

During the subsequent maintenance interval, neural activity is greater in the posterior region that is contralateral to the location of items in VSTM, relative to the ipsilateral region, reflecting selectivity for the task-relevant items held in VSTM.

If task-goals change dynamically after the initial encoding of the events, stimuli maintained in VSTM may gain or lose relevance; therefore, a mechanism for dynamic modulation of specific memoranda would be highly advantageous in optimizing and controlling the limited contents of VSTM. Recent behavioral evidence demonstrates that attention can be directed to specific items held in VSTM (Vandenbroucke, Sligte, & Lamme, 2011; Makovski, Sussman, & Jiang, 2008; Lepsien & Nobre, 2007; Makovski & Jiang, 2007; Matsukura, Luck, & Vecera, 2007; Yeh, Kuo, & Liu, 2007; Makovski, Shim, & Jiang, 2006; Griffin & Nobre, 2003; Landman, Spekreijse, & Lamme, 2003). Presenting a spatial cue during the delay period to indicate which item in VSTM is likely to be probed dramatically improves VSTM performance for cued relative to uncued items. Critically, these retroactive cues (retrocues) are presented long after iconic memory decay and, therefore, do not influence initial encoding into VSTM. However, the mechanisms by which selective attention can bias maintenance in VSTM remain largely unknown.

As mentioned above, current evidence suggests that VSTM is mediated by sustained activation of memoranda-specific perceptual representations in posterior brain areas. A perceptual basis for VSTM could provide a natural mechanism for dynamic biasing even after initial encoding into VSTM. In particular, similar attentional mechanisms that bias competitive processing during perception may operate upon activity in these posterior areas when they are supporting VSTM representations (Dell'Acqua, Sessa, Toffanin, Luria, & Jolicoeur, 2010; Eimer & Kiss, 2010; Kuo, Rao, Lepsien, & Nobre, 2009). For example, shifts of attention during VSTM maintenance could filter out items as they become task irrelevant, thereby reducing memory load and inter-item competition (Edin et al., 2009) and consequently increasing the probability of recall for the relevant cued items.

In this study, we tested whether top-down attentional signals can continue to modulate persistent delay activity underlying VSTM across two experiments. We exploited the CDA as an index of VSTM maintenance to test whether the load of items being actively maintained can be adjusted dynamically as new information becomes available, signaling which memoranda are most relevant for task performance. As common practice in experiments using the CDA measure, at the beginning of each trial participants viewed an arrow cue, instructing them to only encode items in either the left or right visual hemifield. Next, a memory array of multiple colored squares was presented within each visual hemifield. After a retention interval, a test stimulus was presented to probe the contents of VSTM. During this retention interval, attentional orienting was manipulated by providing spatially informative

(spatial) or noninformative (neutral) cues after the memory array, yet before the test probe. These retrocues indicated the location of the single item that would be required to perform the subsequent comparison with the probe stimulus, thus effectively reducing the task-relevant load from multiple items to just one item. Importantly, because this predictive information is presented long after the offset of the memory array, retrocues cannot be used to bias initial processing of the visual stimulus for selective access to VSTM but may influence information that is already being maintained in VSTM.

Consistent with previous studies (Nobre, Griffin, & Rao, 2008; Griffin & Nobre, 2003), we found that recall was faster and more accurate for cued items, relative to uncued items. More importantly, we found that load-dependent neural activity reflecting VSTM maintenance could be modulated by spatial cues that effectively reduced the task-relevant memoranda to one item across two experiments. Our results provide direct evidence that top-down control directly modulates neural activity associated with maintenance in VSTM.

METHODS

Experiment 1

Participants

All participants in this study were right-handed according to the Edinburgh handedness inventory (Oldfield, 1971). Twenty-five participants were recruited. They had normal or corrected-to-normal visual acuity, provided informed written consent, and were financially reimbursed for their time. Data from seven participants were excluded because of poor performance on the task (<60% correct trials) or too few trials remaining after EEG artifact rejection (<25 trials). The behavioral and ERP analyses were performed on the remaining 18 participants (nine women, age range = 21–33 years, mean age = 27 years). All experimental methods had ethical approval from the Central University Research Ethics Committee of the University of Oxford.

