Published in final edited form as:

Brain Res. 2016 July 1; 1642: 226–237. doi:10.1016/j.brainres.2016.03.048.

The lasting memory enhancements of retrospective attention

Sarah Reaves¹, Jonathan Strunk¹, Shekinah Phillips², Paul Verhaeghen¹, and Audrey Duarte¹

¹School of Psychology, Georgia Institute of Technology, Atlanta, Georgia, USA

²Department of Biology, Agnes Scott College, Atlanta, Georgia, USA

Abstract

Behavioral research has shown that spatial cues that orient attention toward task relevant items being maintained in visual short-term memory (VSTM) enhance item memory accuracy. However, it is unknown if these retrospective attentional cues (“retro-cues”) enhance memory beyond typical short-term memory delays. It is also unknown whether retro-cues affect the spatial information associated with VSTM representations. Emerging evidence suggests that processes that affect short-term memory maintenance may also affect long-term memory (LTM) but little work has investigated the role of attention in LTM. In the current event-related potential (ERP) study, we investigated the duration of retrospective attention effects and the impact of retrospective attention manipulations on VSTM representations. Results revealed that retro-cueing improved both VSTM and LTM memory accuracy and that posterior maximal ERPs observed during VSTM maintenance predicted subsequent LTM performance. N2pc ERPs associated with attentional selection were attenuated by retro-cueing suggesting that retrospective attention may disrupt maintenance of spatial configural information in VSTM. Collectively, these findings suggest that retrospective attention can alter the structure of memory representations, which impacts memory performance beyond short-term memory delays.

1. Introduction

Visual Short Term Memory (VSTM) is a capacity limited system that represents visual information after it is no longer available through sensory input. Although capacity is limited and varies by individual, studies have discovered that VSTM capacity and accuracy can be enhanced via spatially informative, retrospective cues (“retro-cues”) (Makovski and Jiang, 2007; Makovski et al., 2008; Matsukura et al., 2007). In these studies, the retro-cue (a small arrow, for example) is presented briefly during the delay period between array presentation and memory probe and indicates which item will later be probed at test. Behavioral results from such studies reveal greater accuracy and faster response times for retro-cue trials that are similar to performance benefits seen when orienting attention before a perceptual array (Griffin and Nobre, 2003; Makovski and Jiang, 2007).

Correspondence to: Sarah Reaves, M.S., 654 Cherry St NW, Atlanta Georgia, 30332-0170, sarahareaves@gmail.com.

Publisher's Disclaimer: This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

There are a few suggested mechanisms for how retrospective attention enhances VSTM performance. One explanation is that, as item representations compete with one another in VSTM, the retro-cue isolates the important “to-be-probed” item, which causes the other items in VSTM to become task-irrelevant and consequently reduces effective memory load (Matsukura et al., 2007). Consistent with this account, research has shown greater retro-cue memory benefits at larger set sizes where interitem interference is higher compared to smaller set sizes (Duarte et al., 2013; Kuo et al., 2012; Lepsien and Nobre, 2007). Another, non-mutually exclusive explanation is that retro-cues reduce the number of comparisons needing to be made between the probe item and representations held in VSTM (Makovski et al., 2008).

The temporal resolution of electroencephalography (EEG) lends itself well to investigating how retrospective attention enhances VSTM performance. An event related potential (ERP) of particular relevance for investigating VSTM maintenance is the “contralateral delay activity” (CDA). The CDA is hypothesized to reflect the same persistent delay period activity observed in the extrastriate cortex in fMRI studies (Anderson et al., 2011; McCollough et al., 2007; Vogel and Machizawa, 2004). The CDA presents as sustained negative-going activity over posterior electrodes in the contralateral hemisphere with respect to the visual field in which task-relevant items were presented. The amplitude of the CDA increases with the number of items accurately held in VWM, but reaches an asymptote at an individual's own working memory capacity, supporting the idea that it reflects VWM maintenance (McCollough et al., 2007). Only two studies have investigated the effects of retrospective attention on VSTM maintenance as measured by the CDA (Duarte et al., 2013; Kuo et al., 2012). Both studies found memory performance benefits for retro-cue trials were more pronounced at higher set sizes, consistent with the idea that retro-cues reduce effective memory load. The ERP results also corroborated the load-reduction hypothesis by revealing that CDA magnitude was reduced after the presentation of retro-cues particularly at the larger set sizes. We additionally found a reduction in P3b latency and amplitude associated with probe items following retro-cues, supporting the hypothesis that retro-cues may also enhance memory performance by reducing the demands on memory updating processes (Duarte et al., 2013).

While an increasing number of studies have investigated interactions between attention and VSTM, relatively little work has assessed the duration of attentional manipulations. Specifically, there have been no studies investigating whether retro-cue effects persist beyond short-term memory delays. Studies manipulating retrospective attention have typically use colored squares, unnamable shapes, or other repeating stimuli. These kinds of stimuli make it impossible to test memory beyond short-term delays. In the present study, we used images of unique, namable objects as stimuli, which allowed us to test memory at both short-term and long-term delays. We were particularly interested in assessing the duration of retro-cue effects because emerging evidence suggests that processes that affect short-term memory maintenance may also affect long-term memory (LTM). Specifically, sustained ERPs measured during short-term memory delay periods can distinguish items that are later remembered from those that are forgotten, supporting the idea that STM maintenance contributes to LTM performance (Khader et al., 2007). Although no work has investigated the lasting effects of retrospective attention, a reasonable prediction is that short-term

memory improvements afforded by retrospective attention persist in LTM performance. To this end, our first goal in the current study was to assess the effects of retro-cuing on both VSTM and LTM performance and the relationship between LTM and ERPs measured during VSTM maintenance.

A second goal of the present study was to investigate the spatial nature of memory representations and whether memory for spatial configural information would be affected by retrospective attention. Emerging evidence suggests that at least some spatial information from the original display is maintained in VSTM representations (Jiang et al., 2000; Kuo et al., 2009). ERP evidence suggests that participants search for targets in VSTM representations in the same manner in which they would search through a perceptual display. Specifically, the posterior-maximal N2pc that is thought to reflect spatial biasing of attention in extrastriate cortex during visual search (Hopf et al., 2004; Hopf et al., 2000) shows a similar latency and scalp distribution whether participants were searching for a target item in a VSTM representations or a perceptual display (Kuo et al., 2009). If spatial information is preserved in short-term memory representations, N2pc effects to the VSTM test probe in trials without a spatially informative retro-cue should be similar to those observed during target selection during visual search. If retro-cues result in discontinued maintenance of uncued “distractor” items, one might predict that the spatial configuration of the array would no longer be task-relevant, as only the cued item would require active maintenance. Consequently, the N2pc, which is observed only when distractors accompany targets in visual arrays (Luck and Hillyard, 1994), and memory for spatial location of cued items may be reduced following retro-cues relative to spatially uninformative “neutral” cues. Alternatively, it is possible that spatial retro-cues enhance memory for an item's location perhaps via a mental “refreshing” type of mechanism (Johnson et al., 2007) while at the same time reducing maintenance of the array's spatial configuration. This prediction would be consistent with results showing that retro-cueing enhances the quality or “precision” of VSTM representations (Makovski and Pertzov, 2015; Williams et al., 2013), although several studies have found no such effect (Murray et al., 2013; Souza et al., 2014). In this case, memory for spatial location of cued items may be enhanced while the N2pc may be reduced following retro-cues relative to uninformative cues.

