BRIEF REPORT

An electrophysiological measure of access to representations in visual working memory

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Abstract

Previous research has demonstrated that the maintenance of visual information in working memory is associated with a sustained posterior contralateral negativity. Here we show that this component is also elicited during the spatially selective access to visual working memory. Participants memorized a bilateral visual search array that contained two potential targets on the left and right side. The task-relevant side was signalled by post-cues that were presented either 150 ms after array offset or after a longer interval (700–1000 ms). Enhanced negativities at posterior electrodes contralateral to the cued side of a target were elicited in response to both early and late post-cues, suggesting that they reflect not only memory maintenance, but also processes involved in the access to stored visual working memory representations. Results provide new electrophysiological evidence for the retinotopic organization of visual working memory.

Descriptors: Working memory, Vision, Spatial cognition, Event-related brain potentials

Visual working memory (WM) is responsible for the short-term storage and maintenance of currently relevant visual events. Recent event-related brain potential (ERP) studies have observed a spatially specific electrophysiological correlate of maintenance activity in WM (Klaver, Talsma, Wijers, Heinze, & Mulders, 1999; McCollough, Machizawa, & Vogel, 2007; Vogel & Machizawa, 2004). In these studies, memory items were presented to the left or right of fixation, and one of these sides was previously cued for subsequent recall. A sustained negativity was triggered during the retention interval at posterior electrodes contralateral to the location of the relevant items. This sustained posterior contralateral negativity (SPCN), which increased in amplitude when the number of to-be-remembered items was increased, was interpreted as an electrophysiological marker of maintaining representations in WM. The location-specificity of the SPCN suggests that such WM representations are retinotopically organized. The SPCN was preceded by a transient posterior N2pc component, which reflects the attentional selection of cued memory items (see also Eimer, 1996; Luck & Hillyard, 1994). Similar contralateral ERP components have also been observed in visual search experiments that required WM for the in-depth processing of briefly presented targets (e.g., Dell'Acqua, Sessa, Jolicœur, & Robitaille, 2006; Mazza, Turatto, Umiltà, & Eimer, 2007).

The purpose of the present study was to investigate whether contralateral posterior ERP components analogous to those previously observed in studies of WM maintenance are also elicited during the *access* to representations in WM. Recent functional brain imaging studies (e.g., Nobre et al., 2004) have uncovered common activity patterns during the orienting of spatial attention to perceptual objects and to objects stored in WM (see Lepsien & Nobre, 2006, for review), suggesting that spatially selective processes in perception and in WM may be based on common neural substrates. Here, we compared the situation where the side of visual search targets was cued prior to the presentation of search arrays with a condition where spatial cues were presented *after* these search arrays. In post-cue blocks, participants first saw a visual array consisting of two differently colored (red and green) semicircles on the left and right side (Figure 1). Each semicircle contained four circles and one diamond, and both diamonds were cut either at the top or at the bottom. This array was presented for 150 ms, and was followed after a brief (150 ms) or longer (700–1000 ms) interval by a post-cue (a red or green square at fixation) that indicated the task-relevant side of the display (i.e., the red or green side, corresponding to the left or right side in randomly intermixed trials). Participants had to report the cut location (top or bottom) for the diamond on the cued side. Because they did not know which side of the array was task-relevant prior to the arrival of the post-cue, both sides had to be encoded and maintained in WM. Following the post-cue, this memory representation could be accessed to determine the shape of the diamond target on the cued side. The search task was identical in pre-cue blocks, except that cues now appeared before each search display, so that the task-relevant side could be immediately selected once the search array appeared.

Pre-cue condition

150 ms   700–1000 ms   150 ms

Post-cue conditions

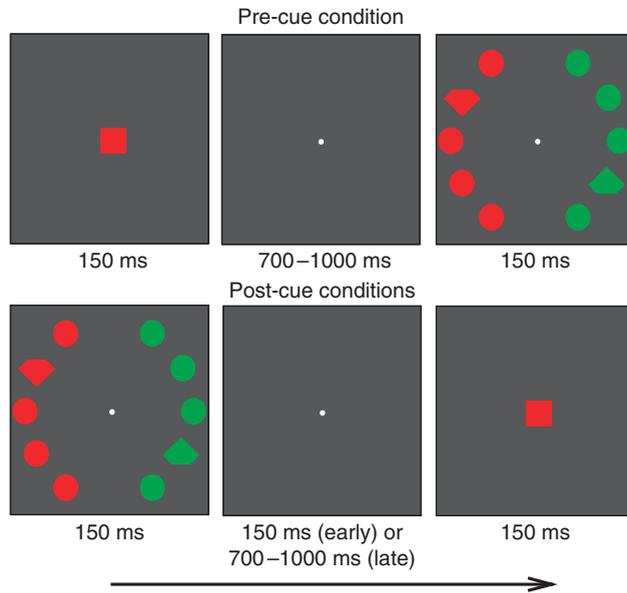150 ms   150 ms (early) or 700–1000 ms (late)   150 ms

Figure 1. Sequence of visual events in blocks with pre-cues (top) and post-cues (bottom).

