOA, $F_{\text{adjusted}}(1, 14) = 4.1$, $MSE_{\text{adjusted}} = 32{,}742$, $p < .1$.

3.2.2.1. Planned comparisons. On trials with a tilted S1, the SPCN latency was significantly longer for the short relative to the long

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[2] Because of the noise on electrodes FC3 and C1, the electrode pairs FC3–FC4 and C1–C2 were excluded from Fig. 4.

SOA, $F_{\text{adjusted}}(1, 14) = 6.9$, $MSE_{\text{adjusted}} = 70{,}446.1$, $p < .05$, suggesting that the arrival of S2 information into VSTM was delayed by Task 1 processes. In contrast, there was no significant SOA effect on SPCN latency for trials with an upright S1, $F_{\text{adjusted}}(1, 14) = 3.0$, $MSE_{\text{adjusted}} = 8934.9$, $p > .10$.

On trials with a SOA of 300 ms, tilted S1 s led to longer SPCN latencies than upright S1 s, $F_{\text{adjusted}}(1, 14) = 5.3$, $MSE_{\text{adjusted}} = 63{,}586.1$, $p < .05$. This suggests that mental rotation, independent of response selection, interferes with the arrival of information into VSTM. This orientation effect was not observed at a SOA of 650 ms, $F_{\text{adjusted}}(1, 14) = 0.61$, $MSE_{\text{adjusted}} = 4104.8$, $p < 1$.

4. Discussion

The present PRP study investigated whether mental rotation affects the progress of deploying visual-spatial attention in a concurrent task. Because mental rotation involves a variable duration of the same process it is capable of causing different degrees of dual-task interference while all other processes remain constant – including deciding whether a character was in normal or mirrored version, and including response selection. With this setup, dual-task interference was elicited that could not be attributed to the involvement of response selection. The N2pc (a real-time measure of the deployment of visual-spatial attention (Luck & Hillyard, 1994)) was attenuated when S2 was presented while subjects performed concurrent mental rotation on S1, and the SPCN (believed to index the storage of information in VSTM (Brisson & Jolicœur, 2007a, 2007b; Vogel & Machizawa, 2004)) to S2 was significantly delayed. The attenuated N2pc showed that spatial attention could not be deployed efficiently to the lateralized target in the Task 2 display as long as mental rotation engaged in Task 1 had not run to completion.

To our knowledge this is the first demonstration of PRP interference in which response selection is neither the delaying, nor the delayed process. The study shows that response selection is not a necessary ingredient of dual-task cost, which undermines the traditional response-selection bottleneck model. The response-selection bottleneck model (Pashler, 1994; Smith, 1967; Welford, 1952, 1980) has been capable of explaining a variety of RT patterns in the PRP paradigm, simply by assuming that response selection is the only process that cannot be performed for two tasks at the same time. While initially response selection was not differentiated, and was described as translation from stimulus codes to response codes (Fagot and Pashler, 1992; McCann & Johnston, 1992), converging evidence in favor of parallel translation of two stimuli has obliged a model that attributes dual-task interference to later processes, such as the actual decision between candidate responses that have been activated in parallel (e.g., Hommel, 1998; Logan & Schulkind, 2000).

Although several so-called central processes, including short-term consolidation (Jolicoeur & Dell'Acqua, 1998), memory retrieval (Carrier & Pashler, 1995) and mental rotation (Van Selst & Jolicœur, 1994) have previously been shown to delay response selection, or to be delayed by response selection, this evidence has never argued against the primacy of response selection processes in causing dual-task interference. It could be, for example, that the involvement of response selection was a necessary condition for delaying a different mental process, due to either capacity limitations as such, or coordinative processes intended to prevent interference in decisions (e.g., Meyer & Kieras, 1997a, 1997b). The current experiment demonstrates, however, that response selection does not need to be involved in dual-task interference, but is only one of a category of demanding processes that causes dual-task interference. In particular, the current study demonstrated attenuation of the N2pc on rotation trials, which indicates that mental rotation interferes directly with visuo-spatial attention processes. The attenuation of the N2pc was observed 190–260 ms after S2, that is 490–560 ms after S1 on short SOAs. Given a mean RT of 857 ms to an upright and 1107 ms to a tilted S1, it is clear that the attenuation of the N2pc cannot be attributed to response selection unless the implausible assumption is made that response selection starts at least 547 ms before the response. We therefore argue that the best explanation is that there was direct interference of mental rotation onto the deployment of attention.