In sum, we pursued several goals in the present study aimed at better understanding the lasting effects of attention manipulations. First, we investigated the duration of retrospective attention effects on memory by testing both short-term and long-term delays, and the relationship between ERPs associated with VSTM maintenance and LTM performance. Second, we investigated the spatial nature of VSTM representations and the influence of retrospective attention on these representations by measuring recognition memory both for items and their locations from the array and ERP correlates of spatially-biased attentional selection.

A schematic for all three of the experimental tasks is shown in **Figure 1**. For the VSTM task, we employed a novel design in which we tested participants' memory for the same concrete objects at both short-term and long-term delays. Each trial began with an arrow cue that indicated whether the participant should encode objects in either the left or right visual field. Next, an array of colored real world objects (e.g. fruit, computer) was briefly presented

in each visual field. For half of the trials, spatially informative “retro-cues” were presented during the delay period that directed the participant's attention toward the location of the to-be-probed item. Participants subsequently decided whether a centrally presented probe object matched one that had been previously presented in the array. For the LTM task, participants were shown objects that were presented as probes during the VSTM task as well as new objects and asked to decide if they recognized them and in which position they were previously presented in the VSTM task. Finally, participants performed a visual search task in which they searched for a target object in an array of objects. This allowed us to compare N2pc components associated with target selection during visual search with those associated with VSTM probes in order to better determine whether visual search operations also contribute to VSTM performance.

2. Results

2.1. Behavioral results

2.1.1. VSTM performance—Item accuracy was estimated using Pr , i.e. $p(\text{hits}) - p(\text{false alarms})$ where chance performance is zero (Snodgrass and Corwin, 1988). Item accuracy for neutral cue trials was 0.72 while accuracy for retro-cue trials was 0.86. Mean response time for correct neutral cue trials was 418.79 ms while reaction time for correct retro-cue trials was 374.34 ms. Accuracy for retro-cue trials was significantly higher [$t(1,18) = 6.108$, $p < 0.001$] and reaction times significantly faster [$t(1,18) = 8.266$, $p < 0.001$] than for neutral cue trials.

If similar processes support performance in visual search and VSTM tasks, we might predict a relationship between performance measures in these tasks. We computed correlations between the size of the retro-cue effect for both accuracy and response time (i.e. retro Pr - neutral Pr , and neutral RT - retro RT) for short-term memory with accuracy and RT measures for the visual search task. The mean level of accuracy for the visual search task was 89% and the mean response time for correct trials was 1201 ms. None of these correlations were significant [$r(18)$'s < 0.4 , p 's > 0.1]. It is perhaps worth noting that there was a trend for participants who were faster in correctly identifying the target objects in the search task to also show a larger retro-cue RT effect in the VSTM task [$r(18) = 0.4$, $p = 0.1$]. It is possible that this correlation might be more evident in a larger sample of participants. Nonetheless, this pattern is supportive of the idea that search operations may contribute to retro-cue effects in VSTM (Griffin and Nobre, 2003).

2.1.2. Long-term item recognition—Item recognition was estimated using Pr . Accuracy was 0.46 for neutral and 0.55 for retro-cued trials. Mean response time to the old/new was 733.53 ms for correctly recognized neutral cue trials and 722.90 ms for correctly recognized retro-cued trials. Accuracy was higher for retro-cued than neutral cued trials [$t(1,18) = 4.49$, $p < 0.001$] but the difference between response times was not reliable [$t(1,18) = 0.79$, $p = 0.44$].

The previous analysis was based on all items presented as probes in the VSTM task regardless of whether they were correctly or incorrectly judged as “matches.” Thus, the accuracy difference between retro-cued and neutral cued trials observed in LTM may be

driven by the greater proportion of correct “matches” for retro-cue than neutral cue trials at VSTM, rather than a persistent retro-cue effect, per se. To address this potential confound, we reanalyzed LTM item recognition only for those items that were correctly judged as “matches” during the VSTM task. Pr estimates were 0.49 for neutral and 0.56 for retro-cued trials. A paired samples t-test confirmed that accuracy was higher for retro-cued than neutral cued trials [$t(1,18) = 2.58$, $p = 0.019$]. Thus, the retro-cue effect observed at LTM is not driven solely by the greater proportion of correct “match trials” presented for retro-cue than neutral cued trials in the LTM task.

To determine whether retro-cue memory benefits differed in magnitude between VSTM and long-term memory, we conducted a Memory Phase (VSTM, LTM) X Cue (retro-cue, neutral cue) repeated measures ANOVA for z scores transformed from the Pr measures of accuracy in order to directly compare accuracy across these phases. This revealed a significant main effect of Memory Phase [$F(1,18) = 27.01$, $p < .001$], Cue [$F(1,18) = 24.75$, $p < 0.001$], and a significant interaction [$F(1,18) = 5.04$, $p = 0.04$]. These results suggest that while accuracy was greater for VSTM than LTM, and retro-cue benefits were observed at both short and long delays, these accuracy benefits were reduced at LTM.

2.1.3. Long-term location memory—We calculated two measures of location memory: exact and coarse location memory. Coarse location memory was calculated as the percentage of hit trials for which the hemifield the target was previously presented in was correctly identified. Chance performance for hemifield memory was 50%. Coarse item location accuracy was 69.02% for neutral cued trials and 68.19% for retro-cued trials. A paired samples t-test revealed no significant difference in coarse location accuracy between the two cue types [$t(1,18) = 0.34$, $p = 0.74$]. To measure exact location memory, we calculated the percentage of hit trials for which both location questions were answered correctly. There were six possible locations (three on each side) making chance performance 16%. Exact item location memory was 44.01% for neutral cued trials and 44.97% for retro-cued trials. A paired samples t-test revealed no difference in exact location accuracy between the two cue types [$t(1,18) = 0.26$, $p = 0.79$].

2.1.4. Performance differences between sessions—In order to produce sufficient numbers of trials for behavioral and ERP analysis, we averaged data over two sessions collected one week apart. In order to rule out the influence of major performance differences between sessions resulting from, for example, practice effects, we compared accuracy and response times between sessions. One participant did not return for the second session leaving 18 participants for this analysis. It was not possible to obtain stable ERPs for all participants from each separate session. We conducted Cue (retro-cue, neutral cue) $\times$ Session (first, second) ANOVAs for Pr and response times for VSTM and LTM separately. Importantly, there was a main effect of Cue for Pr and response time measures for VSTM [$F(1,17)$'s > 37.3 , p 's < 0.0001] and for Pr for LTM [$F(1,17) = 11.9$, $p = 0.003$]. There was no effect of Cue on response times in the long-term delay [$F(1,17) < 1$], similar to what was shown in the across session analysis above. There was also no main effect of Session for any measure [$F(1,17)$'s < 1]. The Cue $\times$ Session interaction was marginally significant for VSTM response times [$F(1,17) = 4.19$, $p = 0.056$] but no other measure. This interaction reflects the

fact that the retro-cue effect for response times was slightly greater for the first than second session. Collectively, these findings rule out the possibility that retro-cue effects are driven primarily by data from one session or the other. They further suggest that significant strategy differences between sessions are unlikely to contribute to our results.

