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**Visual working memory load disrupts the space-based
attentional guidance of target selection**

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ABSTRACT

During visual search, the selection of target objects is guided by stored representations of target-defining features (attentional templates). It is commonly believed that such templates are maintained in visual working memory (WM), but empirical evidence for this assumption remains inconclusive. Here, we tested whether retaining non-spatial object features (shapes) in WM interferes with attentional target selection processes in a concurrent search task that required spatial templates for target locations. Participants memorised one shape (low WM load) or four shapes (high WM load) in a sample display during a retention period. On some trials, they matched them to a subsequent memory test display. On other trials, a search display including two lateral bars in the upper or lower visual field was presented instead, and participants reported the orientation of target bars that were defined by their location (e.g., upper left or lower right). To assess the efficiency of attentional control under low and high WM load, EEG was recorded and the N2pc was measured as a marker of attentional target selection. Target N2pc components were strongly delayed when concurrent WM load was high, indicating that holding multiple object shapes in WM competes with the simultaneous retention of spatial attentional templates for target locations. These observations provide new electrophysiological evidence that such templates are maintained in WM, and also challenges suggestions that spatial and non-spatial content are represented in separate independent visual WM stores.

Keywords: visual working memory; visual attention; memory load; event-related potentials; N2pc component

INTRODUCTION

Visual search for specific target objects is controlled by attentional templates that represent of the features of these targets (e.g., their colour, shape, or size). Such templates, or attentional control setting (e.g., Folk, Remington, & Johnston, 1992; Duncan & Humphreys, 1992), are assumed to be activated prior to a specific search episode, and to bias visual attention towards the location of possible targets once a search display has been presented. Templates for search targets thus play an essential role in the guidance of visual search, and in improving search efficiency (e.g., Wolfe & Horowitz, 2004; Wolfe, 2007). While the importance of search templates is undisputed, the nature of these templates is still poorly understood. One unresolved question concerns the locus of attentional templates. Because templates are activated during the preparation for search, it is generally assumed that they are maintained in visual working memory (WM). In line with this hypothesis, it has been shown that storing visual information in WM for an upcoming memory test can affect the allocation of attention in unrelated visual search tasks that are performed during the memory maintenance period. Responses to search targets are delayed when one of the distractors in the search display matches a feature that is currently held in WM, indicating that this object was able to attract attention (e.g., Olivers, Meijer, & Theeuwes, 2006). This suggests that currently active WM representations can act as attentional templates even when they are irrelevant for a current search task (see Olivers et al., 2011, for further discussion).

If search templates are generally stored in WM, loading WM with search-unrelated information should impair search efficiency, because this information will compete with attentional target templates that are simultaneously held in the same WM store. However, several studies that investigated such links between WM load and attentional guidance by target templates during visual search failed to observe such adverse effects of WM load on search efficiency. For example, Woodman, Vogel, and Luck (2001) found that having to maintain two or four colour objects in WM produced a constant delay of reaction times (RTs) in a concurrent search task, but had no effect on search efficiency (i.e., the increase of RTs as a function of display set size). Analogous results were reported by Oh and Kim (2004, Exp. 2). These studies may have failed to find costs of WM load on the efficiency of template-guided search because observers searched for the same shape-defined search

target throughout the entire experiment. When target objects remain constant, it may no longer be necessary to maintain target templates in WM, because these templates can be transferred to a different long-term memory store, and thus will not compete with other items that are concurrently held in WM.

Evidence for this comes from event-related potential (ERP) studies that measured the contralateral delay activity (CDA) as an electrophysiological marker of WM maintenance (e.g., Woodman & Arita, 2010; Carlisle, Arita, Pardo, & Woodman, 2011). In the experiment of Carlisle et al. (2011), CDA components were measured while participants prepared for visual search across runs of trials where the target-defining colour remained constant. A CDA was present only for the first few trials of each run, but disappeared on later trials of the same run. This suggests that colour-specific target templates are initially held in WM, but are transferred to a different long-term memory store when the same target colour is used for an extended period of time. If this was correct, loading WM should impair search in tasks where search templates also need to be maintained in WM, which is the case when the identity of a search target changes frequently. In line with this prediction, Woodman, Luck, and Schall (2007) demonstrated that a concurrent WM task impaired search efficiency when a particular target shape was cued anew at the start of each trial, but not when this shape remained constant for an extended period. However, this might apply primarily to search templates for a single target-defining feature. Templates for multiple features (e.g., two possible target colours) have been found to be kept at least partially in WM (as reflected by reliable CDA components) even when they remain unchanged for several successive blocks (Grubert, Carlisle, & Eimer, 2016).