If visual WM representations are retinotopically organized, accessing such representations in response to post-cues should give rise to lateralized posterior ERP components similar to those previously observed in ERP studies of WM maintenance. If similar mechanisms are involved in the spatial selection of perceptual objects and objects held in WM (Nobre et al., 2004), lateralized components triggered by post-cues should be similar to those elicited in response to search arrays in pre-cue blocks.

Method

Participants
Out of 16 participants, three were excluded due to eye movement artefacts (saccades to the target or blinks), and one was excluded because of excessive alpha activity. The remaining 12 participants (eight female, mean age: 27.4 years) were all right-handed and had normal or corrected vision.

Stimuli and Procedure
In each trial, two displays were presented (see Figure 1). Search displays contained a circular array of ten elements (five equidistant elements in each hemifield; angular distance of 4.5° from central fixation). Two diamonds in opposite hemifields were presented together with eight circles. Diamonds appeared equiprobably and randomly at each of the five positions in their respective hemifields. Both diamonds were cut either at the top or the bottom (size of cut: 0.4°). As these cut positions were randomly determined for each diamond, they were identical in half of all trials (same-cut trials), and different in the other half (different-cut trials). Stimuli in each hemifield were uniformly colored (equiluminant red or green; CIE x/y values: .635/.339 and .298/.579; luminance: 9.6 cd/m^2), with color-hemifield mappings changing randomly across trials. Cue displays consisted of a red or green square presented at fixation, with cue color determined randomly for each trial. Target, distractors, and cues subtended 1.2° × 1.2°.

Participants had to report the position of the cut (top or bottom) of one diamond by pressing one of two spatially corresponding keys with their index fingers (hand-key assignments counterbalanced within participants). The hemifield of this target diamond was signalled by the color cue. There were three blocked cue conditions. In the pre-cue condition, the cue display was presented for 150 ms, followed by a blank interval of variable duration (700 to 1000 ms, jittered in steps of 60 ms), after which the search array was presented for 150 ms. In the late post-cue condition, the order of cue and search displays was reversed. In the early post-cue condition, search and cue displays were separated by a constant blank interstimulus interval of 150 ms. Intertrial interval was 1500 ms. Eight successive blocks of 40 trials per block were run for each of the three cue conditions, and order of cue conditions was counterbalanced between participants.

EEG Recording and Analysis
The EEG was recorded with a sampling rate of 500 Hz and a bandpass of 0–40 Hz from 23 electrodes attached at standard positions with an elastic cap. Electrodes were referenced to the left earlobe and offline re-referenced to the average of both earlobes. All impedances were below 5 kΩ. Trials with saccades (HEOG exceeding ± 30 μV), blinks (Fpz ± 60 μV), or other artefacts (any other electrode ± 80 μV) were discarded. ERPs were averaged relative to search array onset in the pre-cue condition and relative to cue onset in the two post-cue conditions. Pre-stimulus baselines were 100 ms intervals prior to search array onset and cue onset in the pre-cue and late post-cue conditions, respectively. In the early post-cue condition, a 100-ms baseline prior to search array onset was used.

Averages were computed for same-cut and different-cut trials with correct responses, separately for each of the three cue conditions, and for trials with target diamonds in the left and right hemifields. Mean amplitudes were calculated at lateral posterior electrodes PO7 and PO8 for two post-stimulus time windows (N2pc: 180–250 ms; SPCN: 300–600 ms). ERP analyses focused on different-cut trials, where participants had to use the cues to select the correct response.[1] Repeated-measures ANOVAs were conducted on these mean amplitude values separately for each cue condition with the factors target position (left vs. right) and contralaterality (contralateral vs. ipsilateral to the target position). Additional analyses were conducted across all different-cut trials, with cue condition (pre-cue, early post-cue, late post-cue) as an additional factor. Greenhouse-Geisser corrections for nonsphericity were applied where appropriate.