Behavioral Task

The task of the first experiment is illustrated in Figure 1A. Retrocue type (spatial, neutral) and VSTM load (two-item, four-item) were manipulated within participants, in a two-way repeated measures factorial design.

Stimuli were presented on a CRT screen using Presentation software (Neurobehavioral Systems, Inc., Albany, CA). Each trial began with the onset of a centrally displayed asterisk (500–1000 msec duration, randomized), which signaled the onset of the trial. Next, an arrow pointing to either the left or right visual hemifield was presented at the center of the screen for 200 msec, followed, at a variable interstimulus interval (500–1000 msec duration), by the memory array consisting of two or four colored squares in each hemifield. Participants were instructed to remember

Results

Behavioral results. The behavioral results are summarized in Figure 1 and Table 1. A significant retrocueing effect was observed across all measures, with higher mean d' scores [$F(1, 17) = 58.70, p < .005$], higher mean K measures [$F(1, 17) = 76.72, p < .005$], and faster RT [$F(1, 17) = 252.93, p < .005$] in spatial trials (2.34 ± 0.71 d' score, 2.05 ± 0.54 K value, 528.46 ± 87.71 msec in RT) relative to neutral trials (1.83 ± 0.78 d' score, 1.59 ± 0.42 K value, 648.20 ± 98.02 msec in RT). We also observed a significant main effect of VSTM Load across all measures, showing higher mean d' scores [$F(1, 17) = 113.16, p < .005$], lower K measures [$F(1, 17) = 21.91, p < .005$], and faster RT [$F(1, 17) = 98.85, p < .005$], in two-item trials (2.66 ± 0.52 d' score, 1.59 ± 0.17 K value, 551.41 ± 90.89 msec in RT) relative to four-item trials (1.52 ± 0.56 d' score, 2.06 ± 0.66 K value, 625.25 ± 116.12 msec in RT). Finally, the interaction between Retrocue Type and VSTM Load was significant in all measures [d' score: $F(1, 17) = 6.12, p < .05$; K measure: $F(1, 17) = 40.91, p < .005$; RT: $F(1, 17) = 9.16, p < .05$], owing to a reduction of the load effect associated with spatial retrocues [increased d' score: $t(17) = 2.46, p < .05$; enhanced K measure: $t(17) = 6.44, p < .005$; faster RT: $t(17) = 3.03, p < .05$]. These behavioral results confirmed that participants were able to orient their attention toward the item held in VSTM, resulting in benefits of VSTM performance and consequently attenuating the load effect.

ERP results. The ERP results are plotted in Figure 2. First, we tested for the presence of CDA during the precue interval (500–800 msec) and found a significant main

Table 1. Mean d' Scores, K Measures, and RTs (in msec) and Standard Deviations of the Means of Correct Responses in Each Condition

Experiment 1			
		Neutral Cue	Spatial Cue
d' Score	2-item	2.48 ± 0.44	2.84 ± 0.56
	4-item	1.19 ± 0.46	1.85 ± 0.47
K measure	2-item	1.53 ± 0.16	1.65 ± 0.16
	4-item	1.66 ± 0.58	2.45 ± 0.51
RT (msec)	2-item	603.38 ± 84.22	499.44 ± 68.40
	4-item	693.01 ± 94.86	557.48 ± 99.15
Experiment 2			
	No Cue	Neutral Cue	Spatial Cue
d' Score	1.11 ± 0.43	1.22 ± 0.31	1.84 ± 0.57
K measure	1.59 ± 0.45	1.74 ± 0.38	2.45 ± 0.64
RT (msec)	745.63 ± 64.11	695.27 ± 71.14	538.86 ± 71.83

effect of Visual Hemifield with a greater mean negative amplitude on the contralateral side relative to ipsilateral sides ($F(1, 17) = 37.73, p < .005$). As predicted, we found the CDA to be load-dependent. We observed a significant interaction of VSTM Load and Visual Hemifield [$F(1, 17) = 20.56, p < .005$], owing to a greater increase in voltage negativity over posterior electrodes that were contralateral to the memorized hemifield relative to the ipsilateral hemifield within increasing VSTM load (two-item trial: 0.97 ± 0.97 μV , four-item trial: 1.70 ± 0.99 μV) [$t(17) = 4.54, p < .005$]. There was also a significant main effect of VSTM Load, attributable to a greater negative amplitude for four-item (-2.46 ± 2.58 μV) relative to two-item trials (-1.45 ± 2.07 μV) [$F(1, 17) = 15.13, p < .005$].