While these studies have focused on the conditions under which holding search-unrelated non-spatial information (e.g., a set of colours) in WM affects the control of visual search, other experiments have investigated the impact of spatial WM load on template-guided visual search performance (Woodman & Luck, 2004; Oh & Kim, 2004, Exp. 1). In these studies, observers had to retain a set of locations in WM for a subsequent test while they performed a search task. In contrast to the results observed for non-spatial WM load, visual search efficiency was now found to be impaired even when the identity of search targets remained constant throughout the experiment. This discrepancy suggests that spatial and non-spatial WM utilise different storage mechanisms (e.g., Baddeley & Logie, 1999; Baddeley, 2012), which differ in the way that they interfere with the control of visual

search. Memorising particular locations has been shown to be tightly linked to visual-spatial attention (e.g., Awh, Jonides, & Reuter-Lorenz, 1998), whereas memorising non-spatial features may involve spatial attention to a lesser degree. Because spatial attention shifts between candidate target objects are also required during many visual search tasks, the control of such shifts could be impaired by a concurrent spatial WM task (see Woodman & Luck, 2004, for similar suggestions). In this case, spatial WM load may not directly interfere with the storage of target templates, but with sequential movements of attention during a visual search episode.

Until now, the effects of WM load on the control of visual search by attentional template were investigated in experiments where search targets were defined by a particular non-spatial feature (e.g., a specific colour). This is the typical situation in visual search tasks, where observers have some information about the features of the target object they are looking for, but not about its spatial location. However, attention can also be guided by spatial information. For example, in spatial cueing experiments (e.g., Posner, Snyder, & Davidson, 1980), performance is generally better for targets at cued (spatially attended) as compared to uncued (unattended) locations, reflecting a facilitation of visual processing for objects that appear within the current focus of spatial attention. It is likely that the guidance of spatial attention in such tasks is based on attentional templates for target locations. Such spatial templates may be implemented neurally as sustained baseline shifts of visual activation of neurons with spatially corresponding receptive fields in retinotopic maps (see Driver & Frith, 2000, for discussion). Because the maintenance of task-relevant visual locations requires top-down attentional control (e.g., Awh et al, 1998), it is plausible to assume that, similar to search templates for non-spatial features, such spatial templates are also maintained in WM. If this was the case, a search-unrelated WM task might show interference effects on visual search tasks with spatially defined target objects that are similar to those previously observed during search for non-spatial target attributes (e.g., Woodman et al., 2007).

The goal of the current experiment was to investigate whether and how manipulating WM load affects the attentional selection of target objects in a search task where targets are defined by their location. Two aspects of the experimental design were chosen to maximize the possibility that a concurrent WM task would interfere specifically with preparatory spatial templates in WM. First, we employed a non-spatial WM task that

required participants to memorise either one shape (low load) or four shapes (high load). In contrast to spatial WM tasks, WM for non-spatial features should not interfere with template-unrelated aspects of search (such as the efficiency of shifting attention; Woodman & Luck, 2004). Second, our visual search task required participants to maintain two target locations simultaneously, which should increase the probability that preparatory attentional templates were held in WM (e.g., Grubert et al., 2016). At the start of each trial, a memory sample display with one or four shapes was presented, followed by a retention period of 800 ms. WM load was blocked, with six successive high-load blocks followed by six low-load blocks, or vice versa, counterbalanced across participants. On one third of all trials, a memory test display that contained a single shape at fixation was presented after the retention period. This test item either matched or did not match one of the shapes included in the sample display. On the other two thirds of all trials, a search display appeared after the retention period. This display contained two grey bars in the left and right visual fields, either above or below fixation (see Figure 1). The target bar in these displays was defined by its spatial location. Two locations in opposite quadrants were task-relevant in each block (upper left/lower right, or lower left/upper right), and these spatial target templates remained constant for three successive blocks. Participants had to select the relevant target object, and to report whether this object was horizontally or vertically oriented.

