

Object-substitution masking modulates spatial attention deployment and the encoding of information in visual short-term memory: Insights from occipito-parietal ERP components

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Abstract

If object-substitution masking (OSM) arises from mask representations replacing target representations, OSM should impede the formation of representations in visual short-term memory (VSTM). We utilized event-related potentials to examine the effect of OSM on target processing. An N2pc was observed on trials with delayed-offset masks, indicating that focused attention was directed to the target. The sustained posterior contralateral negativity (SPCN), an index of VSTM storage, was observed in delayed-offset trials only on trials with correct responses. This supports the hypothesis that inaccurate performance on delayed-offset trials arises from a failure to encode the target in VSTM. On co-termination trials, accuracy was high and neither the N2pc nor SPCN was observed. This indicates that, in the absence of masking, the task was accomplished by maintaining a diffuse attentional state that enabled the joint encoding of the potential target items.

Descriptors: Masking, Event-related potentials (ERPs), Sustained posterior contralateral negativity (SPCN), Visual short-term memory (VSTM)

Visual masking has been an important tool for investigating visual perception and cognition (Breitmeyer, 1984). Visual masking refers to the impaired processing of a target stimulus due to the presentation of a second stimulus (the mask) in close temporal and spatial proximity to the target. Enns and Di Lollo (1997) introduced a new form of masking, *object substitution masking*, whose characteristics could not easily be explained by traditional theories of masking (for details, see Di Lollo, Enns, & Rensink, 2000). Enns and Di Lollo (1997) demonstrated that, when attention is not focused at the target location before target presentation, a sparse mask (4 dots surrounding the target) could

strongly mask the target when the mask remained visible after the target was removed from the display (*delayed-offset mask*). This type of “object substitution” masking differs from other forms of masking in that the contours of the mask neither overlapped nor had to be spatially contiguous with the masked target. Furthermore, unlike backward pattern masking and metacontrast masking, it is the delayed offset of the mask, rather than delayed onset of the mask, that produces masking.

Di Lollo et al. (2000) proposed that object substitution masking arises from an object recognition system that relies on reentrant connections between higher and lower level visual processes. According to this account, the initial feed-forward processing of visual stimuli is often incomplete or inadequate for accurate perception. Reentrant signals from higher to lower visual areas aid in resolving perceptual ambiguities by allowing high-level codes to be compared to the initial pattern of activity evoked by the stimulus at lower levels. When the target presentation is brief and the mask stimulus remains visible after the target has been removed from the display, the sensory information available at the lower levels will not be consistent with the reentrant signals arising from processing of the target. Thus, if

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the target cannot be identified during the initial processing, substitution by the mask will occur because subsequent processing will focus on the mask representation that continues to be available in the lower level representations after the termination of the target stimulus. Recently, Boehler, Schoenfeld, Heinze, and Hopf (2008) used magnetoencephalographic recordings to provide support for the role of reentrant signals in object substitution masking. Boehler et al. found that modulation of reentrant activity in primary visual cortex correlated with whether subjects became aware of the target identity.

Object substitution masking is strongly affected by attentional manipulations. Experimental manipulations that facilitate attentional selection of the target (e.g., target location precue, eliminating distractor items, pop-out targets) reduce or eliminate object substitution masking (Di Lollo et al., 2000; Neill, Hutchison, & Graves, 2002; Tata, 2002). In contrast, attentional selection of the mask enhances object substitution masking (Neill et al., 2002; Tata & Giaschi, 2004). According to the reentrant processing model, attention plays a critical role in object substitution masking because it affects the quality of the target representation and the speed with which the target can be identified (Di Lollo et al., 2000; Enns, 2004). When attention can be rapidly deployed to the target item, the initial representation of the target will have a high signal-to-noise ratio, and target identification will be accurate even for briefly presented targets. If, on the other hand, attentional selection of the target item is delayed, target identification will be impaired, and briefly presented targets will be vulnerable to masking during reentrant processing.

Woodman and Luck (2003) have utilized the N2pc event-related potential (ERP) component to investigate the deployment of visual spatial attention in an object substitution masking paradigm. The N2pc is measured as a greater negativity over posterior electrode sites contralateral, relative to ipsilateral, to an attended stimulus, recorded approximately between 200 and 300 ms post stimulus onset (Luck & Hillyard, 1994). The N2pc is thought to reflect the attentional selection of a visual stimulus following a shift to a peripheral location, because brain activity generating the N2pc is specifically contingent on the location of the target stimulus, showing a contralateral distribution, and seems to originate from parietal and occipito-temporal areas (Hopf et al., 2000). It has been suggested that the N2pc reflects the top-down selection of a target according to the presence of task-relevant properties (Eimer, 1996). Woodman and Luck (2003) found that targets masked by delayed offset four-dot masks elicited N2pc components whose amplitudes were not significantly different from the N2pc components elicited by targets that were not masked. Furthermore, the N2pc amplitude elicited by masked targets did not differ significantly between trials with correct responses and trials with incorrect responses. These results suggested that targets masked by object substitution masking were nonetheless detected by the visual system, and elicited a shift of attention to their location, even when they could not be reported accurately.

Woodman and Luck's (2003) results indicate that, despite the fact the attention can be directed to the location of the target, object substitution masking interferes with accurate transfer of target identity information to higher level cognitive processes, such as visual short-term memory (VSTM). VSTM is a fundamental memory system that retains visual features and objects for a short period of time (in the order of several seconds). This memory system appears to be important for efficient perceptual and cognitive processing in tasks that depend on visual input

(Jolicœur & Dell'Acqua, 1998; Jolicœur, Sessa, Dell'Acqua, & Robitaille, 2006a, 2006b). In the present study, we utilized the sustained posterior contralateral negativity (SPCN), an electrophysiological marker of storage in VSTM, to examine the effect of object substitution masking on VSTM representations.