The main hypothesis of interest was whether the load-dependent neural activity reflecting VSTM maintenance (i.e., CDA) could be modulated dynamically by spatial cues that effectively reduced the task-relevant memoranda to one item. Accordingly, we tested whether the amplitude of CDA was attenuated after a spatial cue relative to the neutral cue during the postcue interval (1500–1800 msec). Direct comparison of the voltage difference between ipsilateral versus contralateral side indicated a significant main effect of Load [$F(1, 17) = 8.17, p < .05$], showing greater mean amplitude for four-item (0.28 ± 1.09 μV) relative to two-item trials (-0.22 ± 0.90 μV) [$t(17) = 2.86, p < .05$]. More importantly, we observed a significant three-way interaction among Retrocue Type, VSTM Load, and Visual Hemifield [$F(1, 17) = 4.35, p = .05$]. Follow-up analyses were conducted to clarify the pattern of interaction effect. Analysis of neutral trials still revealed a significant load effect [$t(17) = 3.42, p < .005$] (four-item trial: 0.67 ± 1.20 μV ; two-item trial: -0.32 ± 1.45 μV). In contrast, no difference was found in amplitude of CDA between four-item (-0.11 ± 1.23 μV) and two-item (-0.12 ± 1.04 μV) spatial cue trials ($p > .1$). Overall, the results highlighted that the difference in the CDA between two and four items was reduced after a spatial cue (0.01 ± 1.26 μV) in contrast to a neutral cue (1.0 ± 1.23 μV) [$t(17) = 2.09, p = .05$], revealing a greater reduction in CDA after a spatial cue than after a neutral cue.

To test for a functional link between the neural activity reflected in the CDA and VSTM performance in our task, we also examined the correlation between the increase in amplitude of CDA between two and four items and the increase in K measured on neutral trials between two and four items across participants (Vogel & Machizawa, 2004). During the precue interval, there was a significant relationship between the set size effect on CDA amplitudes and K [Pearson correlation: $r(17) = 0.63, p < .05$]. This finding showed that individual differences in VSTM capacity can be reflected in the measures of delay activity, replicating previous reports of correlations between CDA and VSTM capacity (Vogel & Machizawa, 2004). We also observed a significant correlation on neutral trials in the interval after the cue was presented [$r(17) = 0.43, p < .05$], further demonstrating that the neutral cue did not alter