On trials where the memory sample display was followed by a search display, the memorised shape information was no longer task-relevant and could effectively be discarded once the search display was presented. Because search templates are assumed to be activated during the preparation for search, having to maintain four versus just one shape should still interfere with the activation of spatial target templates during the retention period, and thus affect the template-guided attentional selection of target objects in search displays. To assess whether and how WM load interfered with the allocation of attention to target objects, we recorded EEG during task performance, and measured N2pc components in response to search displays, separately for blocks with high and low WM load. The N2pc is an enhanced negativity that is triggered in response to search displays at posterior scalp electrode sites contralateral to a candidate target object. In standard visual search tasks without a concurrent independent WM task, the N2pc typically emerges at around 200 ms post-stimulus onset. This component is believed to be generated in ventral extrastriate visual areas (Hopf et al., 2000) and to reflect the allocation of spatial attention

to possible targets (e.g., Luck & Hillyard, 1994; Eimer, 1996). Previous studies have shown that the N2pc is sensitive to currently active attentional templates for target features. During search for a particular feature-defined target, all objects that match this target template trigger reliable N2pc components, whereas template-nonmatching objects do not (e.g., Eimer & Kiss, 2008; Leblance, Prime, & Jolicoeur, 2008; Lien, Ruthruff, Goodin, & Remington, 2008).

To date, all N2pc experiments on attentional target selection in visual search have employed tasks that involved templates for specific target features or feature combinations (e.g., Eimer & Grubert, 2014; Berggren & Eimer, 2016). While behavioural effects of space-based attentional preparation have been studied extensively with the spatial cueing paradigm (e.g., Posner et al., 1980), there are no published reports that have measured N2pc components in tasks where target objects were defined by their spatial location, and their attentional selection thus had to be based on spatial templates. Therefore, the first question addressed in the current experiment was whether reliable target N2pc components would also be elicited under conditions where no attentional guidance by non-spatial features was available, and where targets and nontargets could only be discriminated in terms of their spatial locations. If this was the case, the second critical question was whether these N2pcs would be affected by the number of shape objects that had to be maintained during the retention period prior to the onset of a search display. The absence of an effect of non-spatial WM load on the attentional selection of spatially defined target objects could either imply that spatial templates are not maintained in WM at all, or that spatial and non-spatial information are held in separate WM stores (e.g., Baddeley & Logie, 1999; Baddeley, 2012). In either case, there would be no competition between spatial attentional templates for target locations and the concurrent storage of multiple shapes in WM. The alternative possibility is that WM load has a systematic effect on the attentional selection of search targets, as reflected by attenuated and/or delayed target N2pc components when four shapes have to be maintained relative to low WM blocks. Such a result would imply not only that attentional templates for target locations are stored in WM, but also that there is a considerable degree of overlap and thus competition between WM representations of spatial and non-spatial features.

METHOD

Participants

Fourteen participants were recruited to participate in the experiment. Two participants were excluded from data analysis, one due to chance-level performance in the search task and another due to a large number of trials contaminated with eye-movement artefacts (over 2.5 SDs from the group mean). Of the remaining 12 participants, 6 were male, and all were right-handed (M age = 30 years; SD = 6).

Stimuli and Procedure

The experiment was created and executed using E-Prime 2.0 software (Psychology Software Tools, Inc.). Stimuli were presented on a 24-inch BenQ monitor (60 Hz; 1920 x 1080 screen resolution) attached to a SilverStone PC, at a viewing distance of approximately 90 cm. Manual responses were entered via a standard computer keyboard. All stimuli were presented against a black background, with a grey fixation dot ($0.2^\circ \times 0.2^\circ$ of visual angle) continuously present throughout each experimental block. Each trial started with memory sample display (200 ms). After a retention period of 800 ms, either a search display (100 ms duration) or a memory test display (2000 ms duration; see Figure 1) was shown. The interval between the offset of the search or test display on the previous trial and the onset of the memory sample display on the next trial was 2900 ms or 1000 ms, respectively. All stimuli in the memory sample and search displays were grey (CIE colour coordinates: .305/.325). Memory sample displays included one or four outline shapes (square, circle, triangle, hexagon, gate, heart, or star, each covering an area of $1.46^\circ \times 1.46^\circ$). In low WM load blocks, a single shape appeared at fixation. In high WM blocks, four shapes appeared at the four cardinal points around fixation, at an eccentricity from fixation of 1.21° (measured relative to the outer edge of each shape). Memory test displays contained a single shape at fixation, which was presented in blue (.169/.152), to distinguish it from the preceding memory sample display object in low WM load blocks. The search displays contained two rectangular horizontal or vertical bars ($0.45^\circ \times 0.83^\circ$) that both appeared either in the upper or lower visual field at an eccentricity of 2.23° from central fixation.