In contrast to the amplitude effects we observed for the N2pc, the effects on the SPCN can be interpreted as principally due to latency shifts. The convergence of the SPCN waveforms near the end of the measurement window for all four conditions is broadly consistent with the similar accuracy in S2 achieved in all conditions (between 89% and 92%). Most important, however, was the observation that the SPCN wave had different onset latencies in the different conditions (Fig. 3), and in particular that the onset of the SPCN was the most delayed in the condition associated with the largest PRP interference in the mean RT2s, namely the condition in which the SOA was short and S1 was rotated to 140°. These results converge nicely with those of Brisson and Jolicœur (2007a) in showing that entry into VSTM can be systematically delayed by concurrent dual-task interference.

Although these effects were quite substantial, and clearly statistically significant, the delays in SPCN onset cannot explain all of the observed differences in mean response times in Task 2. For the delay of Task 2 with increased task overlap (reduced SOA) we found a behavioral effect of 202 ms when S1 was upright and an effect of 309 ms when S1 was tilted. The observed SPCN effect for SOA 300 ms vs. SOA 650 ms was 60 ms when S1 was upright and 254 ms when S1 was rotated. For the two SOAs, the SPCN latency effect was 29.7% and 82.2% of the behavioral effect, respectively. Even though the comparison of effect sizes is complicated by the fact that ERP latencies are obtained in average waveforms rather than single-trial waveforms, which introduces bias due to smearing in average ERPs, it is still likely that additional delays of processing took place following entry into VSTM, likely at the response-selection stage.

The present results were not compromised by issues of component overlap, despite the presentation of two stimuli in close temporal proximity. First, the main electrophysiological results of interest were derived from double subtraction lateralization waves (N2pc, SPCN), which cancel out any electrical brain activity that is not lateralized systematically with respect to the side of presentation of S2 (see Brisson & Jolicœur, 2007a; Luck & Hillyard, 1994). Given that S1 was presented at the center of the screen and that the independent variables were manipulated orthogonally to the position of S2 in the visual field, S1-related electrical activity was equivalent in the contralateral and ipsilateral waveforms defined relative to the spatial position of S2, and thus this activity was entirely canceled out in the contralateral minus ipsilateral difference waves. Second, the N2pc was attenuated by mental rotation when considering only the trials at the short SOA. The fact that an effect of orientation on the N2pc was observed even when SOA was held constant shows that mental rotation itself was capacity limited or shared capacity-limited processes with other processes. The observed differences cannot be due to differential component overlap of low-level sensory ERPs (given fixed SOA) and so they must be due to different durations of mental rotation.

The question remains which underlying cause can explain the interference between mental rotation, attention, and response selection – processes that do not seem to be related in terms of function, input and output requirements, or computational logic. One way to look at such processes is to consider them as computational routines that take parameters from control processes, as envisioned by the executive control theory of visual attention (ECTVA; Logan & Gordon, 2001). Response selection processes identify and select an appropriate response *given* a particular decision rule; mental rotation processes modify the spatial characteristics of a particular stimulus representation *given* a particular rotation direction; and attentional processes facilitate the processing of stimulus information from a particular location *given* that this is where the target has been located. In other words, all three processes operate conditional on goal-specific input parameters. Whereas the processes themselves can be prepared in advance of the eventual presentation of stimuli, thus rendering them a kind of "prepared reflex" (cf., Hommel, 2000), their online parameterization may require capacity-demanding executive supervision (Logan & Gordon, 2001) or at least be typically accompanied by such supervision to avoid errors (Meyer & Kieras, 1997a, 1997b). Therefore, in this current experiment, the delay might be caused by the control processes imposed on the ongoing processes to switch between mental rotation, response selection and visual-spatial attention and to give the correct response in an as short amount of time as possible.

In conclusion, the present experiment shows that mental rotation and attention shifting not only interact and interfere with response selection (e.g., Brisson & Jolicœur, 2007a), but that they also interfere with each other in a way that reveals their bottleneck properties. Mental rotation can influence the deployment of visual-spatial attention as well as delay the passage of information into VSTM. Because the capacity-limited process of mental rotation – in contrast to response selection – takes considerably more time when a stimulus is rotated further from upright, we were able to manipulate the duration of mental rotation systematically. There is thus strong evidence that dual-task costs are not only created by response selection but by other, earlier, processes as well, and all three processes – response selection, mental rotation and visual-spatial attention – are likely to share a common resource like executive control.

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References

Band, G. P. H., & Miller, J. (1997). Mental rotation interferes with response preparation. *Journal of Experimental Psychology: Human Perception & Performance*, *23*, 319–338.