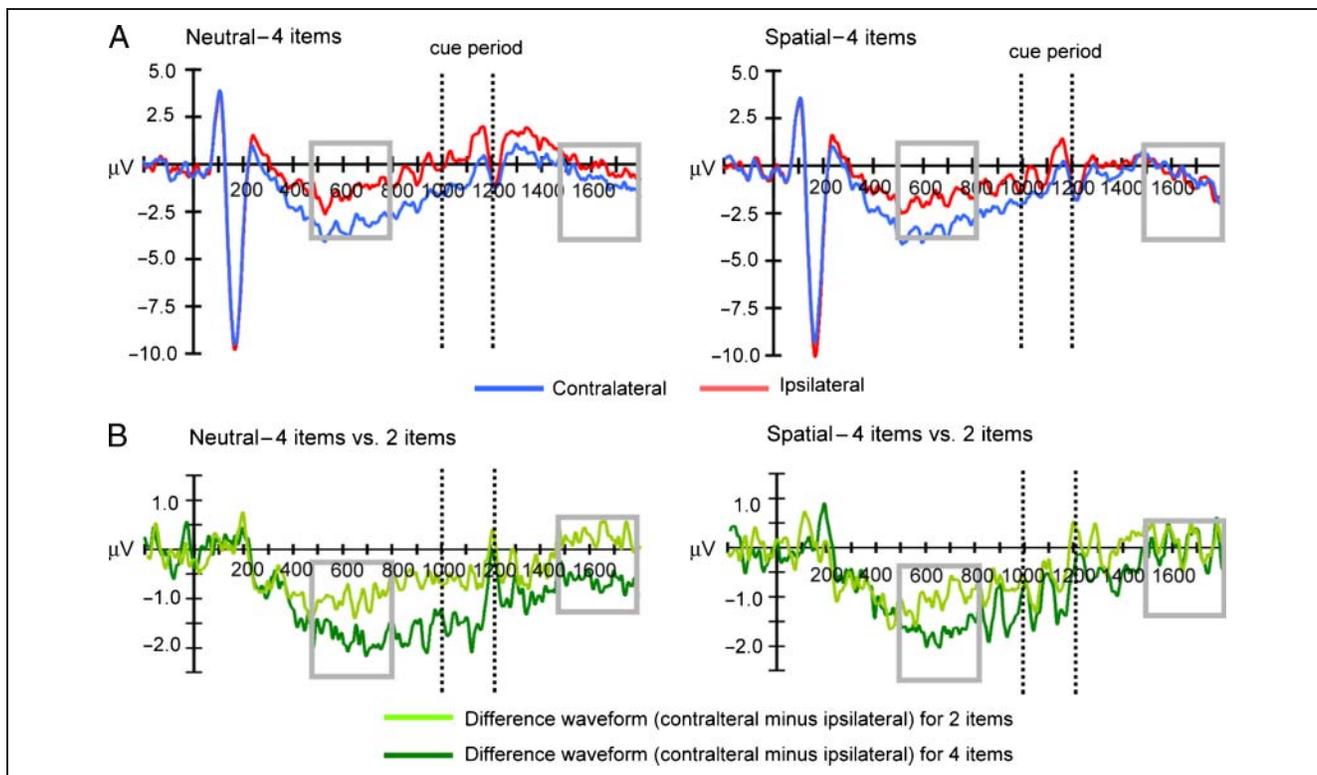


Figure 2. The ERP results of Experiment 1. (A) ERP waveforms averaged across all participants are shown for the four items for neutral (left) and spatial retrocue trials (right) over contralateral (blue lines) and ipsilateral (red lines) posterior parietal–occipital electrode pair: PO7/PO8. Our result shows equivalent CDA for neutral and spatial trials during the precue interval (500–800 msec). The amplitude of CDA is attenuated after a spatial cue, relative to the neutral cue, during the postcue interval (1500–1800 msec). (B) The voltage difference between contralateral versus ipsilateral side is also shown for two items (light green lines) and four items (dark green lines) in the neutral and spatial retrocue conditions, respectively. CDA is load dependent, showing greater CDA for four items than two items during the precue interval (500–800 msec). Spatial retrocues reduced the magnitude of the CDA during the postcue interval (1500–1800 msec). The temporal windows for CDA analyses are indicated by gray squares.

the relationship between the maintenance-related delay activity and capacity estimates.

Experiment 2

The goals of Experiment 2 were to replicate our finding that VSTM maintenance could be dynamically modulated by spatial attention and to ensure that these effects did not simply result from a potential disruption of VSTM maintenance by the presentation of a neutral cue. To rule out any effect related to the mere presentation of a visual stimulus as a cue, we included an additional no-cue condition. In Experiment 2, the memory array always consisted of four colored squares in each hemifield. In the no-cue control condition and in the neutral retrocue condition, stimuli maintained in VSTM did not gain or lose relevance. As in Experiment 1, retrocue type was manipulated within participants in a one-way repeated measures design. All trial types were equiprobable and randomized, and presentation order was randomized within 16 blocks of 24 trials, yielding 384 trials in total (64 target-present and 64 target-absent trials in each retrocue type).

To focus on the modulatory effect of spatial and neutral retrocues in the postcue interval more clearly, the spatial or neutral retrocue was presented at the time we found the CDA to be around its maximal amplitude in Experiment 1: 600–800 msec after the memory array. The earlier presentation of the retrocue enabled us to test the modulatory effect over an extended period and to obtain a more stable measure of the CDA during the postcue interval (1100–1800 msec duration; see Figure 1B for an example). The sequence of events in each trial and all other procedures for EEG recording, processing, and analyses were the same as the previous experiment.

Participants

All participants in this study were right-handed according to the Edinburgh handedness inventory (Oldfield, 1971). Sixteen participants were recruited. They had normal or corrected-to-normal visual acuity, provided informed written consent, and were financially reimbursed for their time. Data from one participant was excluded, owing to too few trials remaining after EEG artifact rejection (<25 trials).

The behavioral and ERP analyses were performed on the remaining 15 participants (eight women and seven men, age range = 21–33 years, mean age = 26.5 years). All experimental methods had ethical approval from the Central University Research Ethics Committee of the University of Oxford.