Participants were instructed to memorise the item(s) in the memory sample display. They were informed that on each trial, either a memory test display or a search display would appear after the retention period. When a memory test display was shown, participants had to report whether the item in the memory test display matched or did not match an item in the sample display. Matching and mismatching test displays were presented with equal probability. When a search display was presented, they had to select the target bar and report its orientation (horizontal or vertical). Search targets were defined by their spatial location, with two locations in diagonal visual field quadrants (top-left and bottom-right or top-right and bottom-left) being task relevant in a given block. Participants were informed about this spatial task set at the start of each block. Two small digits (“14” or “23”, marking the target locations for this block) appeared throughout an experimental block at the top of the screen as a reminder of the currently relevant spatial task-set. The orientation of the target bar (horizontal or vertical) was determined randomly for each search display. The orientation of the distractor bar on the opposite side was identical to the target bar in one third of all search displays, and different in the remaining two third. Participants signalled the orientation of the target bar by using the ‘0’ and ‘2’ keys of the numeric keyboard with their right hand. On trials where a memory test display was presented, they reported a match or mismatch with the preceding memory sample display by pressing the ‘a’ or ‘s’ key with their left hand.

The experiment consisted of 12 blocks (6 low WM load, 6 high WM load), each containing 36 trials. Search displays appeared in 24 trials (12 trials each with a stimulus pair in the upper or lower visual field), and memory test displays on 12 trials (six trials where the memory test item matched an item in the memory sample display, and six trials where there was no match). Six participants completed the low WM load blocks prior to the high WM load blocks, and this order was reversed for the other six participants. Within each WM load condition, each of the two different spatial task sets for the search task was used in three successive blocks. The order of these two spatial sets was counterbalanced across the two WM load conditions for each participant.

EEG Recording and Data Analysis

EEG was DC-recorded from 27 scalp electrodes, mounted on an elastic cap at sites Fpz, F7, F8, F3, F4, Fz, FC5, FC6, T7, T8, C3, C4, Cz, CP5, CP6, P9, P10, P7, P8, P3, P4, Pz, PO7,

PO8, PO9, PO10, and Oz. A 500-Hz sampling rate with a 40 Hz low-pass filter was used, with no other offline filters applied. Channels were referenced online to a left-earlobe electrode, and re-referenced offline to an average of both earlobes. Trials with eye-movements (exceeding $\pm 30 \mu\text{V}$ in the HEOG channels during the interval from 200 ms before to 200 ms after the onset of a search display), eye blinks (exceeding $\pm 60 \mu\text{V}$ at Fpz) and movement-related artifacts (exceeding $\pm 80 \mu\text{V}$ at all other channels) were rejected. Following artefact rejection, ERPs were computed for trials where a search display was presented after the retention period. These trials were segmented into 600 ms epochs (from 100 ms before to 500 ms after the onset of the search display). Averaged ERP waveforms from trials with correct responses were computed for search displays where a target bar appeared in the left or right visual field, separately for low and high WM load blocks. N2pc components were quantified on the basis of ERPs obtained at posterior electrode sites PO7 and PO8 contralateral and ipsilateral to the visual field of the target, where the N2pc component is maximal. To compute and compare target N2pc onset latencies in low and high WM load blocks, a jackknife-based analysis method was employed (see Miller, Patterson, & Ulrich, 1998, for details) for contralateral minus ipsilateral difference waveforms. N2pc onsets were calculated on the basis of an absolute onset criterion of $-0.5 \mu\text{V}$ within the entire 500 ms interval following search display onset. To compute N2pc mean amplitude values, previous N2pc studies of visual search have typically used a pre-defined 200-300 ms post-stimulus window. In contrast to these previous studies, the current experiment employed a dual task design where visual search was combined with a concurrent WM task. Because of the possibility that the additional WM task might affect the timing of N2pc components to search targets, we did not employ a pre-defined N2pc mean amplitude window, but instead based this window on the outcome of the N2pc onset analyses described above. ERP mean amplitudes at PO7 and PO8 were quantified within a 250-350 ms interval following search display onset (reflecting the estimated onset of target N2pcs in low WM load blocks), and between 350-500 ms (reflecting the estimated onset of the contralateral negativity in high WM load blocks).

