THE EFFECT OF RETROSPECTIVE ATTENTION ON MEMORY SYSTEMS

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THE EFFECT OF RETROSPECTIVE ATTENTION ON MEMORY SYSTEMS

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SUMMARY

Prior research has shown that visual working memory (VWM) performance can be improved via retrospective cues ("retro-cues") that spatially indicate which item currently being held in working memory will be probed at test. These studies have utilized electroencephalography (EEG) methods to monitor contralateral delay activity (CDA) event related potentials (ERPs) and assert that retro-cues benefit memory by reducing effective memory load.

Here, we investigated the potential relationship between CDA amplitude and future long-term memory (LTM) performance. Emerging evidence from ERP and fMRI studies suggest that working memory maintenance can contribute to LTM formation, which suggests that memory systems are not as discrete as some models suggest. We investigated the hypotheses that A) the benefits afforded by the retro-cue in VWM will carry over into LTM, and B) CDA amplitude will be modulated by subsequent LTM performance. Results revealed that retro-cuing improved item accuracy at both VWM and LTM delays, suggesting that the two memory systems are interactive. Due to an insufficient amount of subsequent LTM misses, we were unfortunately too underpowered to detect a CDA depending on long-term memory performance. However, we found that posterior slow-wave potentials during the maintenance period did differ by subsequent LTM performance, which further suggests an interactive systems account of memory. We also sought to investigate what exactly the retro-cue cues. Prior research has focused on memory for items, but no study has questioned if the retro-cue also enhances memory for item location. To this end, the present study investigated the effect of retro-cueing on both item identity and item location. LTM Behavioral results revealed a retro-cue benefit for item accuracy but no benefit for item location, suggesting that the retro-cue selectively cues item identity.

CHAPTER 1

INTRODUCTION

Visual Working Memory (VWM) is a capacity limited system that represents visual information after it is no longer available through sensory input. VWM capacity varies by individual and contributes to individual differences in the ability to inhibit irrelevant information in visual search (Bleckley, Durso, Crutchfield, Engle, & Khanna, 2003), focus switching accuracy (Unsworth & Engle, 2008), episodic memory (Unsworth & Spillers, 2010), and fluid intelligence (Oberauer, Schulze, Wilhelm, & Suss, 2005).

Although capacity is limited, studies have discovered that VWM capacity and accuracy can be enhanced via spatially informative, retrospective cues ("retro-cues") (Lepsien & Nobre, 2007; Makovski & Jiang, 2007; Makovski, Sussman, & Jiang, 2008; Matsukura, Luck, & Vecera, 2007). In these studies, the retro-cue (a small arrow, for example) is presented briefly following an array of stimuli and gives an indication as to which item will later be probed. Retro-cues are thought to benefit VWM by reducing memory load. Specifically, as items compete with one another in VWM during the delay period (Bahcall & Kowler, 1999), the retro-cue isolates the important "to-be-probed" item and causes the other items in VWM to become irrelevant and thus reduces effective memory load.

Neuroimaging studies have revealed persistent activity during the delay period in regions of sensory cortex responsible for processing the relevant stimuli (i.e. objects, faces). The similarity in activity between seeing a stimulus and maintaining a representation of that stimulus suggests the activity in the sensory cortex during the delay period reflects VWM maintenance (Ester, Serences, & Awh, 2009; Gazzaley, Rissman, & D'Esposito, 2004; Postle & D'Esposito, 1999; Stokes, Thompson, Cusack, & Duncan, 2009). The temporal resolution of electroencephalography (EEG) lends itself well to studying how retro-cues affect VWM during the delay period. An event related potential (ERP) of particular relevance for investigating VWM 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, Vogel, & Awh, 2011; McCollough, Machizawa, & Vogel, 2007; Vogel & Machizawa, 2004). The CDA appears as sustained negative activity over posterior electrodes, and as the name suggests, the CDA is observed for items held in VWM presented in the contralateral visual hemi-field with respect to the posterior electrode location. 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 span, supporting the idea that it reflects VWM maintenance (McCollough et al., 2007).

Only two studies have investigated the effects of retrospective attention on the CDA. In Kuo, Stokes, & Nobre's (2012) design, participants began a trial by viewing a pre-cue (an arrow pointing left or right) for 200ms which directed attention to one hemifield, followed by a variable interval of 500-1000ms. Next, the memory array, which was manipulated by load to include 2 or 4 colored squares in each visual hemifield, was presented for 200ms followed by an interstimulus interval of 800ms. Next, participants were presented either a retro-cue that indicated which quadrant of the cued hemifield would be probed, or a neutral cue that offered no information about the future probe for

200ms. Following the cue, there was a variable interstimlulus interval of 600-1000ms before the test probe was presented for 200ms. Participants were asked to respond via left or right mouse button if the test probe matched an item in the cued half of the array or not. Behavioral results from this experiment revealed faster reaction times, higher sensitivity scores (d'), and higher capacity measures (Pashler-Cowan K) for retro-cued trials compared to neutral cued trials. These benefits were more pronounced with a cued hemifield load of 4 compared to load 2, which is 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 a retro-cue for both load 2 and load 4 conditions.

Duarte and colleagues also investigated how retrospective attention affects the CDA using a very similar paradigm (Duarte et al., 2013). Here, participants first viewed a pre-cue arrow pointing to the left or the right for 200ms, which indicated which hemifield should be attended. Following an interstimulus interval between 400-600ms, participants were presented with an array containing 2, 3, or 4 colored squares in each hemifield for 200ms. Following the array, participants viewed a fixation cross for 800ms before being presented with either a retro-cue (an arrow pointing to the location of the to-be probed item) or no cue (the fixation cross persisted) for 200ms. After an 800-1000ms interstimulus interval, the test probe was presented for 2000ms and participants indicated whether or not the probe was presented in the memory array via button press. Both younger and older adults participated in this study. Similar to Kuo, Stokes, and Nobre's (2012) results, retro-cues enhanced memory performance (accuracy and reaction time) compared to no-cue trails for younger adults. Older adults did not show an accuracy benefit for retro-cue trials, but retro-cues did enhance reaction time compared to no-cue trials. ERP results revealed that CDA amplitude was attenuated following the retro-cue for both age groups, which, similar to Kuo and colleagues (Kuo et al., 2012), again suggests that retro-cues reduce memory load . Results from both of these studies indicate that VWM representations can be modulated via top-down attention mechanisms to maintain only task-relevant information.