A growing body of evidence (e.g., Dell'Acqua, Sessa, Toffanin, Luria, & Jolicœur, 2010; Jolicœur, Brisson, & Robitaille, 2008; Klaver, Talsma, Wijers, Heinze, & Mulder, 1999; Luria, Sessa, Gotler, Jolicœur, & Dell'Acqua, 2010; McCollough, Machizawa, & Vogel, 2007; Perron et al., 2009; Robitaille, Grimault, & Jolicœur, 2009; Vogel & Machizawa, 2004) 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 and is frequently observed to follow the N2pc (Jolicœur et al., 2008). The amplitude of the SPCN increases as the number of target items increased (Jolicœur et al., 2008; McCollough et al., 2007; Perron et al., 2009; Robitaille et al., 2009; Vogel & Machizawa, 2004), reaching a maximum when the number of stimuli to be encoded equals or exceeds the estimated capacity of VSTM (Vogel & Machizawa, 2004). Importantly, Vogel and Machizawa (2004) found that the SPCN was smaller on incorrect response trials relative to correct trials, suggesting that this activity contributes to accurate performance (see also Dell'Acqua, Sessa, Jolicœur, & Robitaille, 2006; Jolicœur et al., 2006a, 2006b; Robitaille, Jolicœur, Dell'Acqua, & Sessa, 2007, for strong associations between behavioral accuracy and the amplitude of the SPCN in the context of the attentional blink paradigm).

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 (Brisson & Jolicœur, 2007a, 2007b; Jolicœur et al., 2008; Mazza, Turatto, Umiltà, & Eimer, 2007) but not in localization tasks (Mazza et al., 2007; McDonald, Hickey, Green, & Whitman, 2009). Recently, Jolicœur 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., McCollough et al., 2007; Jolicœur et al., 2008) indicate that the SPCN indexes the same processes in both types of tasks.

If object substitution masking is the result of the representation of the mask overwriting the target representation during reentrant processing, delayed-offset masks should interfere with the encoding of the target representation in VSTM. Consequently, VSTM load should be higher on trials in which the target was correctly identified in comparison to trials in which the target was not identified. On trials in which the target was correctly identified, both the target and mask representations would be encoded in VSTM. In contrast, in trials in which the target was not identified, only the mask representation would be encoded in

VSTM. In the present study, we utilized an experimental design that was very similar to that employed by Woodman and Luck (2003). However, we measured the amplitude of the SPCN in addition to the N2pc. In order to avoid low-level stimulus differences across hemifields, each search display contained two potential target items, one in each hemifield, each surrounded by a four-dot mask. Targets had a specific shape (either a circle, square, or diamond) that was specified at the beginning of each block, were presented among distractor triangles, and were accompanied by a non-target shape singleton in the opposite hemifield. In order to localize the target, target-defining features at the mask locations must be rapidly detected. Because target location was varied across trials, participants would most likely be in a diffuse attentional state at the onset of the search display. However, the four-dot masks were highly salient cues indicating potential target locations, and localizing and encoding the masks would facilitate detecting and localizing the target. After the target was located, we expected that participants would direct attention to the target location and attempt to encode the target in VSTM in order to prevent the target identity from being lost due to the target's perceptual representation being overwritten (substituted) by the mask. In accordance with the evidence that SPCN amplitude is sensitive to VSTM load, we expected to observe a larger SPCN amplitude on trials with correct responses in comparison to trials with incorrect responses when mask offset was delayed.

In addition to analyzing the amplitudes of the N2pc and SPCN, we also conducted exploratory analyses of two ERP components related to cognitive processes involved in stimulus evaluation and response-selection. One of these components, the fronto-central N2, is thought to reflect the activity of brain areas involved in post-perceptual executive control and response-selection processes (for a review, see Folstein & Van Petten, 2008). The other component, the parietal P3, is thought to reflect processes involved in evaluation and categorization of task relevant or significant events (e.g., Dell'Acqua, Jolicœur, Vespignani, & Toffanin, 2005; Donchin, Kramer, & Wickens, 1986; Kok, 2001). We did not form any *a priori* hypotheses regarding the effect of object substitution masking on these components, but thought that their additional monitoring could help us achieve a more thorough understanding of the mechanisms underpinning visual information encoding when limited by the presence of the four-dot mask.

Method

Participants

Twenty-five volunteers were paid for their participation. All participants reported no neurological problems and normal or corrected-to-normal vision. Informed consent was obtained from each participant at the beginning of the experiment. One participant was excluded from data analysis due to an excessive rate of ocular and EEG artifacts. Two additional participants were excluded because their behavioral performance showed little evidence of masking and their accuracy on target present delayed-offset trials was too high (>90%) to provide a sufficient number of incorrect response trials for the ERP analyses. The remaining 22 subjects (8 male) ranged in age from 19 to 35 years with a mean age of 24.6 years. For these subjects, an average of 91% of trials were included in the ERP analyses.