Results

Behavioral Data
Mean reaction times (RTs) for blocks with pre-cues, early post-cues, and late post-cues were 562 ms, 620 ms, and 464 ms, respectively (main effect of cue condition: $F(2,22) = 27.8, p < .001$). RTs were faster for same-cut relative to different-cut trials (494 vs. 603 ms; $F(1,11) = 34.1, p < .001$). A cue condition × trial type interaction, $F(2,22) = 16.1, p < .001$, was due to the fact that these RT benefits for same-cut trials were much larger with late and early post-cues (166 and 134 ms), where response preparation on same-cut trials could start after the presentation of the

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[1]Note that because diamond stimuli on the left and right side were identical in same-cut trials, selection of the correct response could take place immediately after the search display. However, in the absence of such same-cut trials, diamond identity on the left and right side would have been perfectly correlated, so that participants could have selected either side to choose the correct response.
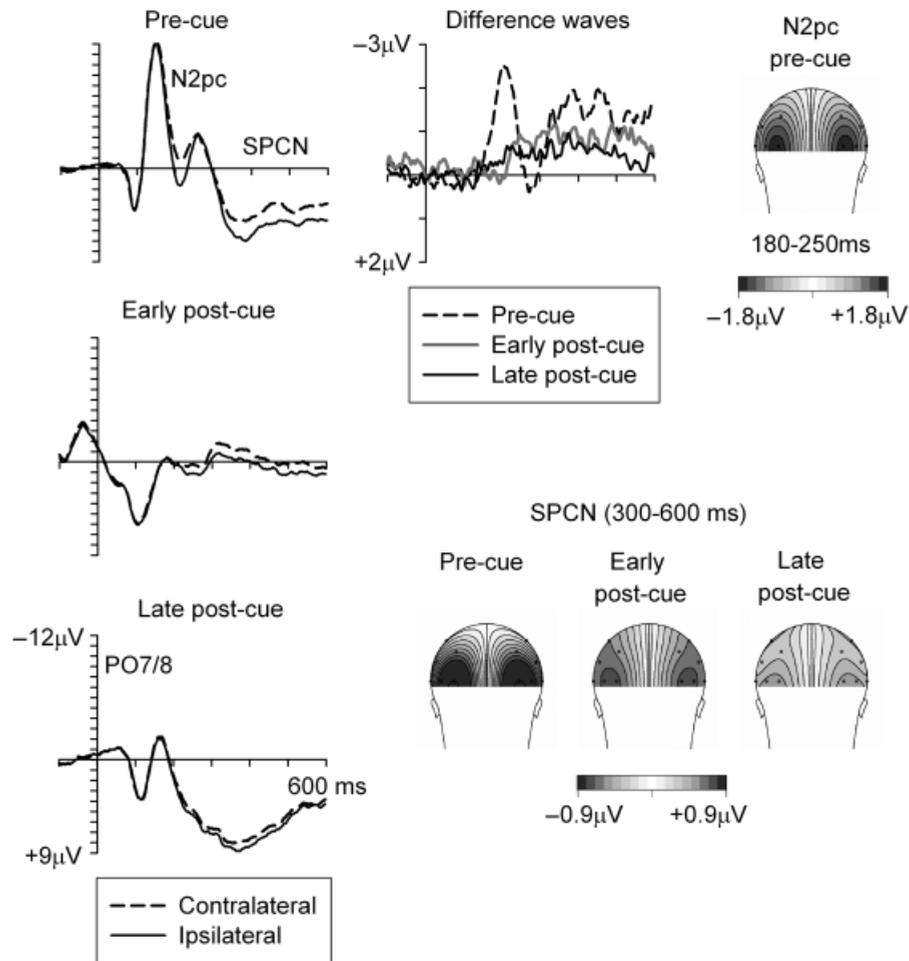
Figure 2. Top: Grand-averaged visual ERPs obtained at electrodes PO7/PO8 contralateral and ipsilateral to the cued side of a target diamond, shown separately for blocks with pre-cues, early post-cues, and late post-cues. Bottom left: Difference waveforms obtained for the three cue conditions by subtracting ERPs at ipsilateral electrodes from contralateral ERPs. Bottom right: Topographical maps representing differences between brain activity over ipsi- and contralateral hemispheres in the N2pc and SPCN time windows, constructed by spherical spline interpolation (Perrin, Pernier, Bertrand, & Echallier, 1989) after mirroring difference amplitudes to obtain symmetrical but inverse amplitude values for both hemispheres.

search array, than with pre-cues (26 ms). Follow-up analyses revealed that RT advantages for same-cut trials were reliable in all three cue conditions, all $F(1,11) > 16.8$, all $p < .01$. The percentage of incorrect responses was 3.7%, 10%, and 5.5%, for pre-cues, early post-cues, and late post-cues, respectively (main effect of cue condition: $F(2,22) = 11.0$, $p < .001$). Premature key presses prior to the onset of the second stimulus were recorded on 5.9% of all same-cut trials in the late post-cue condition, but on less than 1% of trials in all other conditions, resulting in a cue condition × trial type interaction, $F(2,22) = 5.3$, $p < .05$.