The study by Duarte and colleagues (Duarte et al., 2013) also tested a second, non-mutually exclusive explanation for how retro-cues may benefit memory performance. Previous work has suggested that retro-cues reduce the number of comparisons between the test probe and memorized items held in VWM (Makovski et al., 2008). To elaborate, retro cues may reduce the number of items held in VWM (as a reduction in the magnitude of the CDA suggests is happening), which in turn reduces the number of comparisons needing to be made at test. To investigate this hypothesis, Duarte and colleagues monitored the parietal-maximal P300 (P3b) ERP, which reflects working memory updating (Donchin & Coles, 1988; Polich, 2007) , . The more VWM representations needing to be compared with the probe, the more activity there is related to updating the contents of VWM, which leads to increased latencies and amplitudes in the P3b. The logic follows then, if retro-cues reduce the number of comparisons made at test, the P3b should show reduced latency and amplitude compared to non-cued trials. Duarte and colleagues did find that with younger adults, there was a reduction in latency and amplitude associated with retro-cued trials (Duarte et al., 2013). This data, paired with observed modulations in the CDA, suggests that retro-cues reduce both VWM load and comparison demands at test.

The current body of research has focused on how retro-cues benefit working memory, but there has been no research regarding the potential effects of retro-cues on long-term memory. To review, classical models of working memory like Atkinson and Shiffrin’s 1968 model assert that working memory and long-term memory are separable systems (Atkinson & Shiffrin, 1968). Behavioral evidence for a distinction between working memory and long-term memory can be seen in the serial position effect of free recall (Murdock, 1962). In these studies, participants are presented with a list of words and are then asked to recall the list in any order. Studies of this nature produce a serial position curve characterized by primacy and recency effects. To elaborate, participants recall more items from the beginning and end of the list (primacy effect and recency effect, respectively) than items presented in the middle of the stimulus list. The primacy effect is thought to arise from the extra rehearsal time afforded to the early items in the list, which allows those first items to become part of long-term memory. Conversely, the last items in the list benefit from being stored in working memory due to the temporal closeness of hearing the item and being immediately tested, thus producing the recency effect.

A neuroimaging study of the serial position effect also supports the idea of separable systems (Talmi, Grady, Goshen-Gottstein, & Moscovitch, 2005). If items early and late in the list are recalled from separate memory systems, a functional magnetic resonance imaging (fMRI) study should show differing activations for items in early and late positions. This is what Talmi and colleagues found. When items from the beginning of the list were recalled, the hippocampus, which is traditionally associated with long-term memory processes, showed activation. Recalling the items at the end of the list did not produce hippocampal activation but produced activation in frontal and parietal cortices as expected in a working memory task (these areas were also active when recalling early items which is as expected since the items were recalled from long-term memory into working memory in order to make a response). The finding that different brain regions were active depending on serial position supports the separable systems account.

Further evidence for a neurological distinction between memory systems comes from studies of patients like H.M (see Squire, 2009 for review). In order to correct a debilitating seizure disorder, H.M. underwent a bilateral medial temporal lobe resection, which included removing the hippocampus. Although the seizures subsided, H.M. was left with an inability to form new long-term memories after the procedure. H.M.'s working memory, however, remained intact. The discovery that one system can function in the absence of the other (in this case, working memory in the absence of forming new long-term memories) supports a separable systems account.

There is accumulating evidence, however, that memory systems are not so distinct. For example, an fMRI study by Öztekin, McElree, Staresina, and Davachi (2009) investigated possible activation differences in serial positions thought to be maintained in long-term memory (items 1-8 in a 12 item word list; referred to as the passive set), working memory (items 9-11; referred to as the active set), and the focus of attention (item 12). This design differs from the previously described study by Talmi and colleagues (Talmi et al., 2005) in that the item in the last serial position was not hypothesized to be maintained by working memory but instead thought to be maintained by the focus of attention. Oztekin and colleagues hypothesized that including the item in the last serial position in working memory contrasts was affecting the appearance of hippocampal activity. To address this concern, the researchers contrasted the active set (items thought to be in working memory) and the focus of attention, which revealed enhanced hippocampal activity for the active set. This result confirms the suspicion that previous studies had not been properly probing working memory. A second contrast comparing the passive set and the focus of attention revealed enhanced hippocampal activity for the passive set. Together, these results indicate that the hippocampus is activated when accessing both working memory and long-term memory representations. The lack of a neural dissociation between representations in working memory and long-term memory suggests that both systems share a single store.

A study by Ranganath, Cohen, and Brozinsky (2005) offers further evidence for the relatedness of working memory and long-term memory systems. In this study, researchers found that early working-memory processes contribute to long-term memory formation. Using fMRI, these researchers parsed working memory into two types of processes. Early processing during the delay period involved the hippocampus and likely reflected transforming sensory input into memory representations. Later processing (still during the delay period) revealed selective activity in areas usually found in working memory maintenance including the bilateral pre-supplementary motor area, frontal eye fields, dorsal cingulate, and occipital gyri. Importantly, hippocampal activity during the early process predicted later long-term memory performance. Finding hippocampal activity, which has classically been implicated in long-term memory, in association with working memory tasks together with a relationship between this activity and long-term memory performance corroborates the idea that working memory and long-term memory are not independent systems.

Particularly relevant for the present study, research using EEG methods also supports an interactive systems account. A study by Khader and colleagues (Khader, Ranganath, Seemüller, & Rösler, 2007) _ENREF_19measured slow wave ERPs during the delay period in a working memory task and found that ERPs distinguished items that were later remembered from those that were forgotten in a surprise long-term memory task. Specifically, slow wave ERPs were more negative-going over parietal and occipital scalp sites during the delay period for items that were subsequently remembered compared to forgotten items. These results suggest that VWM maintenance can act to strengthen long-term memory traces.

Current Study

In light of this new direction of thinking about the relatedness of memory systems, it is possible that the enhancements afforded by retro-cuing carry over into long-term memory. To this end, the present study assessed the effects of retro-cuing on both working memory and long-term memory performance. We also investigated whether or not the magnitude of the CDA would be predictive of long-term memory performance. In order to assess long-term memory, the present study used images of real-world objects as stimuli, which is a novel stimulus class for investigating both retro-cueing and the CDA.

Another novel aspect of the present study is assessing what exactly the retro-cue is cuing in VWM. Previous research investigating retro-cues has focused on memory for items but there has been no assessment of memory for other features such as spatial location. If spatial location and potentially other features are bound to items in VWM representations, the retro-cue would be expected to enhance memory accuracy for both the item and its location in the original memory array. The present study investigated this possibility by monitoring an ERP termed the N2pc at working memory. The N2pc presents as a negative going waveform over posterior electrodes 200-300 ms following the presentation of a stimulus array and reflects attentional selection in visual search tasks (Eimer, 1996; Luck & Hillyard, 1994). The N2pc is observed at posterior electrodes contralateral to side of the visual field containing the target and may reflect either the suppression of distractors or the enhanced processing of the target (Hickey, Di Lollo, & McDonald, 2009; Kiss, Van Velzen, & Eimer, 2008).