Stimuli

An example of the search array is shown in Figure 1. The stimuli were presented on a video monitor with a black background. The luminance of the stimuli was measured with a Minolta CS-100 chroma meter (Konica Minolta, Ramsey, NJ). With the exception of the exact location of the stimuli, which varied randomly from trial to trial, search arrays were identical on co-termination and delayed-offset trials. Each search array was composed of 20 distractor triangles and two possible target shapes surrounded by four-dot masks. Each hemifield contained one shape surrounded by four dots and 10 distractor triangles. The potential targets and distractor were randomly distributed within $14^\circ \times 9^\circ$ area with each shape separated from its neighbors by a centre-to-centre distance of at least 1.5° . The target shape was selected from a set of three possible shapes (i.e., circle, square, and diamond) at the beginning of each block of trials (see below). On target-present trials, one of the two figures surrounded by the four dots corresponded to the designated target shape for the current block (e.g., a circle) and the other figure surrounded by four dots was selected at random from the two remaining target shapes (e.g., diamond or square). On the target-absent trials, the figures surrounded by the four dots in each hemifield were selected at random, without replacement, from the two figures that were not designated as the target for the current block (e.g., diamond and square). The potential targets and distractors were drawn in white and spanned ($0.9^\circ \times 0.9^\circ$). The mask stimuli consisted of four white dots ($0.2^\circ \times 0.2^\circ$) located at the corners of an imaginary square ($1.4^\circ \times 1.4^\circ$). The luminance of the potential targets and distractors was 30 cd/m^2 , and the luminance of the dots was 48 cd/m^2 . The positions of the two potential target items were selected randomly and independently. The vertical position of the potential targets was confined to a region of 2.5° above or below the horizontal meridian. The horizontal displacement of potential targets was at least 2.5° from the vertical meridian.

Procedure

Participants were instructed to respond based on whether or not a designated target shape was presented in the search array. At the beginning of each block of trials, one of the three possible target shapes (circle, square, or diamond) was designated the target for that block. The order of target shape blocks was varied randomly across participants. The participants responded by pressing the key "1" for the target-present arrays and the key "2" for target-absent arrays on a standard computer keyboard. Rapid responding was not required, and the instructions stressed accuracy.

Participants were seated in a dimly lit, electrically shielded room and viewed the computer monitor from a distance of 57 cm. A chin rest was used to stabilize the head. The participant started each trial by pressing the space bar on a standard computer keyboard. At the start of each trial, a small fixation point was presented at the centre of the display for 600 ms. The search array was then presented for 83 ms. The search array contained the target shape on half of the trials. On co-termination trials, the four-dot masks terminated simultaneously with the search array. On the delayed-offset trials, the four-dot mask remained visible for 600 ms after the search array disappeared. After the participants' response, accuracy feedback was provided by presenting a "+" symbol for correct responses or a "-" for incorrect responses at the centre of the display. The response feedback remained on screen until the participant initiated the next trial.

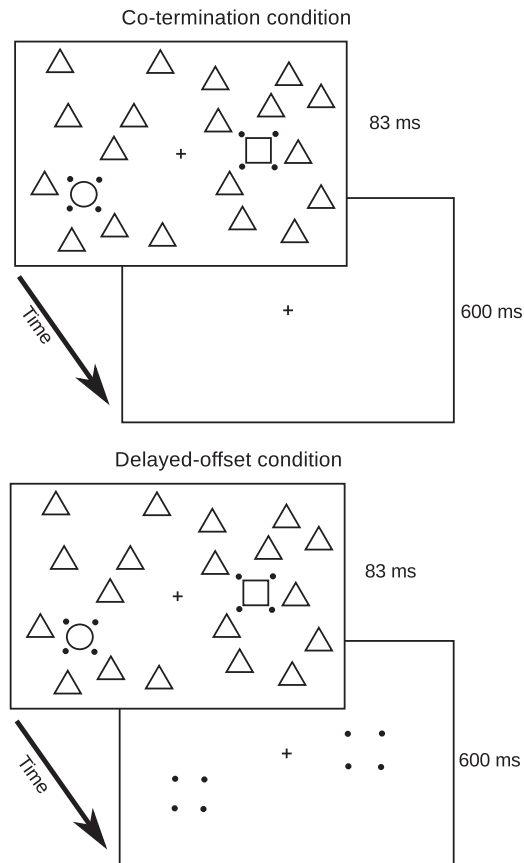


Figure 1. Schematic representation of the search display and trial sequence for both the delayed-offset and co-termination conditions.

Trials from the two experimental conditions were randomly intermixed within each block. Each block contained an equal number of target-present and target-absent trials as well as an equal number of delayed-offset trials and co-termination trials. Participants performed 3 blocks of 8 practice trials and 9 blocks of 96 experimental trials for a total number of 864 experimental trials.

Electrophysiological Recording and Analysis

The electroencephalogram (EEG) was recorded from the left and right mastoids and 64 standard 10–10 scalp sites with active Ag/AgCl electrodes (BioSemi ActiveTwo system, BioSemi B. V., Amsterdam, The Netherlands) mounted on an elastic cap. Eye position was monitored by both the horizontal and vertical electro-oculogram (EOG). The vertical EOG was recorded as the voltage between Fp1 and an electrode placed below the left eye. The horizontal EOG was recorded as the voltage between electrodes placed laterally on the outer canthi. 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 cut-off). Trials containing blinks, eye movements, and EEG artifacts were removed prior to ERP averaging by applying automated artifact detection routines. Blinks and eye movements were detected by a function that detects rapid steps in the voltage of the EOG channels. Artifacts in EEG channels were identified by functions that detect flat sections of EEG and sudden rapid changes in voltage.

For target-present trials, ERP averages were calculated from EEG epochs time-locked to the presentation of the search array. Separate ERP averages were calculated for correct and incorrect response trials for the delayed-offset condition. Response accuracy was high (~90%) in the co-termination condition resulting in an insufficient number of artifact-free incorrect response trials to calculate reliable ERPs for many participants. Therefore, we only analyzed correct response trials for the co-termination condition.