2.2 ERP results

2.2.1.CDA—To capture the CDA prior to cuing, A Cue (retro, neutral) X Hemifield (contralateral, ipsilateral) X Location (frontal, central, posterior) ANOVA was conducted on mean amplitudes for the time window 275-650 ms post array onset (see Methods). The waveforms for each cluster and topographic maps for each cue type can be seen in **Figure 2**. This analysis revealed a significant main effect of Hemifield [$F(1,18) = 47.46$, $p < 0.001$], reflecting more negative-going activity contralateral to the hemifield being attended. No other effects were reliable [$F_s < 1.59$, $p_s > 0.22$]. Analysis of the 1250-1350 ms window following cue offset revealed a main effect of Cue [$F(1,18) = 5.27$, $p = 0.03$] and a main effect of Hemifield [$F(1,18) = 4.69$, $p = 0.04$], but no interactions [$F_s < 2.74$, $p_s > 0.12$] suggesting that the CDA persisted to a similar degree after the cue for both neutral and retro-cue trials.

2.2.2. Subsequent memory ERPs—In order to determine if ERPs during the delay period besides the CDA predicted long-term memory accuracy, we compared ERPs for VSTM hits that were associated with long-term memory hits with those associated with long-term memory misses, collapsed across hemifield. This analysis was performed in 11 participants with sufficient numbers of trials in these conditions. Mean amplitudes for hits at VSTM that were subsequently remembered and those that were subsequently forgotten were calculated for a window 170-300 ms after array presentation, where effects appeared most robust (see Methods). The waveforms and topographic maps can be seen in **Figure 3**. These mean amplitudes were subjected to a Memory (subsequently remembered, subsequently forgotten) X Hemisphere (left, right) X Location (central, posterior) ANOVA. Results of this analysis revealed a significant main effect of Memory [$F(1,10) = 5.26$, $p = 0.04$] but no interactions [$F_s < 0.91$, $p_s > 0.36$]. As can be seen in **Figure 3**, ERPs for subsequent LTM hits were more negative-going than for subsequent LTM misses. Effects were similar albeit less robust for longer time-windows.

2.2.3.N2pc—N2pc analyses were conducted on 13 participants with sufficient numbers of VSTM hits. As described in the Methods, N2pc ERPs were analyzed to the probe for hit trials only, as correct rejection trials were unlikely to be associated with a search through spatial memory representations. Consequently, fewer trials were available for N2pc analyses than the CDA and fewer participants had sufficient numbers of trials for analysis. Topographic maps and ERP waveforms for the N2pc are shown in **Figure 4**. To determine if topographical differences existed between N2pc effects for VSTM and visual search tasks, mean voltage differences between contralateral and ipsilateral activity were subjected to a Location (frontal: FP1/FP2, AF3/AF4, F7/F8, F3/F4, FC1/FC2, FC5/FC6; central: T7/T8, C3/4, CP1/CP2, CP5/CP6; occipital: P7/P8, P3/P4, PO3/PO4, O1/O2) X Task (neutral cue, retro-cue, visual search) repeated measures ANOVA. This ANOVA revealed no significant Location X Task interaction [$F(4,48) = 1.75$, $p = 0.17$]. Given this lack of topographical

difference, we analyzed N2pc effects for a posterior electrode cluster, where effects were more robust and consistent with previous studies (see Methods). A Task (visual search, VSTM retro-cue, VSTM neutral-cue) X Hemifield (contralateral, ipsilateral) repeated measures ANOVA revealed a marginally significant main effect of Hemifield [$F(1, 12) = 4.06, p = 0.07$] and a significant Task X Hemifield interaction [$F(1.82, 21.95) = 7.57, p = 0.004$]. Follow-up paired t-tests revealed a significant N2pc (contralateral activity more negative than ipsilateral activity) for neutral cue trials [$t(1,12) = 2.67, p = 0.02$] and visual search trials [$t(1,12) = 2.49, p = 0.03$]. As can be seen in **Figure 4**, retro-cue trials showed the opposite pattern of activity with ipsilateral waveforms being more negative-going than contralateral waveforms [$t(1,12) = 2.33, p = 0.04$].

Hemifield differences continued to persist 470-900 ms after the onset of the probe most noticeably for both retro-cue and neutral-cue trials (see **Figure 4**). Mean amplitudes measured 470-900 ms after the test probe onset were subjected to a Task (retro, neutral, visual search) X Hemifield (contralateral, ipsilateral) repeated measures ANOVA. This analysis revealed a significant Task X Hemifield interaction [$F(2, 24) = 14.23, p < 0.001$]. Follow-up t-tests revealed greater negativity for contralateral than ipsilateral waveforms for neutral trials [$t(1,12) = 2.26, p = 0.04$], with the opposite pattern for retro-cue trials [$t(1,12) = 5.69, p < .001$]. There were no significant differences between contralateral and ipsilateral activity in the visual search task [$t(1,12) = 1.31, p = 0.21$].

3. Discussion

In the present study we examined the interactions between retrospective attention, VSTM, and LTM. To the best of our knowledge, ours is the first study to investigate the effects of retrospective attention at both short and long-term memory delays. Specifically, we: 1) measured the effect of retrospective attention on item memory performance at short and long delays for the same items, and on memory accuracy for spatial location; 2) assessed whether ERPs reflecting VSTM maintenance predicted LTM performance; and 3) measured the effect of retrospective attention on ERPs reflecting spatial attention. There were three major findings. First, we showed that spatial retro-cues improved memory accuracy at both short and long term delays but did not influence memory for the spatial location of objects. Second, ERPs observed during VSTM maintenance predicted subsequent LTM performance. Third, retrospective attention reduced N2pc ERPs associated with spatially-biased selective attention. These results and their implications are discussed below.

3.1. Retro-cues enhance item but not location memory accuracy in VSTM and LTM

We found the typical retro-cue benefit in VSTM whereby item accuracy and reaction time improved following retro-cue trials compared to neutral cue trials (e.g. Griffin and Nobre, 2003; Landman et al., 2003; Matsukura et al., 2007). The novel behavioral finding in our study was that the item accuracy benefit afforded by the retro-cue was also present in long-term memory performance. We do note, however, that the retro-cuing benefit was greater at the short than the long-term memory delay. This may indicate that whatever protective features the retro-cue offers at VSTM including reducing effective memory load (Duarte et al., 2013; Kuo et al., 2012; Lepsien and Nobre, 2007), refreshing the representation of the

cued item (Murray et al., 2013), or some combination thereof, it does not offer complete protection from memory decay. It would be interesting to assess how VSTM operations like retrospective attention directly affect LTM processes, however we did not probe items at LTM that were not also probed at VSTM. That is, there were no items that were cued at VSTM and only tested at LTM, which could more clearly determine the impact of retrospective attention on LTM formation. Nonetheless, these results suggest that attentional processes can impact more than short-term retention.