Kuo, Rao, Lepsien, and Nobre (2009) monitored N2pc activity during both a visual search task and a VWM task in order to investigate whether searching for target items in VWM representations elicited the same neural activity as searching a perceptual array. Evidence of N2pc activity during a VWM task would suggest that some spatial information is maintained in VWM. The N2pc was found, as expected, during a visual search task where participants were presented with a target item (an abstract shape) and were next asked to search for that item in a stimulus array. Interestingly, the N2pc was also found for a VWM task in which participants were first shown the stimulus array and after a delay presented with a probe item to identify as present or absent in the array. Since the N2pc reflects top-down attentional selection of targets in a spatial search task, evidence of N2pc activity for representations held in working memory suggests that VWM representations maintain some detail of the spatial configuration of the memory array.

Important for the present study, monitoring the N2pc during the working memory task circumvented problems with behaviorally probing for item location following the presentation of a retro-cue. That is, in order to make a decision about an item's location in the memory array, participants need only remember the spatial orientation of the retro-cue to answer correctly. For example, if a participant is shown a retro cue pointing to the upper left location of an array, when the participant is asked which location the item occupied, the participant doesn't need to search through the representation of the visual array, per se; he simply could remember the image of the retro-cue pointing to the upper left location. Monitoring the N2pc also helped the present study investigate the natural, spontaneous properties of VWM. If participants knew memory for location would be immediately probed in the VWM task, they may have adopted a strategy that binds location information. The goal of monitoring the N2pc during working memory was to determine if VWM representations were being searched similar to a visual search task where spatial location and item identity are a bound representation. In order compare N2pc activity at both visual search and VWM, it was critical that the trial structures (timing and visual changes) were identical between the tasks. To this end, we used a pre-cue (an arrow indicating which hemifield to attend to) in the visual search task to mimic the timing and visual change provided by the retro-cues or neutral cues in the VWM task. It is important to mention that previous research has indicated that the N2pc is not influenced by pre-cues (Kiss et al., 2008). In a study by Kiss and colleagues (Kiss et al., 2008), participants were presented with a pre-cue that was either spatially informative regarding which side a target would appear in an array, or spatially uninformative. The N2pc did not differ between informative and uninformative cue trials.

Location memory was behaviorally probed at long-term memory, however, since it was unlikely that participants would remember which retro-cue was presented with which item. Following an item-recognition probe, participants were asked to indicate on which side of the array the item was presented and also in which of three positions the item was located. The present study is the first study to specifically investigate what aspects of a representation retro-cues enhance: the item, item location, or both.

We were also interested in monitoring lateralized old/new activity at long-term memory, which would also indicate retention of spatial information. Such a finding would be consistent with a previous study that found lateralized old/new ERP activity in a long-term task (Gratton, Corbalis, & Jain, 1997). In this study, participants were presented with a series of horizontally or vertically symmetrical shapes on either the left or right side of a screen during study. At test, participants were simply asked to respond "old" or "new" to the now centrally presented shapes (50% of the shapes presented at test were new). Even in the absence of a location probe, lateralized activity was still present such that shapes initially presented in the left visual hemi-field elicited increased negative activity over right hemisphere electrodes and vice versa. These data support the idea that spatial information is bound to items in mnemonic representations even in long-term memory.

To summarize, the present study:

1) Investigated whether retrospective attention facilitates VWM and long-term memory in support of an interactive systems account.
2) Monitored VWM maintenance using the CDA to determine if CDA magnitude would reflect accurate maintenance of information at both working

memory and long-term memory delays, which would also support an interactive systems account.

3) Monitored N2pc activity at working memory and compared this activity to N2pc activity elicited by a visual search task to glean information about the nature of VWM representations.
4) Probed memory for item location at long-term memory to further investigate interactions between events at working memory (retro-cuing, in this case) and later long-term memory performance and the nature of VWM representation.
5) In addition to the location probe, we also monitored lateralized old/new ERP effects at long-term memory to investigate the retention of spatial information.

CHAPTER 2

METHOD

Participants

30 young adults between the ages of 18 and 24 were recruited from Georgia Institute of Technology and the Atlanta community to participate in the study. Of the 30 participants that were recruited, 19 participants are included in the following analyses. 3 participants failed to return for the second session and did not provide enough data during the first session to make any ERP analysis possible. 4 participants were excluded from analysis due to various artifacts in the EEG data (drift due to sweat and malfunctioning electrodes). 4 participants were excluded for excessive bad behavioral responses at long-term memory. Of the remaining 19 participants, 10 were male and 9 were female. The average age was 21 years. All participants were right handed, native English speakers with normal or corrected to normal vision (including the absence of colorblindness). The health screening ensured that no participants reported psychiatric or neurological disorders, vascular disease, or uses psychoactive drugs. Participants were compensated for their time with 1 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.

Neuropsychological Assessment

Each experimental session was divided into two parts: a working memory component and a long-term component. Between the components, neuropsychological assessments were administered. This placement provided a delay in order to ensure proper long-term memory testing. This assessment battery lasted approximately 25 minutes and included measures of processing speed, working 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 & Wolfson, 1985), the Controlled Oral Word Association test (“FAS”) (Benton, 1994), Symmetry Span (Unsworth, Heitz, Schrock, & Engle, 2005), Running Letter Span (Unsworth et al., 2005), and Digit/Symbol Substitution (Wechsler, 1997). The results of this battery will serve as a tool for identifying age group differences in cognition for a future aging version of this study.

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, Dionne-Dostie, Montreuil, & Lepage, 2010), and Massive Memory (Brady, Konkle, Alvarez, & Oliva, 2008) databases, and Google Images. All of the images depict singular, unique objects. The images were edited using Adobe Photoshop to adjust all background colors to white and to constrain image size. All stimuli were presented on a white background. Each object subtended 1.39 degrees of visual angle, similar to dimensions implemented in similar previous ERP studies (Kiss et al., 2008; Kuo et al., 2009; Kuo et al., 2012). Participants were seated 2 feet from the 257 x 300 mm monitor with 1280 x 1024 pixel resolution.

Design

Prior to beginning the experiment, participants engaged in an extensive practice task. To help acclimate the participant with the procedure and response options, the presentation speed of the VWM task began slowly and increased as the practice continued. The first block of 5 trials was at a four second pace (meaning the pre-cue, memory array, and retro-cue were presented for 4 seconds each), the second block contained 10 trials at a two second pace, the third block contained 10 trials at a one second pace, and the fourth block contained 22 trials at the experimental pace (200ms). To conserve object images for the experimental task, the practice task used colored squares as stimuli for the first three blocks. The fourth block began with colored squares for the first ten trials and then shifted to objects for the last twelve trials.