After averaging, the ERPs were digitally low-pass filtered (20 Hz half-amplitude cut-off) to eliminate high frequency noise and were baseline corrected to the mean voltage of the 100-ms pre-target interval. For target-present trials, ipsilateral and contralateral ERP waves for each condition were calculated by averaging corresponding left and right hemisphere electrodes based on the visual field of the target. Electrodes on the midline were averaged across left and right visual field targets.

In order to improve the signal-to-noise ratio of the data used to measure the N2pc and SPCN effects, pooled ipsilateral and contralateral waveforms were calculated by averaging the relevant ERP waves from electrode pairs PO7/PO8 and P7/P8. These electrode locations were chosen because they correspond to the location of the maxima of the N2pc and SPCN topography both in the present experiment and in previously published experiments (e.g., Prime & Jolicœur, 2010). The N2pc and SPCN components were analyzed by comparing the amplitude of the pooled ipsilateral and contralateral ERPs. The N2pc amplitude component was quantified as the mean amplitude between 200 and 300 ms post-stimulus and the SPCN amplitude was quantified as the mean amplitude between 400 and 600 ms post-stimulus. In addition, we also measured the peak of the midline fronto-central N2, the peak of the parietal P3, and the late portion of the parietal P3. The amplitude of the N2 peak was quantified as the mean amplitude between 280 and 310 ms at Fz. The amplitude of the P3 peak was quantified as the mean amplitude between 350 and 450 ms at Pz, and the amplitude of the late portion of the P3 was measured as the mean amplitude between 500 and 600 ms at Pz.

Results

Behavior

As expected, the typical object substitution masking effect was observed. Target detection was significantly less accurate on the delayed-offset trials (74.1%) than on the co-termination trials (88.5%), $F(1,21) = 281.92$, $p < .001$.

ERPs

Grand average ERP waves calculated from the pooled electrodes are shown in Figure 2. The mean of the measured N2pc and SPCN amplitudes are presented in Table 1a. As expected, on correct response trials the pooled ERP waves from the delayed-offset condition are more negative contralateral to the target than ipsilateral to the target in the N2pc and SPCN latency ranges (Figure 2a). In order to assess these differences statistically, the N2pc and SPCN amplitude measurements were entered into separate 2×2 repeated measure analysis of variance (ANOVAs) with factors of Laterality (ipsilateral, contralateral) and Accuracy (correct, incorrect).

Analysis of N2pc amplitude in the delayed-offset condition revealed a main effect of Laterality, $F(1,21) = 5.70$, $p < .03$, indicating that an N2pc wave was generated in the delayed-offset

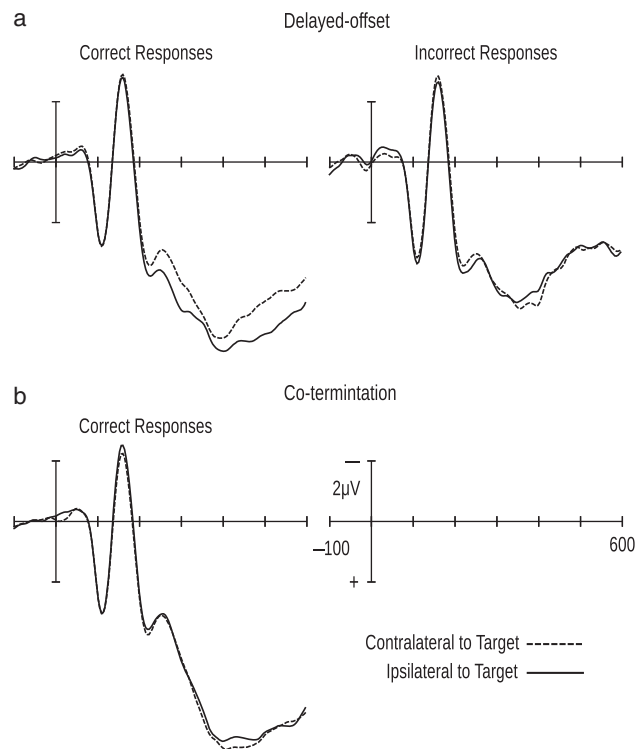


Figure 2. Grand average event-related potentials for pooled occipital electrodes contralateral to and ipsilateral to the target location. Delayed-offset correct response trials, delayed-offset incorrect response trials, and co-termination correct response trials are plotted separately.

condition. Although the N2pc appears larger and longer lasting on correct response trials relative to incorrect response trials, the interaction between Laterality and Accuracy was not significant,

$F(1,21) = 2.19, p > .15$. The main effect of Accuracy was also not significant, $F < 1$. Consistent with the results of Woodman and Luck (2003), the presence of an N2pc effect indicates that the participants were able to localize and direct attention towards the target on delayed-offset trials, irrespective of whether they reported its presence or not.

Analysis of the SPCN amplitude in the delayed-offset condition revealed a main effect of Accuracy, $F(1,21) = 26.61, p < .001$. However, the main effect of Laterality did not reach significance, $F(1,21) = 3.50, p > .075$. Importantly, the interaction between these factors was significant, $F(1,21) = 8.07, p < .01$. Consistent with our hypothesis, paired comparisons of ipsilateral and contralateral ERPs revealed that an SPCN was observed on trials with correct responses, $F(1,21) = 13.71, p < .01$, but not on trials with incorrect responses, $F < 1$.