ERP Data

Figure 2 shows ERPs obtained at PO7/8 contralateral and ipsilateral to the task-relevant side of a visual search display on different-cut trials, separately for all three cue conditions, together with contralateral minus ipsilateral difference waves, and scalp distribution maps for N2pc and SPCN components. In the pre-cue condition, search arrays triggered a substantial N2pc that was followed by an SPCN, as expected. This was substantiated by main effects of contralaterality in the N2pc and SPCN time windows (180–250 ms and 300–600 ms post-stimulus: $F(1,11) = 26.9$ and 13.8; $p < .001$ and .01, respectively).

Most importantly, lateralized occipital components were also clearly triggered in response to both post-cues. Here, a sustained contralateral negativity emerged about 200 ms after post-cue onset, without visible temporal separation of N2pc and SPCN. Significant contralaterality effects were obtained in the SPCN time window for both post-cues ($F(1,11) = 15.6$ and 7.0; $p < .01$ and .03, for early and late post-cues, respectively). A follow-up analysis of SPCN amplitudes conducted across both post-cues found a main effect of contralaterality, $F(1,11) = 13.3$, $p < .01$, but no interaction between post-cue delay and contralaterality, $F < 1$, indicating that SPCN amplitudes did not differ between early and late post-cues.[2] An additional analysis was conducted for both post-cue conditions on ERP mean amplitudes obtained in the 200–300 ms interval after cue onset. As before, main effects of contralaterality were obtained for both early and late post-cues, $F(1,11) = 14.8$ and 5.3; $p < .01$ and .05, respectively, without any post-cue delay × contralaterality interaction, $F < 1$.

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[2]As expected, no reliable SPCN was triggered on same-cut trials in response to early post-cues, $F < 1$, or late post-cues, $F(1,11) = 3.4$, $p = .09$.

Discussion

We investigated whether lateralized posterior ERP components previously found in studies investigating WM maintenance (e.g., McCollough et al., 2007) are also elicited during the spatially selective *access* to stored WM representations. The critical new finding was that post-cues which signalled the side of a memorized search array that contained a target triggered a sustained contralateral negativity at posterior electrodes.[3] Because cues were squares presented at fixation, this effect cannot reflect a lateralized visual response to these cues. Instead, it is likely to be linked to processes involved in accessing stored visual WM representations. The observation that access to stimuli in WM, which had previously appeared in the left or right visual field, gives rise to a contralateral negativity provides new evidence for the retinotopic organization of visual WM (see also Gratton, Corballis, & Jain, 1997, for lateralized ERP responses triggered during the retrieval of visual information from long-term memory). The fact that these contralateral effects were not reliably different for late and early post-cues suggests that the visual WM representations involved are not subject to rapid decay.

Previous functional magnetic resonance imaging (fMRI) studies (e.g., Nobre et al., 2004) have suggested that the spatial selection of perceptual objects and of objects held in WM are based on similar mechanisms. In this case, lateralized components observed in response to post-cues should have been similar to those elicited by search arrays in pre-cue blocks. While the presence of sustained contralateral negativities in both pre- and post-cue blocks is in line with this hypothesis, there were also differences. In pre-cue blocks, the SPCN was preceded by a transient N2pc component (see also Mazza et al., 2007), in line with the fact that targets could be immediately selected after search array onset. In contrast, contralateral negativities emerged later and did not show a biphasic pattern in post-cue blocks. As the scalp distribution of N2pc and SPCN components is very similar (see Jolicœur, Brisson, & Robitaille, 2008), a dissociation of these components based on topographical differences is difficult (but see McCollough et al., 2007). One interpretation of the differences between pre-cue and post-cue blocks is that while the N2pc was strictly time-locked to search array onset in pre-cue blocks, it was delayed and showed more latency variability across trials in post-cue blocks, where it overlapped in time with the SPCN. This hypothesis suggests that the spatially selective access to WM representations is temporally less precise than the spatially selective processing of perceptual events. Such subtle differences in the time course of spatially selecting perceptual versus WM representations may be difficult to detect with fMRI measures. It should also be noted that the presence of contralaterally enhanced posterior negativities in response to post-cues may not exclusively reflect the spatially selective access to WM, as such cues may have also elicited shifts of spatial attention in perceptual space (see Spivey & Geng, 2001, for links between WM access and eye movements towards previous locations of remembered objects).

In summary, the current study demonstrated that access to stored visual WM representations that is guided by their spatial features gives rise to contralateral posterior ERP components that are similar to components previously found during WM maintenance. The presence of such spatially specific ERP modulations supports the claim that visual WM is based on a retinotopic coordinate system.

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[3]The fact that this contralateral negativity was smaller than in previous studies of WM maintenance where WM load was manipulated (e.g., McCollough et al., 2007) is likely due to the fact that search arrays contained only one target item on either side.