Behavioral Analysis

Each behavioral measure (d' score, K measure, and RT) was analyzed using a one-way repeated measures ANOVA (Retrocue Type: spatial, neutral, and no cue).

EEG Analysis

The mean amplitudes of the delay activity were computed between 1100 and 1800 msec (500–1200 msec after appearance of retrocue) during postcue interval at PO7/PO8 contralateral and ipsilateral to the side of the target. A two-way repeated measures ANOVA was computed on the mean amplitudes of the delay activity, testing the effects of Retrocue Type (spatial, neutral, and no cue) and Visual Hemifield (contralateral and ipsilateral to target). Of main interest was the interaction between Retrocue Type and Visual Hemifield.

Results

Behavioral results. The behavioral results are summarized in Figure 1 and Table 1. Overall, participants had bet-

ter performance in spatial trials compared with neutral and no-cue trials. We observed a significant main effect of Retrocue Types across all measures [d' scores: $F(2, 14) = 19.45, p < .005$; K measures: $F(2, 14) = 19.70, p < .005$; RT: $F(2, 14) = 203.71, p < .005$]. Follow-up comparisons showed higher mean d' scores, higher K measure, and faster RT in spatial trials than in both neutral [d' score: $t(14) = 5.11, p < .005$; K value: $t(14) = 4.89, p < .005$, RT: $t(14) = 12.00, p < .005$] and no-cue trials [d' score: $t(14) = 4.80, p < .005$, K value: $t(14) = 5.12, p < .005$, RT: $t(14) = 18.00, p < .005$]. Faster RT was also observed in neutral trials than in no-cue trials [$t(14) = 7.92, p < .005$]. No other significant effect was observed for d' scores or K values ($ps > .1$). As in Experiment 1, participants were capable of orienting their attention toward the item held in VSTM, resulting in benefits of VSTM performance.

ERP results. We tested whether the magnitude of CDA could be influenced by a neutral cue as well as a spatial cue, relative to the no-cue condition. The ERP results are plotted in Figure 3. We first demonstrated a significant main effect of Visual Hemifield [$F(1, 14) = 40.91, p < .005$] and, more importantly, a significant interaction between Retrocue Type and Visual Hemifield [$F(1, 14) = 16.45, p < .005$]. Follow-up analyses showed that the difference in voltage for the ipsilateral side in contrast to contralateral side was significantly larger in both neutral [$t(14) = 3.32, p = .005$] ($0.75 \pm 0.48 \mu\text{V}$) and no-cue trials ($1.46 \pm$