Our results further suggest that retro-cues selectively enhanced item memory but had no effect on location memory, either the hemifield of presentation or the specific vertical location within the hemifield. We had reasoned that if retro-cueing reduces active maintenance of spatial configural information of the array, as only the cued item requires continued maintenance, memory for location might be reduced. Alternatively, if retro-cues increase the precision of VSTM representations (Makovski and Pertzov, 2015; Williams et al., 2013), then memory for both cued items and their locations might be enhanced. It should be noted that cueing effects on memory precision have been identified for an item's spatial orientation (Makovski and Pertzov, 2015) and its color (Williams et al., 2013), which are arguably more integral to the item's identity than is spatial location. Future studies will be necessary to determine whether retrospective attention differentially affects precision for different kinds of features of VSTM representations. We believe our findings are most consistent with the idea that retro-cues enhance VSTM and LTM for item representations, and perhaps certain integral item features, but have no effect on memory for the item's location. Interestingly, our ERP results suggest that retro-cues do interfere with spatially-biased target selection mechanisms in VSTM (discussed below).

3.2.ERPs reflecting VSTM maintenance

This is the first study to show that the CDA is sensitive to complex real-world objects with most previous studies using relatively simple stimuli like colored squares (for example, Anderson et al., 2011; Duarte et al., 2013; Ikkai et al., 2010; Kuo et al., 2012). The present study was not designed to assess the resolution of the representations being maintained. Some previous work has shown that while CDA amplitude increases as the number of simple objects, like colored squares, increases in the memory array, it levels off or decreases as the number of complex objects increases (Dell'acqua et al., 2009; Gao et al., 2009). The authors concluded that for complex objects, the CDA might reflect information load in VSTM that is determined by both number and resolution of the objects. It has further been shown that the resolution of VSTM representations increases with the duration of the memory array (Gao et al., 2013). For short processing times, like that used in the current study and in most similar studies, the CDA reflects maintenance of coarse representations. Additional research in which array presentation time, set size, and stimulus complexity are manipulated would be necessary to better determine the nature of the VSTM representations of the real world highly complex object stimuli used in the current study. We tentatively suggest, however, that CDA reflects maintenance of low-level or coarse representations of the complex objects that are sufficiently vivid to support accurate memory decisions.

We expected the CDA to attenuate following retro-cues compared to neutral cues consistent with the hypothesis that retro-cues filter irrelevant items from active maintenance (Duarte et al., 2013; Kuo et al., 2012; Matsukura et al., 2007). However, we observed no significant differences in CDA magnitude between these trial types. If the CDA reflects the number of items being actively maintained in VSTM (reviewed in Luria et al., 2016) and retro-cues reduce this number in the present experiment from two to one, one might predict a reduction in CDA magnitude following the retro-cue. Previous studies have often investigated the CDA for stimuli that may lack preexisting semantic representations, unlike the stimuli used in the current study. One possible explanation for the lack of attenuation of the CDA following the retro-cue is that the objects were rapidly converted into a semantic code such that maintenance in VSTM was not required. Of course, it was necessary to use such stimuli so that we could measure memory at both short and long delays. Whether or not these complex objects, presented for only 200 ms could be consistently converted into a semantic code circumventing the need for VSTM maintenance is unclear. Some previous evidence has shown that CDA magnitude is reduced when participants maintain words compared to non-words in VSTM (Predovan et al., 2009). These authors reasoned that verbal chunking mechanisms might have acted to reduce the effective load in VSTM. A similar mechanism in which long-term memory representations interact with early visual representations in VSTM may contribute to the current findings.

An alternative explanation for the lack of CDA reduction is related to the potentially limited memory capacity for these complex objects. Some previous behavioral studies suggest that memory capacity is greater for simple stimuli like colored squares than for complex stimuli (Alvarez and Cavanagh, 2004; Eng et al., 2005; Olsson and Poom, 2005). Memory capacity can be further limited by brief presentation rates (see Eng et al., 2005 where presentation rates varied from .5 seconds to 3 seconds). The stimuli used here were small, visually complex items, presented very briefly. Under these conditions, capacity is likely severely limited and the difference between maintaining two and one complex item in VSTM may be minimal, at least as measured by the CDA. Further studies implementing masking procedures to reduce semantic rehearsal during STM delays or studies directly assessing memory capacity for concrete objects by manipulating set size may be necessary to determine which of these accounts may be correct.

An interesting difference that emerged between the current findings and previous studies was that the CDA, which is usually localized to posterior locations, had a fairly widespread distribution here. One possible explanation for this pattern of results is that the use of namable objects enhanced attempts to retrieve or elaborate upon semantic representations of these objects. Although it is always difficult to determine the neural regions underlying ERPs, a wealth of neuroimaging evidence suggests that the inferior frontal and lateral temporal cortices are involved in semantic processing (Gold and Buckner, 2002; Poldrack et al., 1999; Roskies et al., 2001). While we cannot rule out this possibility, it is worth noting that previous findings showed a localized posterior maximal CDA for words that had a similar topography to that for non-words (Predovan et al., 2009). Thus, it seems unlikely that semantic processing alone can account for the relatively widespread CDA in our study. Future EEG and fMRI studies manipulating the lexical accessibility of stimuli will be needed to better understand the regions supporting maintenance in VSTM.

In addition to the CDA, we also observed ERPs over the delay period that predicted long-term performance. Specifically, ERPs, collapsed across visual field and cue type, were more negative going for subsequent hit than for miss (i.e. forgotten) trials. It should be noted that these ERPs were assessed for a subset of the participants ($n = 11$) who possessed sufficient numbers of trials for this analysis. One previous study has shown that ERPs measured during the delay period and sustained over 1-2.5 seconds post-array onset were modulated by long-term memory performance for abstract line drawings of meaningless objects (Khader et al., 2007). A similar effect was observed over a longer period for strings of letters. Topographies of these slow-wave ERPs were modulated by stimulus type such that strings of letters elicited activity at frontal electrodes and line drawings elicited activity at occipital electrodes. Based on these topographical and temporal distinctions, these researchers concluded that long-term-memory formation is dependent on short-term memory maintenance in stimulus-specific brain areas. Specifically, they suggest that verbal rehearsal supported encoding of letter strings while visual imagery supported encoding for abstract objects. Given the posterior distribution of the subsequent memory ERPs in the current study, we tentatively conclude that maintenance of object-specific perceptual rather than conceptual representations supports subsequent long-term memory performance. Although the ERPs in the current study appeared sustained through the delay period, results were most robust for a relatively small time window (170-300 ms). Thus, we cannot definitively conclude that the present subsequent memory ERPs are the same slow-wave ERPs observed by Khader and colleagues. Future studies including a larger group of participants, a longer maintenance period, and various kinds of stimuli, would be necessary to evaluate the mechanisms that support the subsequent memory effects observed here.