The experiment was divided into two sessions with two components contained in each session: a working memory component and a long-term memory component. The two sessions were separated by a two-week delay. The two sessions are imperative to accumulating enough trials. Each session contained 88 working memory trials and 88 long-term memory trials for a total of 176 working memory trials and 176 long-term memory trials across the experiment. Each session required the use of 453 of the 762 objects. To circumvent this problem of not having enough images, the objects in the unreferenced hemi-field were reused in the second session as objects in the cued hemi-field. For example, if the pre-cue on a particular trial pointed to the right visual field, the two objects on the left side of the array, say a rubber duck and a paint pallet, were presented on the cued side of an array in session 2, though not in the same trial. Items presented in the cued hemifield in session 1 were not presented again in session two. It seemed unlikely that participants would remember the objects presented on the non-cued side of the array, especially given the brief presentation time (200ms). As an extra precaution, the two-week delay between sessions served as a buffer to insure that no incidental memories for the non-cued objects remained. We also tested for explicit memory for the non-cued objects in a group of pilot participants to ensure that these items were not encoded. Behavioral and EEG data were combined for the 2 testing sessions.

Working Memory Component

The paradigm is shown in **Figure 1.** The timing and duration of each component in the trial is based on prior research (Brisson & Jolicoeur, 2007; Kuo et al., 2012). Trials began with a pre-cue presented for 200ms. The pre-cue consisted of a small arrow that indicated which side of the array the participant should direct their attention. There was an interstimulus interval that randomly varied between 500 and 1000ms in 50ms increments prior to presenting the memory array for 200ms. The array contained two objects on each side of the array, making the objective set size 2. While it is true that greater modulations in the CDA are observed at greater memory loads, a load of 2 objects has been sufficient to observe a reliable CDA and retro-cueing effects in behavior and ERPs (Kuo et al., 2012; Duarte et al., 2013). Two objects were randomly presented in two of three possible positions in both halves of the array. There was also a place-holder object on both sides of the array consisting of an image scrambled in Photoshop (making the item unidentifiable) in order to keep the array balanced, which was important for assessing lateralized ERPs. That is, it was important that all 6 positions in the array be filled on every trial to keep the visual display consistent for recording ERPs. The three positions on each side of the array created an ellipse-shaped array with a radius subtending 3.21 degrees of visual angle. After the offset of the array, there was a 700ms delay before presenting the neutral or retro-cue for 200ms. These cues, like the objects, were constrained to 1.39 degrees of visual angle. The neutral cue appeared as an asterisk with three intersecting lines. The retro-cues were a modification of this asterisk with arrowheads positioned on one of the six tips of the intersecting lines (See **Figure 1** for an example). The arrow pointed to the location of the to-be probed object and was always a valid cue. Half of the trials contained a retro-cue and the other half contained a neutral cue presented in a pseudorandom order such that no more than 4 trials of one cue type were presented consecutively. An interstimulus interval that varied randomly between 700 to 1100ms in 50ms increments was presented before the probe. The memory probe was presented for 200ms. Half of the trials were match trials in which the probe was presented in the cued hemi-field. The other half of the trials were non-match trials in which the probe was not presented in either the cued or non-cued hemifield. Match and non-match trials were presented in a pseudorandom order such that no more than 4 trials of one type (match, non-match, neutral, retro-cue) were presented consecutively. Following a 700ms interval, the participant was asked if the probe was an item presented in the array or an item that was new, a match or a non-match, respectively. Participants had 1500 to 2000ms to respond. There were 88 trials total per session: 44 neutrally cued trials of which 22 were match trials and 22 were non-match trials and 44 retro-cued trials of which 22 were match trials and 22 were non-match trials. This portion of the experiment lasted approximately 20 minutes.

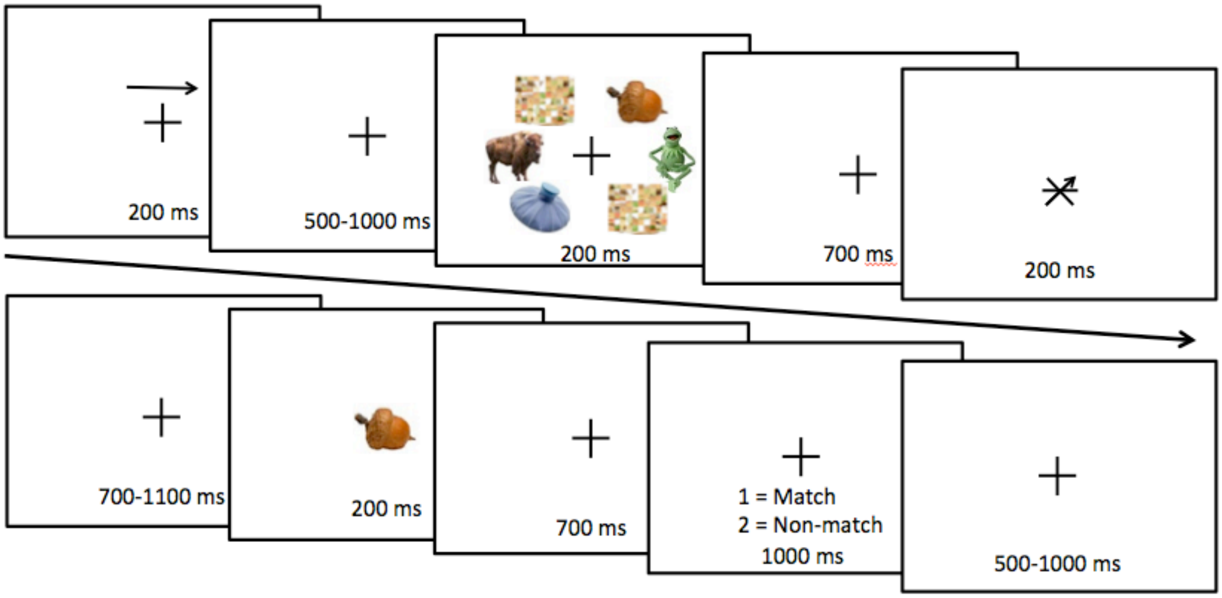


Figure 1. Experimental procedure for the working memory component.

Long-term Memory Component

After completing the neuropsychological battery (described above), the long-term memory task was administered (see **Figure 2**). The match probes from the working memory task were presented again. Non-match probes from the working memory task also appeared again in the long-term task. New object distractors were used as non-match probes for the long-term memory task. The order of neutral and retro-cue match and non-match trials were presented in a pseudorandom order such that no more than 4 trials of the same type were presented consecutively. The probe was presented for 200ms and followed by a fixation cross for 700ms. Participants were then asked three questions about the probe. Participants were first asked if the probe was an item presented during the working-memory component or an item that is new to the participant, old or new, respectively. A second question asked the participant to indicate in which hemi-field the object was presented (right or left) and a third question asked the participant to indicate which specific location (upper, middle, or lower) the object was positioned in in the array. Participants made responses via button press using the numbers 1, 2, and 3 (old:1, new:2; left:1, right:2; upper:1, middle:2, lower:3; old/new responses were counterbalanced so that for half of the participants, new:1, old:2). Participants had 2 seconds to answer each question. There was a 500 to 1000ms interval between trials. The long-term memory component contained 88 trials per session (44 match, 44 non-match) and last approximately 20 minutes.