Brisson, B., & Jolicœur, P. (2007a). 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.

Brisson, B., & Jolicœur, P. (2007b). Electrophysiological evidence of central interference on the control of visual-spatial attention. *Psychonomic Bulletin and Review*, *14*, 126–132.

Carrier, L. M., & Pashler, H. (1995). Attentional limits in memory retrieval. *Journal of Experimental Psychology: Learning, Memory & Cognition*, *21*, 1339–1348.

Cooper, L. A. (1975). Mental rotation of random two-dimensional shapes. *Cognitive Psychology*, *7*, 20–43.

Cooper, L. A. (1976). Demonstration of a mental analog of an external rotation. *Perception & Psychophysics*, *19*, 296–302.

Cooper, L. A., & Shepard, R. N. (1973). Chronometric studies of the rotation of mental images. In G. Chase (Ed.), *Visual information processing* (pp. 75–176). New York: Academic Press.

Corballis, M. C. (1986). Is mental rotation controlled or automatic? *Memory & Cognition*, *14*, 124–128.

DellAcqua, R., & Jolicœur, P. (2000). Visual encoding of patterns is subject to dual-task interference. *Memory & Cognition*, *28*, 184–191.

Eimer, M. (1996). The N2pc component as an indicator of attentional selectivity. *Electroencephalography and Clinical Neurophysiology*, *99*, 225–234.

Fagot, C., & Pashler, H. (1992). Making two responses to a single object: Implications for the central attentional bottleneck. *Journal of Experimental Psychology: Human Perception and Performance*, *18*, 1058–1079.

Hanslmayr, S., Klimesch, W., Sauseng, P., Gruber, W., Doppelmayr, M., Freunberger, R., et al. (2005). Visual discrimination performance is related to decreased alpha amplitude but increased phase locking. *Neuroscience Letters*, *375*, 64–68.

Heil, M., Wahl, K., & Herbst, M. (1999). Mental rotation, memory scanning, and the central bottleneck. *Psychological Research*, *62*, 48–61.

Hommel, B. (1998). Automatic stimulus–response translation in dual-task performance. *Journal of Experimental Psychology: Human Perception & Performance*, *24*, 1368–1384.

Hommel, B. (2000). The prepared reflex: Automaticity and control in stimulus–response translation. In S. Monsell, & J. Driver (Eds.), *Control of cognitive processes: Attention and performance XVIII* (pp. 247–273). Cambridge, MA: MIT Press.

Hopf, J. M., Luck, S. J., Girelli, M., Hagner, T., Mangun, G. R., Scheich, H., et al. (2000). Neural sources of focused attention in visual search. *Cerebral Cortex*, *10*, 1233–1241.

Hopf, J. M., & Mangun, G. R. (2000). Shifting visual attention in space: An electrophysiological analysis using high spatial resolution mapping. *Clinical Neurophysiology*, *111*, 1241–1257.

Jennings, J. R., & Wood, C. C. (1976). The re-adjustment procedure for repeated-measures analyses of variance. *Psychophysiology*, *13*, 277–278.

Johnston, J. C., McCann, R. S., & Remington, R. W. (1995). Chronometric evidence for two types of attention. *Psychological Science*, *6*, 365–369.

Jolicœur, 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., & Dell'Acqua, R. (1998). The demonstration of short-term consolidation. *Cognitive Psychology*, *36*, 138–202.

Kiss, M., Van Velzen, J., & Eimer, M. (2008). The N2pc component and its links to attention shifts and spatially selective visual processing. *Psychophysiology*, *45*, 240–249.

Kiesel, A., Miller, J., Jolicœur, P., & Brisson, B. (2008). Measurement of ERP latency differences: A comparison of single-participant and jackknife based scoring methods. *Psychophysiology*, *45*, 250–274.

Logan, G. D., & Gordon, R. D. (2001). Executive control of visual attention in dual-task situations. *Psychological Review*, *108*, 393–434.

Logan, G. D., & Schulkind, M. D. (2000). Parallel memory retrieval in dual task situations: I. Semantic memory. *Journal of Experimental Psychology: Human Perception & Performance*, *26*, 1072–1090.

Luck, S. J. (2005). *An introduction to the event-related potential technique*. Cambridge MA: The MIT Press.

Luck, S. J., & Hillyard, S. A. (1994). Spatial filtering during visual search: Evidence from human electrophysiology. *Journal of Experimental Psychology: Human Perception & Performance*, *20*, 1000–1014.