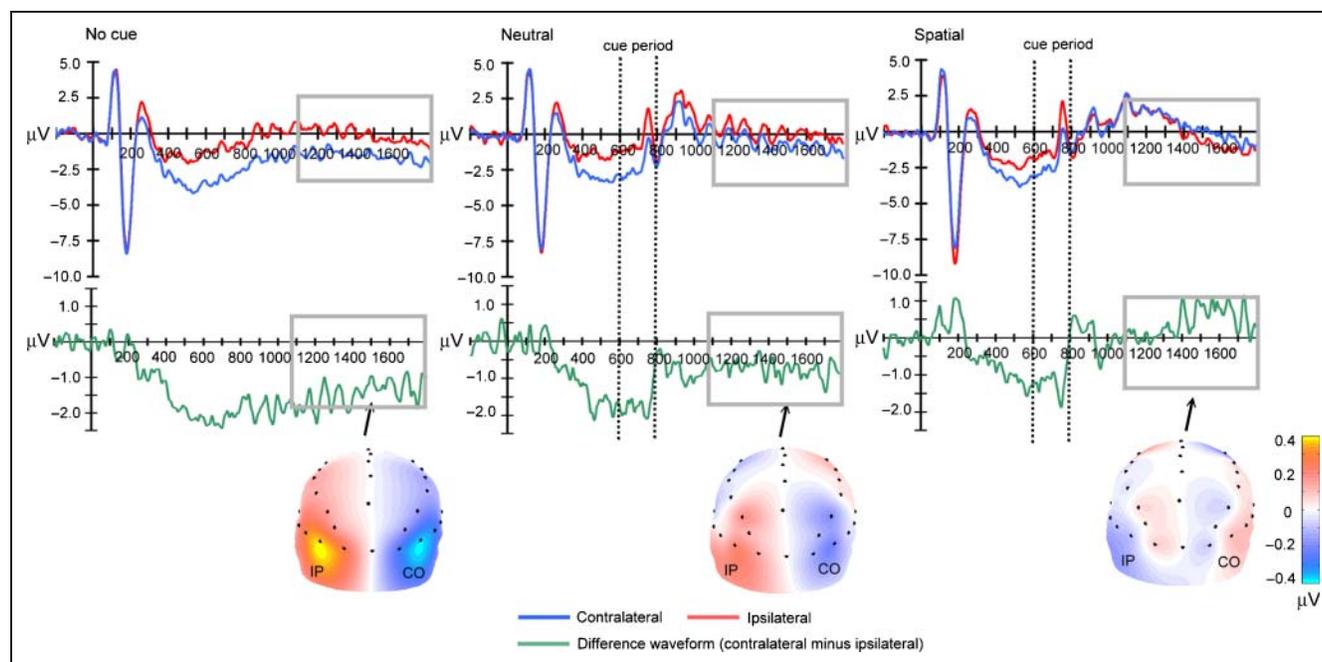


Figure 3. The ERP results of Experiment 2. ERP waveforms averaged across all participants are shown for no-cue (left), neutral (middle), and spatial (right) cue conditions over contralateral (waveforms: blue lines; topographies: right side) and ipsilateral (waveforms: red lines; topographies: left side) posterior parietal–occipital electrode pair: PO7/PO8. The amplitude of CDA is attenuated after a spatial cue, relative to the neutral cue and no-cue condition, during the postcue interval (1100–1800 msec). The voltage difference between contralateral versus ipsilateral side is also shown (waveforms: green lines). The temporal windows for CDA analyses are indicated by gray squares. The topographic maps isolated the lateralized differences in voltage between contralateral (CO) and ipsilateral (IP) sites. These maps show the symmetrical relative differences in voltage, which is more negative over the contralateral scalp and more positive over the ipsilateral scalp. The voltage distributions are shown from posterior perspective. The color scale shows the range of possible voltage values. Blue indicates negative voltage, and red indicates positive voltage.

0.90 μV) [$t(14) = 4.67, p < .005$] than in the spatial trials ($-0.42 \pm 0.99 \mu\text{V}$). We also observed larger CDA for no-cue trials in contrast to neutral cue trials [$t(14) = 3.43, p < .005$], although both were significantly greater than zero [neutral: $t(14) = 6.04, p < .005$; no cue: $t(14) = 6.27, p < .005$].

DISCUSSION

It is now well established that maintenance of information in VSTM is associated with persistent activity in neural ensembles in posterior brain regions that represent the perceptual characteristics of mnemonic information (see Pasternak & Greenlee, 2005, for a review). In this study, we tested whether top-down attention can directly modulate the maintenance of VSTM representations across two ERP experiments. By manipulating the spatially predictive information of an attentional retrocue, we showed that maintenance-related activity is modulated by changes in the task relevance of particular items in VSTM, as indicated by spatially informative retrocues. Specifically, spatial retrocues reduced the magnitude of persistent delay activity, consistent with a reduction in the effective memory load. This neural modulation was also consistent with behavioral benefits of spatial retrocuing. Presumably, reducing the number of task-irrelevant items stored in VSTM increases the probability of recall for the cued item.

The pattern of behavioral results replicates and extends previous studies, confirming that VSTM performance can be regulated by orienting attention to the internal representation of the task-relevant item (Griffin & Nobre, 2003; Landman et al., 2003). Spatial retrocues were accompanied by faster RT, higher d' scores, and K measures relative to neutral retrocue and no-cue conditions. This behavioral facilitation associated with spatial retrocues was more pronounced as VSTM load increased (Nobre et al., 2008; Lepsien & Nobre, 2006), consistent with the hypothesis that attentional selection during VSTM maintenance effectively reduces the number of items that need to be retained. These behavioral results are in accordance with previous studies that have demonstrated that attentional retrocues presented beyond the phase of VSTM encoding can still shape internal representations (Nobre et al., 2008), providing further evidence that VSTM representations can be modulated dynamically to accommodate changing task-goals.