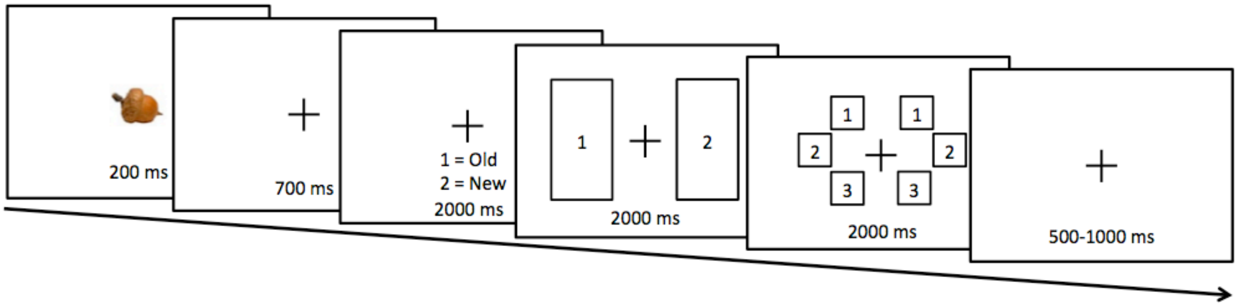


Figure 2. Experimental procedure for the long-term memory component.

Visual Search Task

At the end of session 2, participants completed the visual search task. The same objects used in the VWM and long-term memory components were used as stimuli. The paradigm is shown in **Figure 3**. Critically, the timing of the visual search task is identical to that of the working memory task such that the delay between target and search array is identical to the delay between the array and probe in the working memory task. A mini block of 16 trials served as a practice session. To begin, a target item was presented centrally for 200ms. Participants were instructed that this is the item they will be searching for in the stimulus array. Next, participants viewed a fixation cross for 700ms.

Following the fixation cross, a pre-cue was presented for 200ms indicating which half of the array participants should direct their attention. Next, there was an interstimulus interval of 700 to 1100ms that varied in increments of 50ms. A stimulus array was then be presented for 200ms. Following array presentation, there was a 700ms fixation cross. Following fixation, participants had 1500 to 2000ms to indicate via key press if the target matched an item presented in the array or not (match: 1, non-match: 2). 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 in order to avoid participant fatigue.

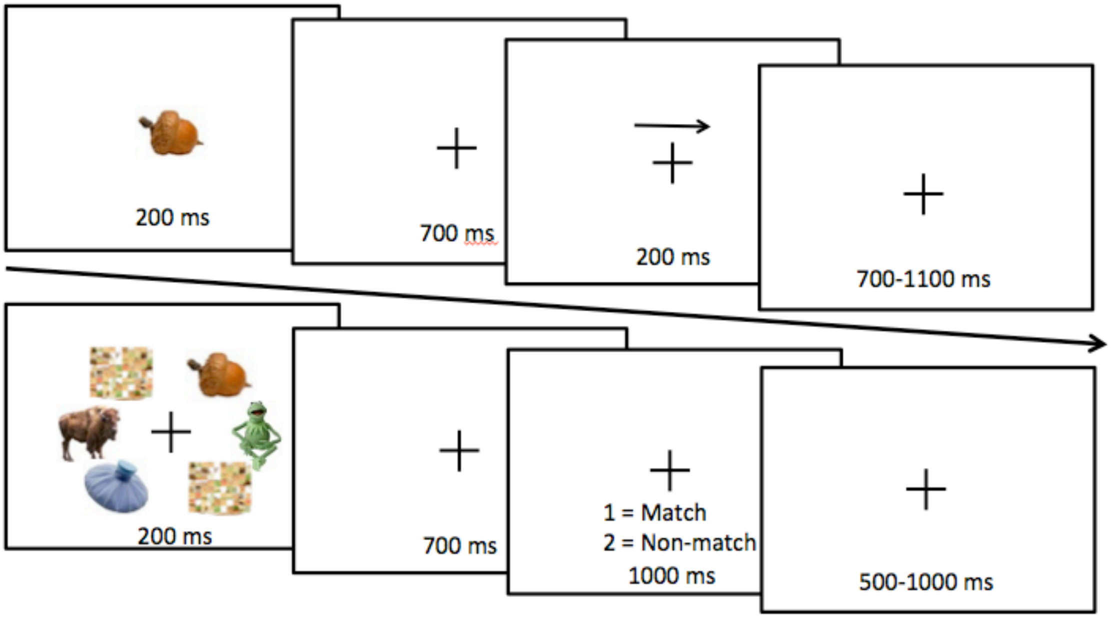


Figure 3. Experimental procedure for the visual search component.

Behavioral Analysis

Working Memory Component

A target was defined as a probe item that matched an item in the memory array. Hits were defined as a "match" response to a target present trial, correct rejections were defined as a "non-match" response to a target absent trial, misses were defined as a "non-match" response to a target present trial, and false alarms were defined as a "match" response to a target absent trial. Accuracy was calculated using a “Pr” discrimination measure: hit rate – false alarm rate, making chance 0 (Snodgrass & Corwin, 1988). A paired samples t-test was used to compare neutral cue and retro-cue accuracy. We also calculated Cohen’s d (Cohen, 1988) to measure effect size (i.e. (mean accuracy for retro-cue trials – mean accuracy for neutral-cue trials)/ pooled standard deviation)). Response times for correct trials (hits and correct rejections) for retro-cue and neutral cue trials were compared using a paired-samples t-test.

Long-term Memory Component

Targets at long-term memory were items that were presented as probes during the working memory component. As in the working memory component, hits were defined as a "match" response to a target present trial, correct rejections were defined as a "non-match" response to a target absent trial, misses were defined as a "non-match" response to a target present trial, and false alarms were defined as a "match" response to a target absent trial. Accuracy was again calculated as hit rate – false alarm rate, making chance 0 (Snodgrass & Corwin, 1988). A paired samples t-test was used to compare neutral cue and retro-cue item accuracy. We also calculated Cohen’s d (Cohen, 1988) to measure effect size (i.e. (mean accuracy for previously retro-cue trials – mean accuracy for previously neutral-cue trials)/ pooled standard deviation)). Item accuracy from the long-term memory task and the VWM task was subjected to a Memory Phase (VWM, long-term memory) X Cue (retro-cue, neutral cue) repeated measures ANOVA to assess memory decay. In the case of a significant interaction, paired samples t-tests will be used to determine the source of the effect. Item probe response times for correct trials were compared using a paired-samples t-test.