RESULTS

Behavioural data

As expected, accuracy in reporting the presence or absence of a match between memory sample and test displays on trials where memory test displays were shown was much higher in low WM load blocks relative to high WM load blocks (error rates: $M = 2$ vs. 18 %; $t(11) = 5.94$, $p < .001$, $d = 2.70$). Correct RT data on trials where search displays were presented were faster in blocks with low WM load relative to high WM load blocks ($M = 812$ vs. 856 ms). However, this difference was not statistically reliable ($t(11) = 1.67$, $p = .12$). The absence of a significant WM load effect on RTs to search displays may be the result of the fact that WM load was blocked, with general task practice effects (i.e., faster RTs in the second half of the experiment) masking the effects of WM load. An Analysis of Variance (ANOVA) with the within-participants factor WM Load (Low, High) and between-participants factor Task Order (low WM load blocks prior to high WM load blocks, or vice versa) did indeed obtain an interaction between both factors ($F(1,10) = 4.99$, $p < .05$, $\eta_p^2 = .33$). For participants who completed the high WM blocks first, there was a 96 ms cost associated with high WM load ($M = 898$ vs. 802 ms; $t(5) = 2.67$, $p < .05$, $d = 1.19$). For participants who were tested in low WM load blocks prior to high load blocks, no reliable difference was present ($M = 821$ ms versus 815 ms for low versus high WM load; $t < 1$, $p > .80$). Error rates on trials with search displays were generally low and did not differ between low and high WM blocks ($M = 1.58$ vs. 2.33 %; $t(11) = 1.68$, $p > .10$).

N2pc components

Figure 2 (top panel) shows ERPs elicited in response to search displays at electrodes PO7/PO8 contralateral and ipsilateral to the side of a target object, separately for low and high WM blocks. To visualise the time course of target N2pc components, N2pc difference waveforms obtained by subtracting ipsilateral from contralateral ERPs are also shown (bottom panel). While target objects elicited a clear N2pc component with an onset latency of about 250 ms in low WM blocks, the target N2pc was strongly attenuated and delayed in blocks where WM load was high. To quantify the N2pc delay induced by high as compared to low WM load, a jackknife-based procedure was employed with an absolute onset criterion of -0.5 μV . This analysis revealed a highly significant N2pc onset delay difference of about 100 ms between low and high WM blocks ($M = 249$ vs. 354 ms; $t_c(11) = 12.01$, $p < .001$), in line with the time course of the N2pc difference waves shown in Figure 2 (bottom panel).

ERP mean amplitudes obtained during the 250-350 ms post-stimulus time window were entered into a 2x2 repeated-measures ANOVA, with the factors WM Load (Low, High) and Laterality (Ipsilateral, Contralateral). A significant main effect of Laterality ($F(1,11) = 13.19, p < .005, \eta_p^2 = .55$) confirmed the reliable presence of N2pc components. Importantly, a highly significant Load x Laterality interaction ($F(1,11) = 18.74, p = .001, \eta_p^2 = .63$) was obtained, suggesting that N2pc amplitudes were affected by WM load. In blocks where WM load was low, a reliable target N2pc was present (contralateral versus ipsilateral: $M \text{ diff} = -.85 \mu\text{V}; t(11) = 5.77, p < .001, d = 0.40$). In contrast, no significant target N2pc was found during the 250-350 post-stimulus time window in high WM load blocks ($M \text{ diff} = -.19 \mu\text{V}; t(11) = 1.09, p > .25$). This is in line with the result of the N2pc onset latency analysis, which suggested that a contralateral negativity to target objects only emerged around 350 ms after search display onset in high WM load blocks. To assess whether this delayed effect was reliable, an additional ANOVA was conducted for the 350-500 ms post-stimulus time interval. In this analysis, a main effect of Laterality ($F(1,11) = 20.28, p = .001, \eta_p^2 = .65$) was again obtained, but there was no interaction between Load and Laterality ($F < 1$), indicating that a contralateral negativity was now present in both low and high WM load blocks. This was confirmed by subsequent comparisons of contralateral and ipsilateral ERPs, which revealed significant differences for both low and high WM load (both t 's $> 3.14, p$'s $< .01$).

N1 component

As can be seen in Figure 2 (upper panels), the early non-lateralised visual N1 component in response to search displays also appeared to be affected by concurrent WM load, with strongly attenuated N1 amplitudes in high WM load block. Because this difference was not predicted, we only conducted an exploratory analysis of N1 mean amplitudes (averaged across electrodes PO7 and PO8) in the 150-200 ms time interval after search display onset. This analysis confirmed that the N1 attenuation in high versus low WM load blocks was reliable ($M \text{ diff} = -4.60 \text{ vs. } -2.28 \mu\text{V}; t(11) = 3.16, p < .01, d = 0.51$).