Our result is also in line with previous evidence that CDA reflects VSTM maintenance and its magnitude correlates with VSTM capacity (Vogel & Machizawa, 2004). The strength of persistent activity varied as a function of VSTM load before appearance of retrocues. Moreover, the correlation between the CDA and capacity estimates was still evident after appearance of the neutral cue, demonstrating that the CDA continues to provide a valid index of VSTM maintenance, even after the presentation of a potentially distracting visual stimulus.

More importantly, our ERP data revealed that the magnitude of persistent activity was sharply attenuated by appearance of spatial retrocues. This finding supports the hypothesis that top-down attention in VSTM may share properties with attentional mechanisms that modulate perceptual analysis to bias competition in favor of the task-relevant information. Previously, Lepsien and Nobre (2007) used fMRI to test for modulation of maintenance-related activity in an object-based VSTM task. They showed that retrocues signaling the relevance of the face or scene in the previous two-item array for performance of a subsequent probe-match comparison modulated activity in perceptual areas preferentially processing faces (posterior fusiform gyrus) or scenes (parahippocampal gyrus). However, these results were ambiguous. Their task design made it unclear whether the cue-related modulations within these areas reflected changes to maintenance-related activity or anticipation of a specific category of probe stimulus (face or scene). Indeed, in a recent follow-up study, Lepsien, Thornton, and Nobre (2011) provides further evidence that anticipatory attention to relevant probe items can influence activity in visual areas. We were careful, therefore, to design our task in a way that would preclude any effect of anticipatory spatial attention to the cue or probe arrays.

In our task, the changes in the magnitude of lateralized neural activity in this task can only reflect changes in spatiotopic VSTM maintenance during the retention period. Spatial and neutral retrocues were presented *centrally* and, therefore, should not result in changes in the lateralization of neural activity. The continued correlation between CDA amplitude and capacity measures after neutral cues confirms this to be the case. Probe stimuli also appeared centrally and did not differ across the conditions of interest. A single color probe stimulus was presented at fixation, and the participant had to decide whether it was one of the items in the initial memory array. There was no basis, therefore, for the formation of any anticipatory spatial bias that could interfere with our CDA measure. Although lateralized markers of VSTM markers and spatial attention can often co-occur in many experimental designs (for a discussion, see Stokes, 2011), these were de-coupled within the present task design.

Our results also revealed some attenuation of the CDA in neutral retrocue trials, relative to no-cue trials in Experiment 2. We speculate that the CDA may reflect neural activity correlated to tonic firing in extrastriate visual areas during the delay, which is known to be sensitive to perceptual interference (Miller et al., 1993). Interestingly, this CDA decrement was not accompanied by a change in accuracy or sensitivity.

The nature of VSTM is still not fully understood. However, recent studies have suggested that VSTM may involve similar neural codes to those that mediate perceptual information (Dell'Acqua et al., 2010; Astle, Scerif, Kuo, & Nobre, 2009; Kuo et al., 2009; Jiang, Olson, & Chun, 2000; Gratton, 1998). We suggest that the shared neural organization for

perceptual and VSTM representations provides a common framework for top-down attentional modulations that optimize task-relevant processing during multiple domains of processing—perception, VSTM, and possibly beyond. Top-down attentional signals during VSTM maintenance can bias internal representations on the basis of the original spatial configuration of the perceptual inputs.

In conclusion, evidence that retrocues can modulate VSTM maintenance through top-down attentional orienting has important implications for views about the nature of VSTM. In particular, our findings provide further support for the view that VSTM representations are flexible and can be modulated dynamically according to changing goals and expectations (Kuo, Yeh, Chen, & D'Esposito, 2011; Kuo et al., 2009; Lepsien & Nobre, 2006, 2007). Top-down attentional orienting can modulate the maintenance of the short-lived representations within VSTM and bias competition in a favor of the most task-relevant information. We suggest that dynamic modulation of maintenance-related activity is likely to operate in conjunction with other optimizing mechanisms, such as attention-dependent encoding into VSTM (Murray et al., 2011; Schmidt et al., 2002) and selective biasing of search/retrieval processes (Nobre et al., 2008). As in perception, we argue that goal-dependent biases do not operate at a single bottleneck but at multiple stages between stimulus and response, depending on how task-goals and expectations are determined and how they unfold over time.

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