We calculated two measures of item location accuracy. The first measure was concerned with whether or not participants remembered which hemifield the item was presented in during the VWM task. This measure of coarse item location accuracy was calculated as the proportion of item hits associated with correct hemifield location judgments divided by the total number of item hits. The second measure of location accuracy for exact location, which required participants to answer both the hemifield question and the vertical location question correctly. Exact item location accuracy was defined as the proportion of item hits associated with correct location judgments for both side of screen and vertical location divided by the total number of item hits, making chance 0.16 (i.e. 6 possible locations). Paired samples t-tests were used to compare retro-cue and neutral cue item accuracy, retro-cue and neutral cue coarse location accuracy measures, retro-cue and neutral cue exact location accuracy measures, and response times for correct trials (hits and correct rejections) for retro-cue and neutral cue trials.

Visual Search Task

Hit rate was defined as the conditional probability that a participant responded “target present” given that a target was present in the array. False alarm rate was defined as the conditional probability that a participant responded “target present” given a target was not present in the array. Perceptual sensitivity to detect targets was calculated as Pr, as in the WM and LTM tasks (Snodgrass & Corwin, 1988).

ERP 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 elecrooculogram (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. Off-line, the mastoid electrodes were used as reference and data was digitally band-pass filtered between 40Hz and 0.01 Hz. Vertical and horizontal eye movements were removed via a method based on independent component analysis by using a feature available in the EEG lab toolbox for Matlab (Delorme & Makeig, 2004). Epochs containing uncorrected artifacts (+/- 100 microvolts) were removed. Also excluded from analysis were trials with incorrect behavioral responses or reaction times less than 200ms.

ERP Analysis

CDA

One purpose of using EEG methodology in the present study was to determine if retro-cuing modulated activity associated with VWM maintenance when objects are used as stimuli. We were also interested in assessing weather or not the CDA, as an index of VWM maintenance, would be modulated by subsequent long-term memory performance. The EEG data was segmented into epochs starting 200ms pre-array onset and lasting until 1800ms post-array onset, consistent with the timing of the shortest trial in which the probe onsets at 1800ms and also with similar previous studies (Kuo et al., 2012). ERP mean amplitude was measured for both contralateral and ipsilateral target activity.

Similar to previous research (Kuo et al., 2012; Duarte et al., 2013), mean amplitudes of the CDA were computed for two time windows: 275-650ms after memory array onset and 1250-1350ms after memory array onset in order to capture the CDA before and after presentation of the cue. As common in other studies, mean amplitudes were averaged across hemisphere and electrodes where the CDA appeared most robust (PO3/O4 and P7/8) as a method for increasing sensitivity to detect CDA modulations (Jost, Bryck, Vogel, & Mayr, 2011). Mean amplitudes of delay period activity were subjected to Hemifield (contralateral, ipsilateral) x Cue (retro-cue, neutral cue) repeated measures ANOVAs for each separate time window in order to detect the CDA pre-cue and compare any cuing effects post-cue. For working memory hit trials, mean amplitudes of delay period activity during the pre-cue time window (275-650ms) were also subjected to a Long-Term Memory Accuracy (long-term memory hit, long-term memory miss) X Hemifield (contralateral, ipsilateral) ANOVA to determine if there were differences in the CDA depending on subsequent long-term memory performance. We ran this analysis specifically for working memory hits because we were primarily interested in how accurate working memory maintenance could predict later long-term memory performance. Cue type isn't an interesting factor in this analysis since the time-window is prior to the cue. That is, at the time of amplitude measurement, participants are unaware of which cue they will see so there shouldn't be any differences in amplitude depending on cue-type. Any significant interactions were followed up with subsidiary analyses to determine the source of the effect. Huynh-Feldt corrections are reflected in the error term when appropriate.

N2pc

Another purpose of using EEG in the present study was to investigate the nature of VWM representations by comparing any N2pc activity at working memory with the N2pc we expected to find in the visual search task. In both the visual search task and the working memory task, only correct responses to target present trials were assessed (i.e. hits), which is consistent with previous research (Kuo et al., 2009). For both tasks, the EEG data was segmented into epochs starting 200ms pre-array onset and lasting until 900ms post-array onset. N2pc mean amplitude was computed 240-300ms after array presentation and averaged at parietal/occipital electrodes (P7P8, P3/P4, PO3/PO4, and O1/O2) for both tasks (Kuo et al., 2009). In order to compare possible N2pc activity at working memory with the N2pc expected at visual search, mean amplitudes were subjected to a Task (retro-cue at working memory, neutral cue at working memory, visual search) X Hemifield (contralateral, ipsilateral) X Electrode Pair (P7P8, P3/P4, PO3/PO4, and O1/O2) repeated measures ANOVA. Any significant interactions were followed up with subsidiary analyses to determine the source of the effect. Huynh-Feldt corrections are reflected in the error term when appropriate.

Lateralized Old/New effects

We also used EEG to monitor lateralized old/new activity in order investigate the retention of spatial information at long-term memory. The EEG data was segmented into epochs starting 200ms before probe presentation and ending 1800ms after probe presentation (similar to Gratton et al., 1997). Old/new effects appeared most evident 550-800 ms after the probe. To investigate lateralized activity and topographical location, mean amplitude was measured for contralateral and ipsilateral target activity (that is, contralateral and ipsilateral to the hemifield in which the target was presented during the

VWM task) at electrode pairs AF3/AF4, F7/F8, CP1/CP2, P3/P4, and PO3/PO4. Similar to Gratton and colleagues (Gratton et al., 1997), mean amplitudes were subjected to a Hemifield (contralateral, ipsilateral) X Electrode Pair (AF3/AF4, F7/F8, CP1/CP2, P3/P4, PO3/PO4) repeated measures ANOVA to detect any lateralized differences. In the case of a significant interaction, subsidiary analyses will determine the source of the effect.

CHAPTER 3

PREDICTIONS

Behavioral Predictions

Based on the previously discussed literature regarding the relatedness of VWM and long-term memory, we predicted that working memory and long-term memory are interactive systems and that retro-cues would enhance memory performance measured at both working memory and long-term memory delays. Furthermore, in the case that the interactive systems account holds true, the location probe at long-term memory could shed light on the nature of VWM representations and what aspect of that representation the retro-cue enhances. If VWM representations are picture-like in the sense that item and location information are bound and those bound representations are accessible in long-term memory (Gratton et al., 1997), retro-cue benefits at long-term memory would be observed for both the item and the location. Conversely, if VWM representations are more abstract in the sense that constituent features of the object like identity and location are not bound together, retro-cue benefits at long-term memory would be observed for the item only.

ERP Predictions for CDA

We expected that CDA magnitude would reflect accurate maintenance of information at both working memory and long-term memory delays in agreement with an interactive systems account. That is, trials that were subsequently forgotten at long-term memory would show a reduced CDA magnitude compared to trials that are subsequently remembered. As in previous studies (Kuo et al., 2012), we expected that the magnitude of the CDA would be reduced following the presentation of a retro-cued compared to neutrally cued trials during the working memory task.