Inspection of Figure 2b reveals virtually no differences between ipsilateral and contralateral ERPs for correct response trials in the co-termination condition. Statistical analysis of the effect of Laterality in the N2pc and SPCN latency ranges for this condition indicated that neither an N2pc nor an SPCN wave was present, both $F_s < 1$. These results stand in contrast to those of Woodman and Luck (2003) who found reliable N2pc effects for both delayed-offset and co-termination trials. In order to ensure that the differences observed between the delayed-offset and co-termination conditions were reliable, we submitted the N2pc and SPCN amplitude measures from correct response trials to an ANOVA with factors of Laterality (ipsilateral, contralateral) and Masking (delayed-offset, co-termination). Consistent with the differences found between the results of the separate analysis for each masking condition, analysis of N2pc amplitude revealed a significant interaction between the factors, $F(1,21) = 8.46, p < .01$, supporting the interpretation that the N2pc was larger in delayed-offset trials than in co-termination trials. The main effect of Laterality, $F(1,21) = 3.62, p < .08$, approached significance

Table 1. Mean Amplitude Measures

			Electrode Side		
Component	Condition	Accuracy	Ipsilateral	Contralateral	Contra-Ipsi
N2pc	Delayed-offset	Correct	3.74	3.14	-0.60
		Incorrect	3.46	3.28	-0.18
SPCN	Co-termination	Correct	3.38	3.46	0.08
	Delayed-offset	Correct	5.59	4.72	-0.87
		Incorrect	3.13	3.18	0.05
	Co-termination	Correct	6.91	7.05	0.14

				Target Presence	
Component	Electrode	Condition	Accuracy	Present	Absent
N2	Fz	Delayed-offset	Correct	2.48	1.37
			Incorrect	1.47	1.72
P3-peak	Pz	Co-termination	Correct	3.28	2.70
		Delayed-offset	Correct	11.12	9.21
			Incorrect	9.22	9.32
		Correct	11.80	9.86	
P3-late	Pz	Co-termination	Correct	9.22	7.77
		Delayed-offset	Correct	12.82	9.45
			Correct		

Note: a. Mean amplitude measures (in μV) of the pooled event-related potential (ERP) averages for sites ipsilateral and contralateral to the target location in the N2pc (200–300 ms) and SPCN (400–600 ms) latency windows. b. Mean amplitude measures (in μV) of the ERP averages at indicated electrodes for the N2 (280–310 ms), P3-peak (350–450 ms), and P3-late (500–600 ms) intervals.

but the main effect of Masking did not, $F < 1$. Similarly, an analysis of SPCN amplitude revealed a significant interaction between Laterality and Masking, $F(1,21) = 11.40$, $p < .01$, consistent with the interpretation that the SPCN was larger in delayed-offset trials than in co-termination trials. In addition, both the main effect of Laterality, $F(1,21) = 5.18$, $p < .04$, and Masking, $F(1,21) = 21.11$, $p < .001$, were significant. The significant interactive effects of masking and laterality observed across the above analyses demonstrate that the different results obtained in the analysis of the N2pc and SPCN components between the delayed-offset and co-termination conditions are statistically reliable.

In addition to the N2pc and SPCN effects, masking and target accuracy also affected the amplitude of the fronto-central N2 (Figure 3) and parietal P3 (Figure 4) peaks. Mean amplitude measures for these components are presented in Table 1b. For target-present trials, the amplitude of the N2 was largest for delayed-offset trials with incorrect responses, intermediate for delayed-offset trials with correct responses, and smallest for co-termination trials with correct responses, $F(2,42) = 12.83$, $p < .001$. Subsequent paired comparisons revealed that the difference in N2 amplitude between incorrect and correct trials in the delayed-offset condition was significant, $F(1,21) = 11.56$, $p < .01$. Similarly, the N2 amplitude for trials with correct responses differed between the delayed-offset and co-termination conditions, $F(1,21) = 4.36$, $p < .05$. A significant difference across conditions was also obtained for target-absent trials, $F(2,42) = 4.23$, $p < .03$. For these trials, paired comparisons revealed that N2 amplitude was smaller on co-termination trials than on delayed-offset trials with correct responses, $F(1,21) = 11.86$, $p < .01$. The difference between co-termination trials and delayed-offset trials with incorrect responses approached significance, $F(1,21) = 3.39$, $p < .08$. For the delayed-offset condition, the difference between trials with correct and incorrect trials was not significant, $F < 1$.

Masking and target accuracy affected both the amplitude and morphology of the parietal P3. For target-present trials in the delayed-offset condition, the amplitude of the parietal P3 peak was significantly higher for trials with correct responses than for trials with incorrect responses, $F(1,21) = 19.39$, $p < .001$. Although the amplitude of the P3 peak was not significantly different between delayed-offset and co-termination trials with correct responses, $F(1,21) = 3.44$, $p > .07$, there were significant differences in the amplitude of the later portion of the P3 wave (500–600 ms), $F(1,21) = 32.31$, $p < .001$. A different pattern of results

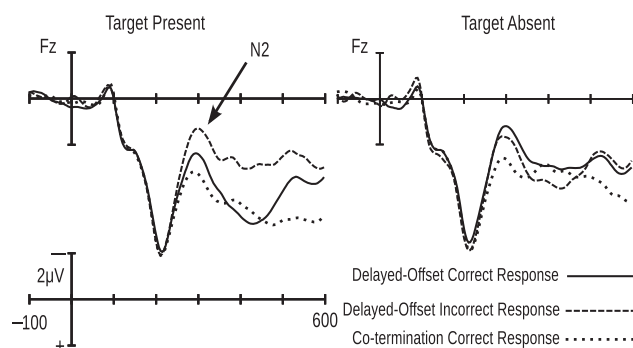


Figure 3. Grand average event-related potentials from electrode Fz for delayed-offset correct response trials, delayed-offset incorrect response trials, and co-termination correct response trials. Target present and target absent trials are plotted separately.

was obtained for target-absent trials. For these trials, the amplitude of the parietal P3 peak for delayed-offset trials with correct responses did not differ from delayed-offset trials with incorrect responses, $F < 1$, or from co-termination trials with correct responses, $F(1,21) = 2.56$, $p > .12$. However, there were significant differences in the amplitude of the later portion of the P3 wave for delayed-offset and co-termination trials with correct responses, $F(1,21) = 13.16$, $p < .01$.