DISCUSSION

The present experiment employed the N2pc component as an electrophysiological marker of attentional target selection to investigate whether increasing concurrent WM load affects the allocation of attention to target objects in another task where targets were defined spatially, and their selection thus had to be guided by attentional templates for target locations. Participants memorised either one or four different shapes during a retention interval that was followed either by a search display that contained a response-relevant target object or by a memory test display. The key finding was that N2pc components elicited in response to target objects in search displays were strongly delayed (by approximately 100 ms) in high WM load blocks where four shapes had to be retained relative to low WM blocks with only a single to-be-remembered shape. This suggests that visual WM load had a strong effect on attentional allocation processes that were controlled by spatial attentional templates. In other words, the retention of multiple shapes in WM interfered with the activation of templates for target locations during the preparation for search. It is notable that this type of interference occurred in spite of the fact that the WM task required the maintenance of non-spatial features (object shapes), whereas the attentional selection task was exclusively space-based. It has previously been suggested that spatial and non-spatial visual information are held in separate WM stores (e.g., Baddeley, 2012). If spatial and non-spatial WM storage processes operated in a strictly independent fashion, there should have been little if any interference in the present experiment between the maintenance of multiple object shapes and the control of target selection by attentional templates for spatial locations. The strong effects of non-spatial WM load on the speed of space-based attentional target selection processes revealed in the present study do not support the idea that spatial and non-spatial WM processes are entirely separate. Instead, they suggest that there are close links between the storage of spatial and non-spatial features in WM.

While target N2pc components revealed clear costs of high WM load on the space-based attentional selection of target objects, a corresponding effect of high versus low WM load on target RTs was numerically present, but not statistically reliable. This is most likely due to the fact that WM load was blocked in the current experiment, with six successive low WM load blocks followed by six high load blocks, or vice versa. With such a blocked WM load manipulation, RT variance resulting from general task practice effects could conceal any genuine RT differences between high and low WM load. In line with this hypothesis, a

recent study from our lab that investigated the effects of WM load on the guidance of search by templates for target colours ([BLINDED]) found that high WM load produced reliable costs on RTs to search targets when high and low WM load trials were mixed within experimental blocks, but not when WM load was blocked.

Previous investigations of the effects of WM load on attentional templates for non-spatial target features have suggested that such templates are held in WM only under conditions where target identity changes frequently across trials (e.g., Woodman et al., 2007). However, templates for multiple features (e.g., two possible target colours) remain in WM even when they are constant for extended periods (Grubert et al., 2016). Under these conditions, search-unrelated WM load will also affect attentional guidance by non-spatial attentional templates. This was shown in our recent study ([BLINDED]), where observers searched for targets defined by either of two possible colours, and clear effects of high versus low WM load on N2pc components to these targets were found when the two target colours remained the same across the entire experiment. The present experiment had a similar design, as participants had to maintain two possible target locations, and the same two locations remained relevant for three successive blocks. The fact that WM load modulated target N2pc components thus suggests that spatial templates for multiple task-relevant locations are held in WM even when these locations do not change across trials. A possibility that could be tested in future studies is that constant attentional templates for a single target location may be represented in a different long-term memory store, and will therefore no longer be affected by a concurrent WM task.

We interpret the delay of target N2pc components with high as compared to low concurrent WM load as reflecting competitive interactions between spatial search templates and representations of memorized shapes in WM. However, this interpretation could be challenged by assuming that these load-induced N2pc effects are not related to differences in the quality of attentional guidance by spatial templates under high versus low WM load, but are instead the result of other template-unrelated mechanisms. For example, Woodman and Luck (2004) have argued that WM load can affect the efficiency of serial attention shifts between objects during visual search. However, their argument only applies to the load of spatial WM tasks, but not to non-spatial WM. In the present experiment, participants had to memorize object shapes whose location was entirely irrelevant, as memory test items were always presented at fixation. This type of task should minimize the

involvement of space-based maintenance processes, and thus the impact of these processes on template-unrelated attentional processes.

One could also argue that the load-related target N2pc delay observed in the present experiment is unrelated to template-based attentional guidance processes, but instead reflects a more general effect of high versus low cognitive load. According to the load theory (e.g., Lavie, 2005), the cognitive demands associated with WM maintenance impair the ability of top-down control processes to filter out irrelevant information, and thus increase the probability of distractor stimuli capturing attention. While this theory is primarily concerned with the inhibition of unattended stimuli, it could in principle be extended to also include cognitive control processes associated with the selection of task-relevant information. In this case, increasing the load of a WM task could produce impairments in the speed or efficiency of attentional target selection in another task, as was indeed observed in the present study. This would apply not only to the space-based selection processes studied in the present experiment, but also to all other studies that investigated the effects of WM load on the selection of targets defined by non-spatial attributes. However, because load theory does not specify the exact processes that are responsible for the effects of cognitive load on perceptual selectivity, such an explanation may be entirely compatible with the account proposed here. Attentional target selection may be impaired when WM load is increased because target templates compete with other items that are currently stored in WM. Such competition processes might thus provide a mechanism that underlies the cognitive load effects postulated by load theory, and could also be responsible for the inability to ignore irrelevant information when WM load is high.