3.3.Retro-cues interfere with spatially-biased target selection

The N2pc for neutral trials exhibited the same time course and topographical distribution to that observed in a visual search task using the same concrete object stimuli. These results suggest that participants search through VSTM representations in the same manner as they search for targets in a physically present display in a visual search task (Kuo et al., 2009). We reasoned that by reducing maintenance demands to one item representation, spatial configural information of the array would become irrelevant and ERPs reflective of spatially-biased target selection, namely the N2pc, would be reduced following retro-cueing. A non-mutually exclusive possibility is that the N2pc would be reduced following retro-cueing as demands on focused attention during probe selection were eased because the number of distracting objects was reduced (Luck and Hillyard, 1994). Consistent with these predictions, the N2pc to the VSTM probe was reduced for retro-cue relative to neutral cue trials. Considering the N2pc results alone one might conclude that memory for spatial information would be reduced. However, the behavioral data suggest that retro-cues had no effect on spatial location memory for cued items. We believe that the most parsimonious explanation for these results is that spatial retro-cues, and perhaps other kinds of retro-cues as well, disrupt normal maintenance of the relative positions of target and distractors from the array without attenuating memory for the target item's absolute position. Further study in which memory for relative positions of array items would be necessary to test this hypothesis.

A final interesting finding was the sustained difference between contralateral and ipsilateral ERPs following the N2pc for both neutral and retro-cue trials. Specifically, for neutral cue trials contralateral ERPs were more negative going than ipsilateral ERPs as for the N2pc with the reversed pattern for retro-cue trials over posterior electrode locations. Given the timecourse, topography, and pattern of this activity, it is likely that it reflects another post-probe CDA component. The CDA, also known as the sustained posterior contralateral negativity (SPCN), is often observed after the N2pc in visual search tasks that presumably engage VSTM as needed to make decisions about target items (e.g. Eimer, 1996; Jolicoeur et al., 2008; Jolicoeur et al., 2006). We speculate that these hemifield differences may indicate the updating/refreshing of location information in VSTM in anticipation of the future location probe at long-term memory. The lack of sustained ERP differences for the visual search task, in which there were no explicit maintenance demands, is consistent with this hypothesis. The reversed polarity of this effect for retro-cue trials may indicate that the manner in which the retro-cue isolates the to-be probed item changes the way location information is updated and maintained.

4. Conclusions

With a novel design, we were able to show that retrospective attention affects not only short-term memory but also long-term memory performance for real world objects. CDA amplitude was unaffected by retro-cues, which would be expected if retro-cues reduced effective memory load for the objects as has been shown for simple shapes. It could be that the availability of semantic representations reduced demands on VSTM maintenance operations or alternatively, that memory capacity for these complex objects was lower than what would be expected for simpler stimuli. Future studies comparing performance and CDA components for different kinds of stimuli will be needed to differentiate between these possibilities. An additional interesting avenue for future research would be to investigate whether individuals with memory impairments like older adults also receive long-term memory benefits from retrospective attentional cues. Our N2pc results also shed light on the nature of visual short-term memory representations. These representations may contain information about spatial location but they are also highly flexible. That is, spatial information can be reconstructed as needed in order to meet the demands of task goals and expectations.

5. Method

5.1. Participants

30 young adults between the ages of 18 and 24 were recruited from the Georgia Institute of Technology and the Atlanta community to participate in the study. All participants gave written informed consent as required by the Institutional Review Board. Of the 30 participants, 11 were excluded because they possessed too few trials to obtain stable ERPs for several of our events of interest and had excessive EEG artifacts (e.g. alpha) that exacerbated the issues associated with low numbers of trials. For example, some participants had pronounced resting alpha activity in addition to low memory accuracy such that there was insufficient power to detect a CDA, which is computed only for correct trials. Of the

remaining 19 participants, 10 were male and 9 were female. All participants were right handed, native English speakers with normal or corrected to normal vision (including the absence of colorblindness). No participants reported psychiatric or neurological disorders, vascular disease, or using psychoactive drugs. Participants were compensated with one extra credit per hour of participation for a psychology class or \$10.00 per hour. A \$20.00 bonus was given to all participants who completed both experimental sessions.

5.2. Neuropsychological Assessment

A 25-minute neuropsychological assessment battery was administered between the short-term memory and long-term memory tasks. The main purpose of this assessment was for future comparisons with older adult participants to be discussed in a forthcoming manuscript. The battery included measures of processing speed, short-term memory, executive function, semantic memory, and long-term memory. The following tests were administered: forward and backward digit span and verbal list learning from the Memory Assessment Scale battery (Williams, 1991), Trail Making tests A and B (Reitan and Wolfson, 1985), the Controlled Oral Word Association test (“FAS”) (Benton, 1994), Symmetry Span (Unsworth et al., 2005), Running Letter Span (Unsworth et al., 2005), and Digit/Symbol Substitution (Wechsler, 1997).

5.3. Materials

762 color images of real world objects were used as stimuli. These objects were collected from Hemera Technologies Photo-Objects DVDs, Bank of Standardized Stimuli (Brodeur et al., 2010), and Massive Memory (Brady et al., 2008) databases, and Google Images. All of the images depict singular, unique objects on a white background. Each object subtended 1.39 degrees of visual angle, similar to dimensions implemented in previous ERP studies (Kiss et al., 2008; Kuo et al., 2009; Kuo et al., 2012). Participants were seated 2 feet from the monitor.

5.4. Design

Prior to beginning each session of the experiment, participants engaged in an extensive practice of the VSTM and LTM tasks. To help acclimate the participant with the procedure and response options, the presentation speed of the VSTM task began slowly and increased to the experimental pace as the practice continued. For the first 5 trials, the pre-cue, memory array, and retro-cue were presented for 4 seconds each. For the next 10 trials this pace was doubled, then doubled again for the next 10 trials, and then finally the last 22 trials were presented at the experimental pace. The VSTM practice took approximately 20 minutes to complete. Participants practiced 10 trials of the LTM task at experimental pace, which took approximately 5 minutes to complete. Participants repeated the LTM practice prior to completing the long-term memory experimental task. Finally, participants also completed 16 practice trials of the visual search task immediately before beginning the second session.

The experiment was divided into two sessions separated by a two-week delay. Each session contained 88 short-term memory trials and 132 long-term memory trials for a total of 176 short-term memory trials and 264 long-term memory trials across the experiment. Additionally, at the end of session 2, participants completed a visual search task consisting

of 176 trials. Objects in the unreferenced hemi-field of the short-term task in session one were reused in the second session as objects presented in the cued hemi-field. This was necessary in order to obtain a sufficient number of trials for both behavioral and ERP analysis. The two-week delay between sessions was implemented in order to reduce the likelihood that objects presented in the non-cued visual field would be remembered during the second session. In order to ensure that participants did not remember previously non-cued items, we conducted a separate behavioral study in 7 subjects in which we measured explicit recognition for cued, non-cued objects, and new objects in an item recognition task similar to that used in the present experiment. We found no evidence that items from the non-cued hemifield were remembered after the delay (average hit-false alarm = .04). Consequently, behavioral and EEG data were combined across testing sessions for the short-term memory task and for the long-term memory task.