Discussion

In the present study, we found that an SPCN wave was present in delayed-offset trials with correct responses but not in delayed-offset trials with incorrect responses. In accordance with the abundant evidence that SPCN amplitude is sensitive to working memory load (e.g., Jolicœur et al., 2008; Perron et al., 2009; Vogel & Machizawa, 2004), we conclude that these results provide clear support for our hypothesis that inaccurate performance on delayed-offset trials arises from a failure to encode the target in VSTM. Given the salience of the four-dot masks and their importance for target selection, it is likely that these stimuli were always attended and that a representation of these stimuli was transferred to VSTM. On delayed-offset trials in which the target presence was correctly reported, VSTM likely contained a representation of the target item and representations of the four dots from the target mask and most likely also of the four dots in the other hemifield. In contrast, on delayed-offset trials in which the target presence was missed, VSTM memory likely contained representations of the bilateral pair of four-dot masks only. Because the two masks were presented in opposite hemifields, encoding both masks would not produce a lateralized SPCN wave.¹ Consequently, only the SPCN wave produced by encoding of the target on correct response trials was observed. This conclusion is consistent with observer reports that the area within the four dots sometimes appears empty when the mask offset is delayed (Di Lollo et al., 2000).

At present, the exact nature of the target and mask representations in VSTM cannot be precisely specified. The currently available evidence indicates that the number of object representations used to store the mask and target depends on the exact paradigm being used. In experiments involving apparent motion displays, Lleras and Moore (2003) obtained results consistent with both the mask and target being stored in a single object representation. In contrast, Kahan and Lichtman (2006) and Kahan and Enns (2010) found evidence consistent with the existence of separate target and mask object representations. We cannot be certain which encoding strategy was used by the participants in the current study. Thus, there are two possible accounts for the current results. First, it is possible that separate target and mask representations were formed in VSTM on correct response trials, and inaccurate performance on delayed-offset trials arise from a failure to form the target representation. This possibility is consistent with the abundant evidence that SPCN amplitude is sensitive to the number of items encoded in VSTM (e.g., Vogel & Machizawa, 2004). Alternatively, a joint target plus mask representation may have been formed on correct

¹If only the mask in the target hemifield was encoded into VSTM, we would expect that the SPCN would be observed on both correct and incorrect response delayed-offset trials. Although the SPCN would be larger on correct delayed-offset trials (target+mask), an SPCN due to the mask would also be observed on incorrect delayed-offset trials. This possibility is inconsistent with the present results.

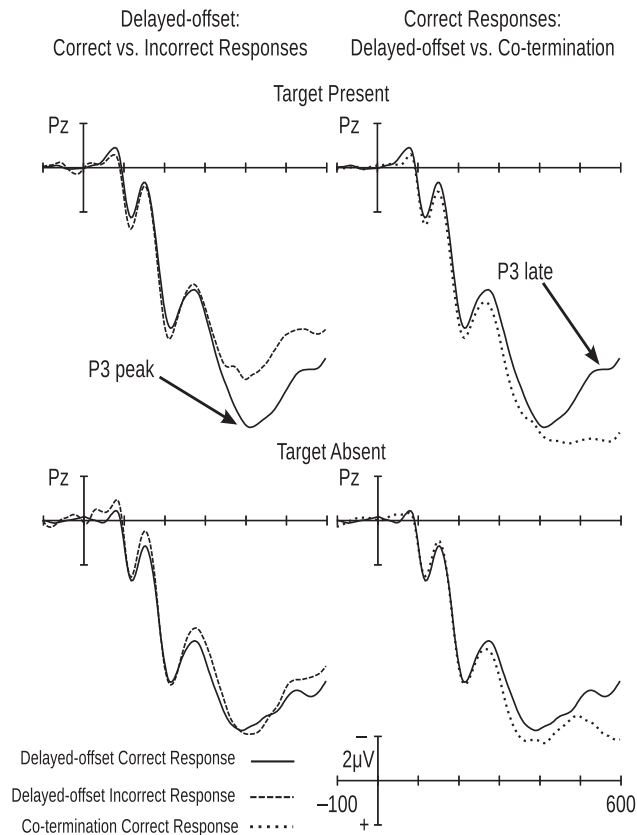


Figure 4. Grand average event-related potentials from electrode Pz. Correct versus incorrect response trials in the delayed-offset condition are shown in the left column. Correct response trials for the delayed-offset and co-termination conditions are shown in the right column. Target present trials are shown in the upper row, and target absent trials are shown in the lower row.

response trials, and inaccurate performance on delayed-offset trials arises from a failure to encode the target features into this representation. This possibility is consistent with recent evidence that SPCN amplitude is also sensitive to the information content of the items in memory (Luria et al., 2010; Woodman & Vogel, 2008). Regardless of the exact encoding strategy used by participants in the current study, the present SPCN results indicate that inaccurate performance on delayed-offset trials arises from a failure to encode the target in VSTM.

Accordingly, the present SPCN results are consistent with Di Lollo and colleagues' account of object substitution masking. According to this account, object substitution masking reduces response accuracy because the original target representation is sometimes replaced by the mask representation during reentrant processing before the target can be identified. It is reasonable to conclude that the overwriting of the target representation would prevent the formation of a stable target representation in VSTM. The present results support this conclusion and provide further evidence that object substitution masking does not arise from processes that only influence the quality or signal-to-noise ratio of the target representation in VSTM (e.g., Enns, 2004).