In this context, it is important to note that the onset of target N2pc components in the present experiment was substantially delayed relative to earlier electrophysiological studies where visual search was investigated in the absence of a concurrent WM task (e.g., Luck & Hillyard, 1994; Eimer & Kiss, 2008; Leblanc et al., 2008; Lien et al., 2008). While N2pcs typically emerged around 200 ms post-stimulus in these studies, they were delayed by about 50 ms in blocks where WM load was low, and by about 150 ms in high WM blocks. There are several possible reasons for this delay. First, it is possible (although unlikely) that the space-based target selection processes investigated here are generally slower than the feature-guided selection mechanisms studied in previous N2pc experiments of visual search. It is also possible that the uncertainty about whether a search display or a memory test

display would appear after the retention interval could have contributed to the delay of N2pc components to search targets in the present experiment. The most plausible interpretation of these N2pc delays is that they primarily reflect the effects of concurrent WM load. It is important to note that even in the low WM load blocks, participants had to perform a dual task. The requirement to retain a single shape in WM may have delayed the N2pcs to search targets by about 50 ms relative to earlier single-task visual search experiments, due to a competition with the currently active spatial target templates. This hypothesis will have to be confirmed in future investigations of links between WM load and search target selection that include a single-task baseline condition.

In high WM load blocks, this delay was most pronounced, as a reliable contralateral negativity only emerged around 350 ms after search display onset. It is unclear whether this late contralateral component should still be interpreted as an N2pc. In previous ERP studies of visual search, a sustained posterior contralateral negativity (SPCN) was observed around this point in time, following the earlier N2pc component (e.g., Mazza, Turrato, Umiltà, & Eimer, 2007; Jolicoeur, Brisson, & Robitaille, 2008). The SPCN is usually interpreted as reflecting the attentional processing of visual objects in WM as a result of their initial attentional selection (but see Grubert, Fahrenfort, Olivers, & Eimer, 2017, for evidence that an SPCN component can be elicited without a preceding N2pc). Regardless of whether the late negativity in high WM blocks reflects a delayed N2pc or an SPCN, the critical observation remains that increasing WM load delayed the emergence of spatially selective contralateral ERP components, thus providing clear electrophysiological evidence that the selective attentional processing of target objects was impaired by WM load.

While load theory generally regards WM load as a type of cognitive load that impairs the ability to filter out unwanted information (Lavie et al., 2004; Lavie, 2005, 2010), it has more recently been argued that the demands associated with visual working memory storage represents a different perceptual type of load (Konstantinou & Lavie, 2013). In this study, increasing the number of features that had to be maintained in visual working memory was found to reduce perceptual sensitivity to other objects, analogous to the effects of perceptual load found in other experiments (e.g., Lavie, 2005). A similar phenomenon might underlie another unexpected finding of the current experiment. Increasing WM load not only affected N2pc components to target objects, but also resulted in an attenuation of posterior N1 components elicited by the search displays. N1 amplitudes

were reliably smaller in high WM load blocks relative to low load blocks (see Figure 2). This effect was bilateral and independent of the position of target objects, suggesting that it is generated in a generic target-nonspecific fashion during the early sensory processing of search displays. An amplitude decrease of an early visual-evoked ERP component by the concurrent retention of visual features in WM is a novel observation (but see Rose et al., 2005, for a similar N1 modulation that was linked to the retention demands of n-back tasks), and it would be premature to provide a detailed account about the basis of this effect. In line with the suggestions by Konstantinou and Lavie (2013), the N1 attenuation with high concurrent WM load might reflect an effect of perceptual load that is associated with maintaining multiple object shapes in visual WM memory, and affects the sensory processing of new visual information. A different way of describing this effect is to characterize it in terms of a trade-off between external attention that is directed towards incoming visual signals and internal attention that is allocated to currently active WM representations (e.g., Chun, Golomb, & Turk-Browne, 2011). The posterior visual N1 component is known to be highly sensitive to manipulations of selective attention (e.g., Mangun & Hillyard, 1991; Eimer, 1994), and the attenuation of N1 amplitudes triggered by search displays in high WM load blocks could reflect the fact that attentional mechanisms were strongly engaged in the maintenance of internal WM representations, thus limiting the degree to which attention could be simultaneously allocated to stimuli in the external world. If these suggestions can be substantiated in future research, this would imply that search-unrelated WM load can have two different effects on the processing of visual search displays. These effects operate at different stages, can be dissociated with ERP measures, and may reflect the perceptual and cognitive types of load described by load theory (Lavie, 2005, 2010). At an early sensory stage that is reflected by visual N1 components, WM load impairs the perceptual processing of all visual input in a non-selective way, in a way that is similar to other manipulations of perceptual load. At a subsequent target selection stage where N2pc components are generated, WM load interferes with the operation of search target templates. Similar to other types of cognitive load, this interference results in an impairment of target selectivity.