ERP Predictions for N2pc

We predicted that an N2pc would be elicited at the probe during the VWM task and at the visual array during the visual search task, and that the time course and topography would be equivalent across the two tasks. This would suggest that both tasks are utilizing the same kind of search process, similar to prior research (Kuo et al., 2009). Such a finding would support the idea that VWM representations are picture-like in the sense that item representations are bound with spatial information.

ERP Predictions for Long-term Memory Lateralized Old-New Effects

At long-term memory, we predicted that old-new ERPs would be more pronounced over the hemisphere contralateral to the visual hemifield in which the target was initially presented (similar to Gratton et al., 1997). Even if the retro-cue was not found to enhance location memory performance, lateralized old-new effects could still be observed which would indicate that spatial information is bound to item representations in long-term memory.

CHAPTER 4

RESULTS

Behavioral Results

Working Memory

Item accuracy was estimated using Pr, i.e. p(hits)-p(false alarms), making chance 0. Item accuracy for neutral cue trials was 72.41% while accuracy for retro-cue trials was 86.17% (**Figure 4**). Mean accuracy for retro-cue and neutral-cue trials was compared using a paired samples t-test. Results of this t-test indicated that accuracy for retro-cue trials was significantly higher than accuracy for neutral cue trials [$t(1,18) = 6.108$, $p < .001$]. Calculating Cohen's d resulted in an effect size of 1.33. Mean response time for correct neutral cue trials was 418.79ms while reaction time for correct retro-cue trials was 374.34ms (**Figure 4**). A paired samples t-test revealed that reaction time was indeed significantly faster for retro-cue trials compared to neutral cue trials [$t(1,18) = 8.266$, $p < .001$].

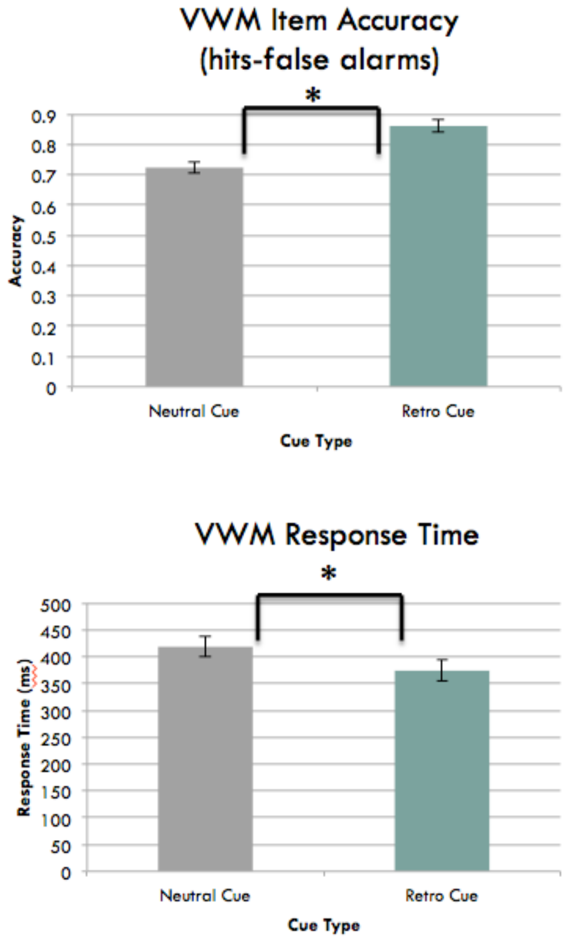
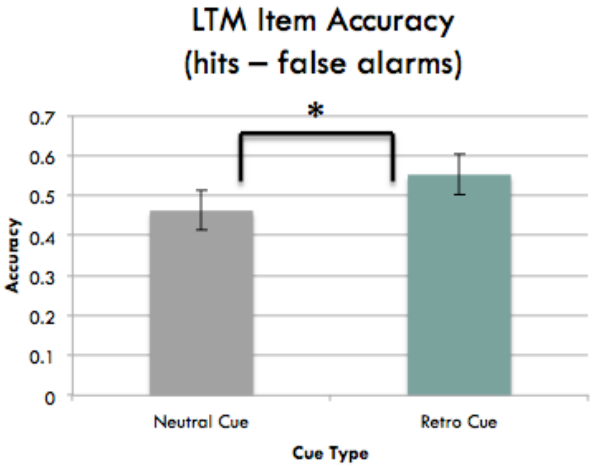


Figure 4. Accuracy and Response times by cue-type for the VWM component.

Long-term Item Memory

Item recognition was again estimated using Pr. Item accuracy and response time can be seen in **Figure 5.** Previously neutral cued item accuracy was 46.24% while previously retro-cued item accuracy was 55.26%. Mean accuracy for retro-cued and neutral-cued trials was compared using a paired samples t-test. Results indicated that accuracy for retro-cued trials was significantly higher than accuracy for neutral cued trials [$t(1,18) = 4.493$, $p < .001$]. Calculating Cohen's d resulted in an effect size of .40. A

Memory Phase (VWM, long-term memory) X Cue (retro-cue, neutral cue) repeated measures ANOVA revealed a significant main effect of Memory Phase [$F(1,18) = 42.49$, $p < .001$], Cue [$F(1,18) = 40.48$ $p < .001$], and a marginally significant interaction [$F(1,18) = 4.18$, $p = .06$]. Paired sample t-tests revealed that accuracy was significantly greater at VWM compared to long-term memory for both cue types (for retro-cue phase comparison, [$t(1,18) = 6.69$, $p < .001$] and for the neutral cue phase comparison, [$t(1,18) = 5.90$, $p < .001$]). Mean response time for correct neutral cue trials was 733.53ms while reaction time for correct retro-cue trials was 722.90ms. A paired samples t-test revealed that there were no significant differences in response time between the two cues [$t(1,18) = 0.79$ $p = .44$].



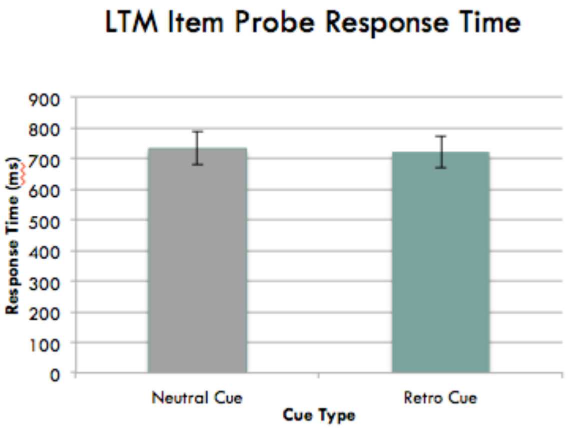


Figure 5. Accuracy and Response times by cue-type for the long-term memory component.