5.4.1. Visual short-term memory task—The paradigm is shown in **Figure 1**. The timing and duration of each trial were based on similar prior research (Brisson and Jolicoeur, 2007; Kuo et al., 2012). Each trial began with a precue that indicated the side of the screen to which participants should direct their attention. Half of the trials were presented with a left hemifield cue and half with a right hemifield cue. Precues were presented in a pseudorandom order such that no more than 4 trials with the same precue were presented consecutively. The memory array consisted of 6 possible object positions with two objects presented in each side of the array. There was also a “place-holder” object on both sides of the array consisting of a scrambled, unidentifiable object in order to keep perceptual load balanced across the hemifields (this is important for the analysis of lateralized ERP components). The scrambled object occurred in each location of the array equally often across the trials of the experiment and the order of trials was randomized across each session of the experiment. The memory array had a radius subtending 3.21 degrees of visual angle. The retro-cue arrow pointed to the location of the to-be probed object and was always valid. The neutral cue appeared as an asterisk with three intersecting lines with no arrowhead. The neutral and retro-cues, like the objects, were constrained to 1.39 degrees of visual angle. Half of the trials contained a retro-cue and the other half contained a neutral cue. Half of the trials were match trials, that is, trials in which the probe was presented in the cued hemifield, and the other half were non-match trials in which the probe was not presented in either hemifield. Participants responded with the index and middle fingers of their right hand pressing one button for match and another for non-match. Trials were presented in a pseudorandom order such that no more than four trials of one type (match, non-match, neutral, retro-cue) were presented consecutively. To avoid participant fatigue, the task was divided into 8 mini blocks of 11 trials with a 10 second break between each block.

5.4.2. Long-term memory task—After completing the neuropsychological test battery (described above), the long-term memory task was administered (see **Figure 1**). The probes from the VSTM task were presented again (“old” items) along with half as many new objects. Old and new trials were presented in a pseudorandom order such that no more than four trials of the same type were presented consecutively. Participants were asked three questions about each presented object during the long-term memory task. First, participants were asked whether the presented item was an “old” item or a new item. The second

question asked whether the object was presented on the left side of the visual array or the right side of the array in the VSTM task. The third question asked participants to identify which of the three vertical positions the object occupied in the array (top, middle, or bottom). The second and third questions were presented to the participant regardless of their response to the old/new question in order to keep motor responses consistent across trials. Participants responded with the index, middle, and ring fingers of their right hand. We assessed location memory during the long-term memory task only and not during the VSTM task because we reasoned that participants would only need to remember the orientation of the retro-cue and not the location of the array item per se in order to make location judgments. It seemed less likely that participants would remember these retro-cues after a long delay. Behavioral data (discussed below) support this prediction. The long-term memory component lasted approximately 30 minutes. The task was divided into 4 blocks of 33 trials with a 30 second break between each block. Some previous findings suggest that LTM traces may contain spatial information associated with VSTM representations (Gratton et al., 1997). Although we recorded EEG during the LTM test, the low number of trials for contralateral and ipsilateral match trials did not allow for stable ERPs to be estimated for this analysis.

5.4.3. Visual search task—At the end of session 2, participants completed the visual search task, as shown in **Figure 1**. Each trial began with a centrally presented target object followed by an arrow pointing left or right indicating which side of the upcoming array the participant should search for the target. The arrow was always valid. No uninformative (i.e. non-directional) cues were used. The search array was presented with the same visual constraints as the array in the VSTM task (a radius subtending 3.21 degrees of visual angle and objects constrained to 1.39 degrees of visual angle). The same objects used in the VSTM and long-term memory tasks were used as stimuli. The timing of the visual search task was identical to that of the VSTM task such that the delay between target and search array was identical to the delay between the array and probe in the short-term memory task. This identical timing was critical for the comparison of N2pc components between the VSTM and visual search tasks. Participants were asked to determine whether or not the target object was found in the search array, pressing one button for match/target present and one for non-match/target absent using the first two fingers of their right hand. There were 88 target present trials and 88 target absent trials for a total of 176 trials. The trials were divided into 11 mini blocks of 16 trials.

5.5. EEG Acquisition

Scalp recorded EEG data was collected from 32 silver/silver chloride electrodes using an ActiveTwo amplifier system (Biosemi, Amsterdam, Netherlands). Electrodes were placed on the right and left mastoid for use as an off-line reference. To record vertical electrooculogram (VEOG), two electrodes were placed above and below the left eye. To record horizontal electrooculogram (HEOG), two electrodes were placed on the outer canthi of both the left and right eyes. EEG data was recorded with 24 bit resolution and a sampling rate of 512 Hz. Electrodes placed on the mastoids were used as off-line references and data was digitally bandpass filtered between 40Hz and 0.01 Hz. Vertical and horizontal eye movements were removed via a method based on independent component analysis (ICA) by using the EEG

lab toolbox for Matlab (Delorme and Makeig, 2004). Epochs containing uncorrected artifacts (± 100 microvolts) were removed. Extensive comparative analyses confirmed that correction of eye movement artifacts via ICA and rejection of all trials containing eye movement artifacts produced virtually identical patterns of N2pc and CDA ERP results, as has been shown previously (Drisdelle et al., 2014). Consequently, in order to increase the number of available trials and increase power, we applied ICA corrections. Finally, all trials with incorrect behavioral responses during the VSTM task or with reaction times less than 200ms were excluded.

5.6.ERP Analysis

5.6.1.ERPs reflecting VSTM maintenance—To monitor VSTM maintenance, we measured two ERPs of interest: the CDA and sustained activity collapsed across hemifield. EEG data for all correct trials (hits and correct rejections) was segmented into epochs starting 200 ms pre-array onset and lasting until 1800 ms post-array onset.

CDA amplitude was measured as the difference between contralateral and ipsilateral target activity (i.e. collapsed across left and right visual fields). Similar to previous research mean amplitudes of the CDA were computed for two time windows: 275-650 ms after memory array onset and 1250-1350 ms after memory array onset in order to capture the CDA before and after presentation of the cue (Kuo et al., 2012; Duarte et al., 2013). Mean amplitudes were averaged across hemisphere and electrodes where the CDA appeared most robust as a method for increasing sensitivity to detect CDA modulations (e.g. Jost et al., 2011; McCollough et al., 2007; Vogel and Machizawa, 2004). Visual inspection suggested that the differences between contralateral and ipsilateral ERPs were evident at anterior as well as posterior electrodes, as can be seen in **Figure 2**. In order to capture all significant effects during the delay period, we included frontal electrodes (FC5/FC6 and F3/F4), central electrodes (CP5/CP6 and T7/T8), and posterior electrodes (PO3/PO4 and P7/P8). That is, two electrode pairs were averaged at each of the three locations. Mean amplitudes of delay period activity were subjected to Hemifield (contralateral, ipsilateral) $\times$ Cue (retro-cue, neutral cue) $\times$ Location (frontal, central, posterior) repeated measures ANOVAs for each separate time window.

We also measured ERPs, collapsed across contralateral and ipsilateral hemifields, which previous research has shown to be related to short-term memory maintenance and modulated by subsequent long-term memory performance (Khader et al., 2007). Visual inspection suggested that differences between long-term memory hits and misses were most evident in the early part of the VSTM delay period at central (C3 and C4) and posterior (PO3 and PO4) electrodes. Analyses were conducted for a 170-300 ms window. Analyses performed for a longer window and additional electrodes revealed numerically similar but less robust effects. Activity associated with subsequent long-term memory hits and misses was compared using a Memory (subsequently remembered, subsequently forgotten) $\times$ Hemisphere (left, right) $\times$ Location (central, posterior) ANOVA to determine if there were differences in activity depending on subsequent long-term memory performance.