Overall, the current experiment provided novel electrophysiological evidence that non-spatial WM load interferes with the guidance of attentional target selection by search templates for target locations. This implies that these spatial attentional templates are held

in visual WM, where they compete with other concurrently active non-spatial WM representations, suggesting that spatial and non-spatial WM are less distinct than is often assumed.

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Figure captions

Figure 1: Example experimental trial sequence (not to scale). On each trial, participants encoded one (low load) or four (high load; as shown here) distinct shape objects from a memory sample display. Following a delay period, a search display (100 ms duration) or a memory test display (2000 ms duration) was presented. Participants had to either match the test display item to an item in the memory sample display, or to report the orientation of the target bar in the search display. Search displays contained a pair of lateral bars in the upper or lower visual field, and targets were defined by their location (top-left/bottom-right, or vice versa).

Figure 2: (Upper panels) Grand average ERPs obtained in response to search displays at lateral posterior electrode sites PO7/PO8 contralateral and ipsilateral to the side of the target object. ERPs are shown for the 500 ms interval following search display onset, separately for blocks with low and high WM load. (Lower panel) N2pc difference waveforms obtained by subtracting ipsilateral from contralateral ERPs for low and high WM load blocks. The N2pc measurement window (250-350 ms) is indicated by grey bars.

Figure 1

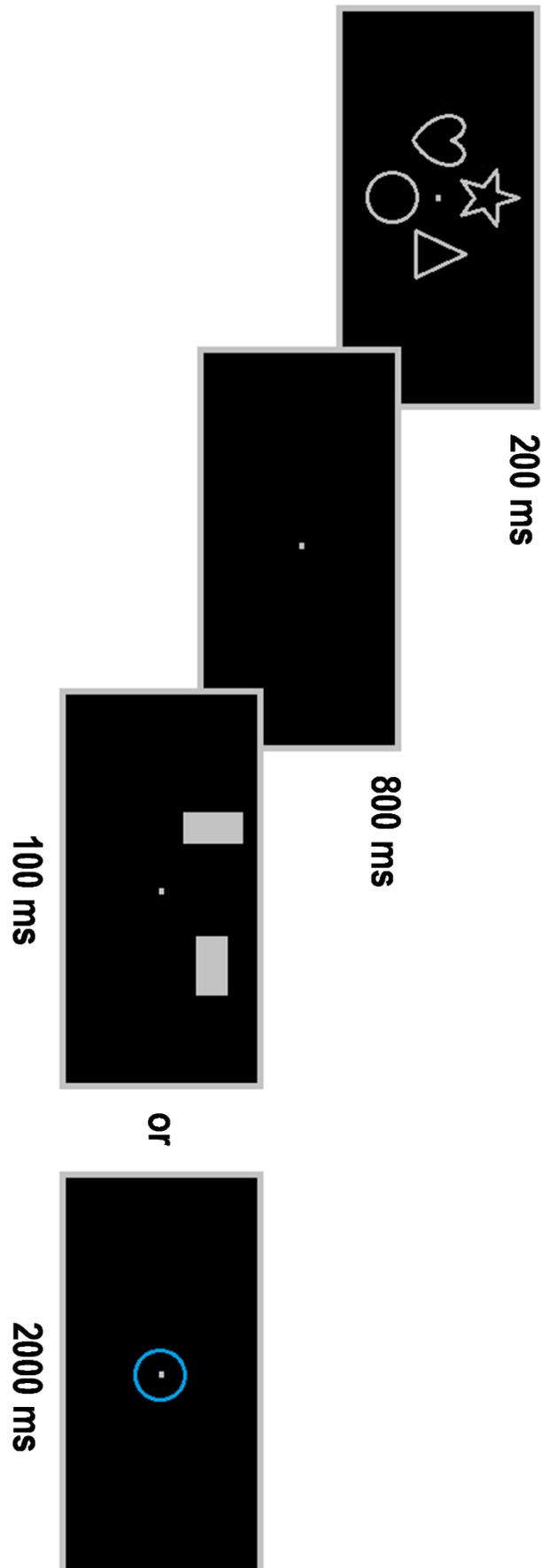


Figure 2