The present SPCN results are also consistent with prior results that indicate that object substitution masking interferes with the encoding and retention of object representations. Reiss and Hoffman (2007) found that object substitution masking eliminated the typical N170 ERP amplitude difference between faces

and non-face stimuli. This result provides strong evidence that object substitution masking interferes with encoding processes necessary for object recognition. Furthermore, in an object substitution masking experiment, Carlson, Rauschenberger, and Verstraten (2007) utilized fMRI to demonstrate that targets that could not be correctly identified did not form persisting neural representations in lateral occipital cortex. Finally, Woodman (2010) found that the error-related negativity (ERN) was elicited on incorrect co-termination trials, and not on incorrect delayed-offset trials. This result indicates that object substitution masking interferes with the formation of a persistent representation of the target necessary for the detection of response errors.

One issue not addressed by the current results is what factors determine whether or not the target representation will be encoded in VSTM. According to the reentrant processing model of Di Lollo et al. (2000), the critical factor is the speed with which attention can be directed to the target location. However, the N2pc represents a relatively late manifestation of attentional processing (> 200 ms post onset) and it is possible that attentional modulation of target processing begins at earlier processing stages. Consequently, the onset latency of the N2pc only provides an upper limit for the latency at which attention is first engaged at the target location. Thus, neither the present results nor those of Woodman and Luck (2003) are able to test the reentrant model's predictions regarding the speed of attentional deployment.

Replicating the key finding from Woodman and Luck (2003), the present study found that an N2pc wave was generated in the delayed-offset condition. This finding provides additional evidence that observers are able to discriminate target and distractor features sufficiently well to attend to the target's location in the delayed-offset condition. Despite the lack of a significant interaction with target accuracy, the amplitude and duration of the N2pc appeared smaller for incorrect response trials than for correct response trials in the delayed-offset condition. Interestingly, Woodman and Luck (2003) observed a similar pattern of results. This may indicate that, on average, more attentional resources were directed to the target location on correct response trials than on incorrect response trials. However, the signal-to-noise ratio for incorrect response trial ERPs was relatively low. Further research will be required to determine if this pattern of results is reliable.

One unexpected result of the current study was the absence of N2pc and SPCN effects in the co-termination condition. At first blush, these results appear to suggest that attention was not directed towards the target item and that nothing was encoded in VSTM. However, the high response accuracy obtained in this condition indicates that this interpretation cannot be correct. It is important to recall that lateralized measures such as the N2pc and SPCN are insensitive to bilateral activity. A more likely interpretation is that, in the absence of masking, participants were able to accomplish the task by maintaining a diffuse attentional state that enabled the joint encoding of the potential target items in each hemifield. We assume that participants adopted a diffuse attentional state at the beginning of each trial because the target could appear unexpectedly in either visual hemifield. An initial search for the target was thus required before attention could be focused on the target. As three very distinctive shape singletons were used in this study, it seems plausible to assume that subjects could encode both shapes and determine whether one was a target when the perceptual input was not degraded by substitution masking. This account is

consistent with the ambiguity resolution theory of visual attention (Luck, Girelli, McDermott, & Ford, 1997) and prior evidence that the N2pc is not always observed in tasks that require the detection of targets defined by salient features (Luck & Ford, 1998). In contrast to the present results, Woodman and Luck (2003) did find an N2pc in their co-termination condition. However, the size of their target stimuli ($0.585^\circ \times 0.585^\circ$) was approximately two-thirds the size of those used in the present experiment ($0.9^\circ \times 0.9^\circ$). The smaller stimulus size used by Woodman and Luck (2003) may have increased the task difficulty and induced the participants to use a more focused attentional state for co-termination trials.

Recently, Hickey, Di Lollo, and McDonald (2008) found evidence indicating that the N2pc observed in response to balanced displays, such as those used in the present experiment, reflects the summation of two distinct components. One component, the Nt, is a relative negativity observed contralateral to the target. The second component, the Pd, is a relative positivity observed contralateral to the distractor (ipsilateral to the target). If the absence of an N2pc in the co-termination condition is due to participants adopting a diffuse attentional state, we would expect that the Pd component would be absent and the Nt component would be present over both hemispheres. Thus, we would expect that the ERPs elicited ipsilateral to the target on delayed-offset trials would be more positive than those on co-termination trials in the N2pc time range. Furthermore, a diffuse attentional state on co-termination trials may reduce the magnitude of the Nt resulting in a greater negativity on delayed-offset trials relative to co-termination trials contralateral to the target in the N2pc time range. As can be seen in Figure 5, this general pattern of effects was observed in the present experiment. *Post hoc* analyses of the effect of mask duration on ERP amplitude in the N2pc interval revealed that the ERPs ipsilateral to the target were significantly more positive in the delayed-offset condition than in the co-termination condition, $F(1,21) = 5.21, p < .04$. However, mask duration did not significantly affect the amplitude of the ERPs contralateral to the target, $F(1,21) = 3.35, p > .08$. Although these results are consistent with our proposal that participants adopted a diffuse attentional state in the co-termination condition, further research will be required in order