5.6.2.ERPs reflecting spatial attention: N2pc—N2pc amplitude was measured as the difference between contralateral and ipsilateral target activity (i.e. collapsed across left and right visual fields). Only correct responses to target-present trials were assessed for the N2pc analysis (i.e. hits), consistent with previous research. In the visual search task, EEG data was segmented into epochs starting 200 ms pre-array onset and lasting until 900 ms post-array onset and N2pc mean amplitude was computed 240-300 ms after array presentation at an electrode-pair cluster containing PO3/PO4 and O1/O2, where effects were most evident and consistent with prior research (Kuo et al., 2009). In the VSTM task, EEG data was segmented into epochs starting 200 ms pre-probe onset and lasting until 900 ms post-probe onset and N2pc mean amplitude was computed 240-300 ms after probe presentation at the same electrode-pair cluster. In order to compare N2pc activity between visual search and VSTM tasks, mean amplitudes were subjected to a Task (retro-cue, neutral cue, visual search) X Hemifield (contralateral, ipsilateral) repeated measures ANOVA.

For all ERP analyses, significant interactions were followed up with subsidiary analyses to determine the source of the effects. Huynh-Feldt corrections are reflected in the error term when appropriate.

Acknowledgements

This research was supported by National Institutes of Health Grant T32 AG00175. We thank all of our research participants.

References

- Alvarez GA, Cavanagh P. The capacity of visual short-term memory is set both by visual information load and by number of objects. *Psychol Sci.* 2004; 15:106–111. [PubMed: 14738517]
- Anderson DE, Vogel EK, Awh E. Precision in visual working memory reaches a stable plateau when individual item limits are exceeded. *The Journal of neuroscience : the official journal of the Society for Neuroscience.* 2011; 31:1128–1138. [PubMed: 21248137]
- Benton AL, Hamsher K, Sivan AB. *Multilingual Aphasia Examination.* 1994
- Brady TF, Konkle T, Alvarez GA, Oliva A. Visual long-term memory has a massive storage capacity for object details. *Proceedings of the National Academy of Sciences.* 2008; 105:14325–14329.
- Brisson B, Jolicoeur P. The N2pc component and stimulus duration. *Neuroreport.* 2007; 18:1163–1166. [PubMed: 17589319]
- Brodeur MB, Dionne-Dostie E, Montreuil T, Lepage M. The bank of standardized stimuli (BOSS), a new set of 480 normative photos of objects to be used as visual stimuli in cognitive research. *PloS one.* 2010; 5:e10773. [PubMed: 20532245]
- Dell'acqua R, Jolicoeur P, Luria R, Pluchino P. Reevaluating encoding-capacity limitations as a cause of the attentional blink. *Journal of Experimental Psychology: Human Perception and Performance.* 2009; 35:338–351. [PubMed: 19331492]
- Delorme A, Makeig S. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics. *Journal of Neuroscience Methods.* 2004; 134:9–21. [PubMed: 15102499]
- Drisdelle, BL.; Aubin, S.; Jolicoeur, P. Eye movements in attention and memory experiments involving N2pc and SCPN: Not as problematic as one might suppose?. *Society for Psychophysiological Research; Atlanta, GA.* 2014.
- Duarte A, Hearons P, Jiang Y, Delvin MC, Newsome RN, Verhaeghen P. Retrospective attention enhances visual working memory in the young but not the old: an ERP study. *Psychophysiology.* 2013; 50:465–476. [PubMed: 23445536]
- Eimer M. The N2pc component as an indicator of attentional selectivity. *Electroencephalography and Clinical Neurophysiology.* 1996; 99:225–234. [PubMed: 8862112]

- Eng HY, Chen D, Jiang Y. Visual working memory for simple and complex visual stimuli. *Psychon Bull Rev.* 2005; 12:1127–1133. [PubMed: 16615339]
- Gao Z, Ding X, Yang T, Liang J, Shui R. Coarse-to-fine construction for high-resolution representation in visual working memory. *PLoS One.* 2013; 8:e57913. [PubMed: 23469103]
- Gao Z, Li J, Liang J, Chen H, Yin J, Shen M. Storing fine detailed information in visual working memory--evidence from event-related potentials. *J Vis.* 2009; 9:17. [PubMed: 19761332]
- Gold BT, Buckner RL. Common prefrontal regions coactivate with dissociable posterior regions during controlled semantic and phonological tasks. *Neuron.* 2002; 35:803–812. [PubMed: 12194878]
- Gratton G, Corbalis PM, Jain S. Hemispheric organization of visual memories. *Journal of Cognitive Neuroscience.* 1997; 9:92–104. [PubMed: 23968182]
- Griffin IC, Nobre AC. Orienting attention to locations in internal representations. *Journal of Cognitive Neuroscience.* 2003; 15:1176–1194. [PubMed: 14709235]
- Hopf JM, Boelmans K, Schoenfeld MA, Luck SJ, Heinze HJ. Attention to features precedes attention to locations in visual search: evidence from electromagnetic brain responses in humans. *Journal of Neuroscience.* 2004; 24:1822–1832. [PubMed: 14985422]
- Hopf JM, Luck SJ, Girelli M, Hagner T, Mangun GR, Scheich H, Heinze HJ. Neural sources of focused attention in visual search. *Cerebral Cortex.* 2000; 10:1233–1241. [PubMed: 11073872]
- Ikkai A, McCollough AW, Vogel EK. Contralateral delay activity provides a neural measure of the number of representations in visual working memory. *Journal of Neurophysiology.* 2010; 103:1963–1968. [PubMed: 20147415]
- Jiang Y, Olson IR, Chun MM. Organization of visual short-term memory. *Journal of Experimental Psychology. Learning, Memory, and Cognition.* 2000; 26:683–702.
- Johnson MR, Mitchell KJ, Raye CL, D'Esposito M, Johnson MK. A brief thought can modulate activity in extrastriate visual areas: Top-down effects of refreshing just-seen visual stimuli. *Neuroimage.* 2007; 37:290–299. [PubMed: 17574442]
- Jolicoeur P, Brisson B, Robitaille N. Dissociation of the N2pc and sustained posterior contralateral negativity in a choice response task. *Brain Research.* 2008; 1215:160–172. [PubMed: 18482718]
- Jolicoeur P, Sessa P, Dell'Acqua R, Robitaille N. On the control of visual spatial attention: evidence from human electrophysiology. *Psychological Research.* 2006; 70:414–424. [PubMed: 16184394]
- Jost K, Bryck RL, Vogel EK, Mayr U. Are old adults just like low working memory young adults? Filtering efficiency and age differences in visual working memory. *Cerebral Cortex.* 2011; 21:1147–1154. [PubMed: 20884722]
- Khader P, Ranganath C, Seemüller A, Rösler F. Working memory maintenance contributes to long-term memory formation: Evidence from slow-event-related brain potentials. *Cognitive, Affective, & Behavioral Neuroscience.* 2007; 7:212–224.
- Kiss M, Van Velzen J, Eimer M. The N2pc component and its links to attention shifts and spatially selective visual processing. *Psychophysiology.* 2008; 45:240–249. [PubMed: 17971061]
- Kuo BC, Rao A, Lepsien J, Nobre AC. Searching for targets within the spatial layout of visual short-term memory. *Journal of Neuroscience.* 2009; 29:8032–8038. [PubMed: 19553443]
- Kuo BC, Stokes MG, Nobre AC. Attention modulates maintenance of representations in visual short-term memory. *Journal of Cognitive Neuroscience.* 2012; 24:51–60. [PubMed: 21736457]
- Landman R, Spekreijse H, Lamme VA. Large capacity storage of integrated objects before change blindness. *Vision Research.* 2003; 43:149–164. [PubMed: 12536137]
- Lepsien J, Nobre AC. Attentional modulation of object representations in working memory. *Cerebral Cortex.* 2007; 17:2072–2083. [PubMed: 17099066]
- Luck SJ, Hillyard SA. Spatial filtering during visual search: evidence from human electrophysiology. *Journal of Experimental Psychology: Human Perception and Performance.* 1994; 20:1000–1014. [PubMed: 7964526]
- Luria R, Balaban H, Awh E, Vogel EK. The contralateral delay activity as a neural measure of visual working memory. *Neuroscience and Biobehavioral Reviews.* 2016; 62:100–108. [PubMed: 26802451]
- Makovski T, Jiang YV. Distributing versus focusing attention in visual short-term memory. *Psychon Bull Rev.* 2007; 14:1072–1078. [PubMed: 18229477]