McCann, R. S., & Johnston, J. C. (1992). Locus of the single-channel bottleneck in dual-task interference. *Journal of Experimental Psychology: Human Perception and Performance*, *18*, 471–484.

McCollough, A. W., Machizawa, M. G., & Vogel, E. K. (2006). Electrophysiological measures of maintaining representations in visual working memory. *Cortex*, *43*, 77–90.

Meyer, D. E., & Kieras, D. E. (1997a). A computational theory of executive cognitive processes and multiple-task performance: I. Basic mechanisms. *Psychological Review*, *104*, 3–65.

Meyer, D. E., & Kieras, D. E. (1997b). A computational theory of executive cognitive processes and multiple-task performance: Part 2. Accounts of psychological refractory-period phenomena. *Psychological Review*, *104*, 749–791.

Miller, J., Patterson, T., & Ulrich, R. (1998). Jackknife-based method for measuring LRP onset latency differences. *Psychophysiology*, *35*, 99–115.

Pashler, H. (1991). Shifting visual spatial attention and selecting motor responses: Distinct attentional mechanisms. *Journal of Experimental Psychology: Human Perception and Performance*, *17*, 1023–1040.

Pashler, H. (1994). Dual-task interference in simple tasks: Data and theory. *Psychological Bulletin*, *116*, 220–244.

Pashler, H., & Johnston, J. C. (1989). Chronometric evidence for central postponement in temporally overlapping tasks. *Quarterly Journal of Experimental Psychology*, *41A*, 19–45.

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.

Predovan, D., Prime, D., Arguin, M., Gosselin, F., Dell'Acqua, R., & Jolicœur, P. (2009). On the representation of words and nonwords in visual short-term memory: Evidence from human electrophysiology. *Psychophysiology*, *46*, 191–199.

Prime, D. J., & Jolicoeur, P. (2009). Mental rotation requires visual short-term memory: Evidence from human electric cortical activity. *Journal of Cognitive Neuroscience*, *22*, 2437–2446.

Robitaille, N., & Jolicœur, P. (2006). Effect of cue-target interval on the N2pc. *Neuroreport*, *17*, 1655–1658.

Ruthruff, E., Miller, J., & Lachmann, T. (1995). Does mental rotation require central mechanisms? *Journal of Experimental Psychology: Human Perception & Performance*, *21*, 552–570.

Sharbrough, F., Chatrian, G. E., Lesser, R. P., Lüders, H., Nuwer, M., & Picton, T. W. (1991). American electroencephalographic society guidelines for standard electrode position nomenclature. *Journal of Clinical Neurophysiology*, *8*, 200–202.

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.

Smith, M. C. (1967). Theories of the psychological refractory period. *Psychological Bulletin*, *67*, 202–213.

Telford, C. W. (1931). The refractory phase of voluntary and associative responses. *Journal of Experimental Psychology*, *14*, 1–36.

Ulrich, R., & Miller, J. (2001). Using the jackknife-based scoring method for measuring LRP onset effects in factorial designs. *Psychophysiology*, *34*, 816–827.

Van Selst, M., & Jolicœur, P. (1994). Can mental rotation occur before the dual-task bottleneck? *Journal of Experimental Psychology: Human Perception & Performance*, *20*, 905–921.

Vogel, E. K., & Machizawa, M. G. (2004). Neural activity predicts individual differences in visual working memory capacity. *Nature*, *428*, 751–784.

Wascher, E., Hoffmann, S., Sänger, J., & Grosjean, M. (2009). Visuo-spatial processing and the N1 component of the ERP. *Psychophysiology*, *46*, 1270–1277.

Wascher, E., & Wauschkuhn, B. (1996). The interaction of stimulus- and response-related processes measured by event-related lateralizations of the EEG. *Electroencephalography and Clinical Neurophysiology*, *99*, 149–162.

Welford, A. T. (1952). The “psychological refractory period” and the timing of high-speed performance—A review and a theory. *British Journal of Psychology*, *43*, 2–19.

Welford, A. T. (1967). Single channel operation in the brain. *Acta Psychologica*, *27*, 5–22.

Welford, A. T. (1980). Choice reaction time: Basic concepts. In A. T. Welford (Ed.), *Reaction times* (pp. 73–128). New York: Academic Press.

Woodman, G. F., & Luck, S. J. (1999). Electrophysiological measurement of rapid shifts of attention during visual search. *Nature*, *400*, 867–869.

Woodman, G. F., & Luck, S. J. (2003). Serial deployment of attention during visual search. *Journal of Experimental Psychology: Human Perception & Performance*, *29*, 121–138.