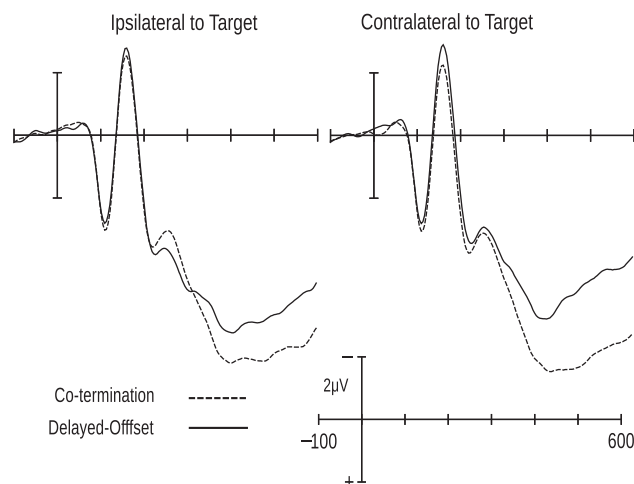


Figure 5. Grand average event-related potentials (ERPs) for pooled occipital electrodes on delayed-offset and co-termination trials with correct response. ERPs contralateral to and ipsilateral to the target location are plotted separately.

to characterize the nature of attentional deployments in the present paradigm.

Although the exact processes indexed by the N2 peak remain a topic of exploration and debate, there is considerable evidence that the N2 peak indexes post-perceptual processes involved in executive control and response-selection (for a review, see Folstein & Van Petten, 2008). Furthermore, there is strong evidence that the amplitude of the N2 is sensitive to the degree of conflict between response alternatives (e.g., Botvinick, Cohen, & Carter, 2004; Nieuwenhuis, Yeung, van den Wildenberg, & Ridderinkhof, 2003; van Veen & Carter, 2002). Thus, the finding that N2 amplitude was larger for delayed-offset trials than for co-termination trials indicates that there was greater conflict in the delayed-offset condition than in the co-termination condition. This difference was found for both correct and incorrect delayed-offset trials. This indicates an increase in response selection conflict even for delayed-offset trials in which the correct response was selected. The evidence for increased cognitive conflict in the delayed-offset condition provided by the N2 amplitude effects suggests that object substitution masking decreased the confidence with which the present-absent decision was made. These results are consistent with Di Lollo et al.'s (2000) reentrant processing model. According to this model, the target's initial perceptual representation is maintained for a longer duration in the co-termination condition, and the observer is able to compare their perceptual hypothesis to this representation. This should result in a higher degree of confidence in the response decision. In contrast, because target representations are overwritten by the mask representation in the delayed-offset condition, response decisions are only informed by the initial processing of the target. This would likely decrease confidence in the response decision, regardless of accuracy. In addition, the N2 results indicate increased conflict for incorrect response trials relative to correct response trials for target-present trials in the delayed-offset condition. This effect suggests that, although the presence of the target was not accurately reported, the initial processing of the target was sufficient to detect its presence. The high level of conflict indicated by the large amplitude N2 observed for these trials may arise from a conflict between the initial processing of the target and the final decision to respond with a 'target absent' response.

Generally, the P3 amplitudes appeared to reflect confidence in the decision about target presence or absence. The largest P3 was observed in the co-termination, target-present, correct trials, in which accuracy was the highest (and conflict, as indexed by N2 amplitude, was lowest). P3 was generally lower (for correct trials) when the target was absent, relative to target-present trials, suggesting that subjects had greater confidence when they could positively identify the target. Later in processing, in the late P3 window, co-termination trials were also associated with larger amplitudes than delayed-offset correct trials, suggesting that confidence tended to be generally greater in the co-termination condition, reflecting the higher overall response accuracy in this condition. The late P3 difference between co-termination and delayed-offset trials was particularly large for target-present trials, suggesting that the delayed-offset condition was associated with a poorer perceptual quality (leading to lower confidence) than the co-termination condition. These late effects (P3 and late-P3) may be delayed consequences of earlier attempts to deal with perceptual quality by deploying spatial attention to a possible target location, in the delayed-offset condition, with only partial success. The high signal-to-noise ratio produced by the

co-termination condition appears to have enabled both a late-selection attentional strategy, producing no lateralized selection-related components (N2pc and SPCN), low decision conflict (small N2), and high confidence (larger P3 and late P3).

The striking differences in N2pc and SPCN amplitude between delayed-offset and co-termination trials associated with a correct response are among the most notable results from the present work. The presence of the N2pc is consistent with a deployment of focal attention to the target, leading to a later SPCN, consistent with the formation of a lateralized memory trace in VSTM. The trigger for this allocation of attention was the delayed offset of the four-dot mask, as no such lateralized effects were observed in co-termination trials. As co-termination and delayed-offset trials were intermixed at random in each block of trials, what is particularly remarkable about this outcome is that the difference between co-termination and delayed-offset trials became manifest to subjects 83 ms after the onset of the search display, that is, upon target and distractors offset. Interestingly, the onset of the N2pc was somewhat later in present work (about 200 ms) relative to other studies in which the N2pc typically

begins earlier (e.g., see Robitaille & Jolicoeur, 2006, for a much earlier N2pc onset). Object-substitution masking may trigger a need for focal attention in order to resolve the difference in temporal dynamics between the target and the mask. When attentional engagement at the target location is not sufficiently strong or timely, inefficient transfer of the target representation to VSTM ensues, and this was reflected in our view in the sharply reduced SPCN on the delayed-offset with incorrect responses that is particularly evident in Figure 2. The present results show that careful measurements of brain dynamics, based on electrical brain activity, can reveal subtle consequences of variations in perceptual signal quality early in processing. A mismatch between reentrant and bottom-up representations can trigger a rapid deployment of visual spatial attention (revealed by the N2pc) designed to resolve the discrepancy and protect the short-term consolidation of a stable representation in VSTM (Jolicoeur & Dell'Acqua, 1998). The complex dynamics of these processes highlight the usefulness of the event-related potential method for the study of perceptual and cognitive processing in the human brain.

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