- Makovski T, Pertzov Y. Attention and memory protection: Interactions between retrospective attention cueing and interference. *Q J Exp Psychol (Hove)*. 2015;1–21.
- Makovski T, Sussman R, Jiang YV. Orienting attention in visual working memory reduces interference from memory probes. *Journal of Experimental Psychology. Learning, Memory, and Cognition*. 2008; 34:369–380.
- Matsukura M, Luck SJ, Vecera SP. Attention effects during visual short-term memory maintenance: protection or prioritization? *Perception and Psychophysics*. 2007; 69:1422–1434. [PubMed: 18078232]
- McCollough AW, Machizawa MG, Vogel EK. Electrophysiological measures of maintaining representations in visual working memory. *Cortex; a journal devoted to the study of the nervous system and behavior*. 2007; 43:77–94.
- Murray AM, Nobre AC, Clark IA, Cravo AM, Stokes MG. Attention restores discrete items to visual short-term memory. *Psychol Sci*. 2013; 24:550–556. [PubMed: 23436786]
- Olsson H, Poom L. Visual memory needs categories. *Proceedings of the National Academy of Sciences of the United States of America*. 2005; 102:8776–8780. [PubMed: 15937119]
- Poldrack RA, Wagner AD, Prull MW, Desmond JE, Glover GH, Gabrieli JD. Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex. *Neuroimage*. 1999; 10:15–35. [PubMed: 10385578]
- Predovan D, Prime D, Arguin M, Gosselin F, Dell'acqua R, Jolicoeur P. On the representation of words and nonwords in visual short-term memory: evidence from human electrophysiology. *Psychophysiology*. 2009; 46:191–199. [PubMed: 19055498]
- Reitan, R.; Wolfson, D. *The Halstead-Reitan Neuropsychological Test Battery: Therapy and clinical assessment*. AZ Neuropsychological Press; Tucson: 1985.
- Roskies AL, Fiez JA, Balota DA, Raichle ME, Petersen SE. Task-dependent modulation of regions in the left inferior frontal cortex during semantic processing. *Journal of Cognitive Neuroscience*. 2001; 13:829–843. [PubMed: 11564326]
- Snodgrass J, Corwin J. Pragmatics of measuring recognition memory: applications to dementia and amnesia. *Journal of Experimental Psychology*. 1988; 116:34–50. [PubMed: 2966230]
- Souza AS, Rerko L, Lin HY, Oberauer K. Focused attention improves working memory: implications for flexible-resource and discrete-capacity models. *Atten Percept Psychophys*. 2014; 76:2080–2102. [PubMed: 24874258]
- Unsworth N, Heitz RP, Schrock JC, Engle RW. An automated version of the operation span task. *Behavior Research Methods*. 2005; 37:498–505. [PubMed: 16405146]
- Vogel EK, Machizawa MG. Neural activity predicts individual differences in visual working memory capacity. *Nature*. 2004; 428:748–751. [PubMed: 15085132]
- Wechsler, D. *Wechsler memory scale*. Psychological corporation; San Antonio: 1997.
- Williams J. *Memory assessment scales professional manual*. 1991
- Williams M, Hong SW, Kang MS, Carlisle NB, Woodman GF. The benefit of forgetting. *Psychon Bull Rev*. 2013; 20:348–355. [PubMed: 23208769]

Highlights

- The duration of retrospective attention effects was investigated.
- Retro-cuing improved both VSTM and LTM memory accuracy.
- Slow-wave ERPs observed during VSTM predicted subsequent LTM performance.
- Retrospective attention can alter the structure of memory representations.

Figure 1.

Schematic of the experimental design showing example stimuli and task requirements. The short-term memory schematic depicts a retro-cue trial, indicating that the item in the first position on the right side of the array will be probed (the acorn). The acorn is presented again as a probe during the long-term memory task in which participants are asked if the item was present during the short-term memory task and where the object was located in the array (the correct answers here would be responding '2' for the right side of the array followed by '1' to indicate the uppermost position). The visual search schematic depicts a trial where the acorn is the target item and only the right side of the array should be searched.

Figure 2.

CDA effects during VSTM delay period. ERPs are shown for neutral and retro-cue trials, time-locked to the onset of the memory array, over contralateral and ipsilateral scalp sites averaged across 3 electrode location clusters: frontal, central, posterior. The greater negative magnitude for contralateral than ipsilateral targets represents the CDA. Black rectangles indicate the time windows for analysis. Dotted vertical lines indicate the cue presentation onset. Only one side of the scalp is shown as the CDA represents activity averaged across hemispheres. Small circles represent electrode locations as viewed from above. The circled locations indicate the electrodes chosen for CDA analysis.

Figure 3.

VSTM delay period ERPs predictive of subsequent long-term memory. Delay period ERPs collapsed across cue type and hemifield are shown for representative electrodes. Gray rectangles indicate the time windows for analysis. Small circles represent electrode locations as viewed from above. The circled locations indicate the electrodes chosen for analysis.

Figure 4.

N2pc effects for VSTM and visual search tasks. ERPs are shown for neutral and retro-cue trials, time-locked to the onset of the memory probe, and for visual search trials, time-locked to the onset of the search array, over contralateral and ipsilateral scalp sites for an averaged electrode cluster. The greater negative magnitude for contralateral than ipsilateral targets represents the N2pc. Black rectangles indicate the time windows for analysis. Only one side of the scalp is shown as the N2pc represents activity averaged across hemispheres. Small circles represent electrode locations as viewed from above. The circled locations indicate the electrodes chosen for analysis. Contralateral minus ipsilateral voltage difference waves are also plotted. Black rectangles indicate the time window for analysis.