Long-term Location Memory

To measure coarse location memory, we calculated the percentage of hit trials for which the hemifield the target was previously presented in was correctly identified (**Figure 6**). For previously neutral cued items that were recognized at long-term memory, coarse item location accuracy was 69.02%. For trials that were previously retro-cued and recognized at long-term memory, coarse item location accuracy was 68.19%. A paired samples t-test revealed no significant difference in coarse location accuracy between the two cue types [*t*(1,18) = .34, *p* = .74]. To measure exact location memory, we calculated the percentage of hit trials for which both location questions were answered correctly (i.e. which hemifield the item was presented in and which vertical position within the hemifield the item was presented in had to be answered correctly to be considered accurate) (**Figure 6**). For trials that were previously neutral cued and recognized at long-term memory, exact item location accuracy was 44.01%. For trials that were previously retro-cued and recognized at long-term memory, exact item location accuracy was 44.97% . A paired samples t-test revealed no difference in location accuracy between the two cue types [*t*(1,18) = .26, *p* = .79].

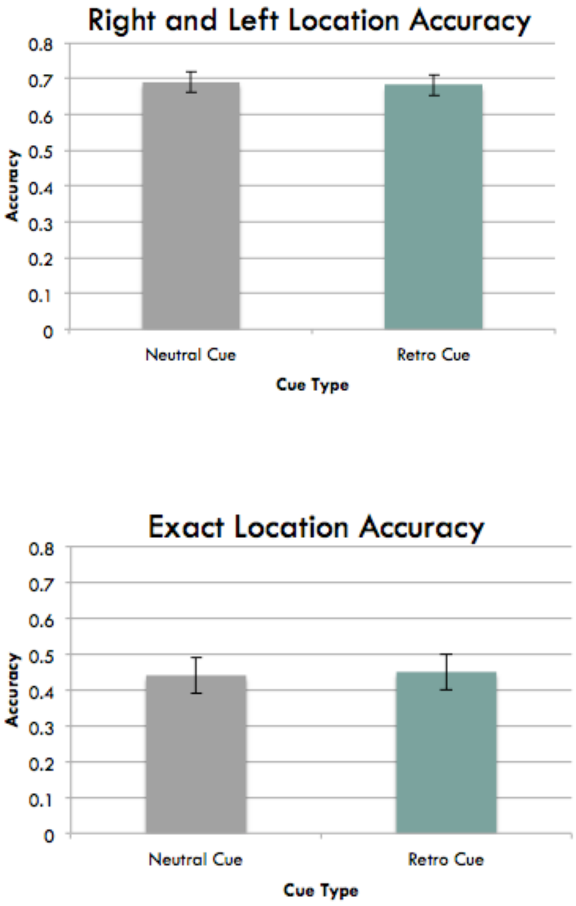


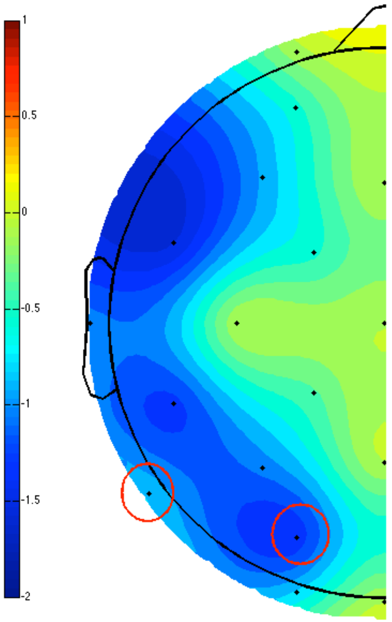
Figure 6. Location accuracy for correctly identifying which hemifield the test item was previously presented in (Right and Left Location Accuracy), and location accuracy for remembering both the hemifield and the specific vertical location within the hemifield (Exact Location Accuracy).

ERP Results

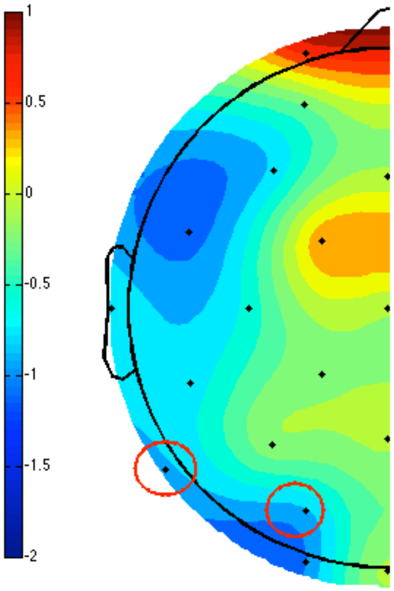
CDA

To capture the CDA prior to cuing, A Cue (retro, neutral) X Hemifield (contralateral, ipsilateral) ANOVA was conducted on mean amplitudes for the time window 275-650ms post array onset for hits and correct rejections at a (PO3/PO4)/(P7/P8) electrode cluster. See **Figure 7** for topographic maps and **Figure 8** for cluster wave-forms for each cue. This analysis revealed a significant main effect of Hemifield [$F(1,18) = 27.22, p < .001$], reflecting more negative-going activity contralateral to the hemifield being attended. Neither the main effect of Cue [$F(1,18) = 0.36, p = .56$] nor the interaction [$F(1,18) = .27, p = .61$] were significant. Upon visual inspection, it appeared that the CDA persisted after neutral cue trials from 1250-1350ms post-array onset but did not continue after retro-cue trials (see **Figure 8)**. Mean amplitudes in this time window were subjected to a Cue (retro, neutral) X Hemifield (contralateral, ipsilateral) ANOVA to test for the interaction. This analysis revealed a main effect of Hemifield [$F(1,18) = 4.90, p = .04$], but no main effect of Cue [$F(1,18) = 2.47, p = .13$], and there was no interaction [$F(1,18) = .52, p = .48$].

In order to test if the CDA differed depending on subsequent long-term memory performance, we collapsed across cue type and analyzed the CDA separately for trials that were subsequently remembered at long-term memory and trials that were later forgotten. Unfortunately, we were severely underpowered for this analysis due to a lack of VWM hits that were subsequently forgotten at long-term memory. Dividing the long-term memory misses by contralateral and ipsilateral presentation left only 6 participants with more than 7 long-term memory miss trials in each hemifield condition. For these six participants, mean amplitudes for a time window 275-650ms post array onset were subjected to a Memory (subsequently remembered, subsequently forgotten) X Hemifield (contralateral, ipsilateral) ANOVA. There was no main effect of Hemifield [*F*(1,5) = 2.19, *p* = 0.20], meaning there was no detectible CDA, the main effect of Memory was not significant [*F*(1,5) = 1.64, *p* = 0.26], and neither was the interaction [*F*(1,5) = .01, *p* = 0.93].



Retro-Cue: Contralateral - Ipsilateral; 275-650 ms



Neutral Cue: Contralateral - Ipsilateral; 275-650ms

Figure 7. Retro-cue and Neutral cue CDA topography. Only one hemisphere is shown since the CDA represents activity averaged across hemispheres. Electrode sites used in the cluster (P03/PO4 and P7/P8) are circled.

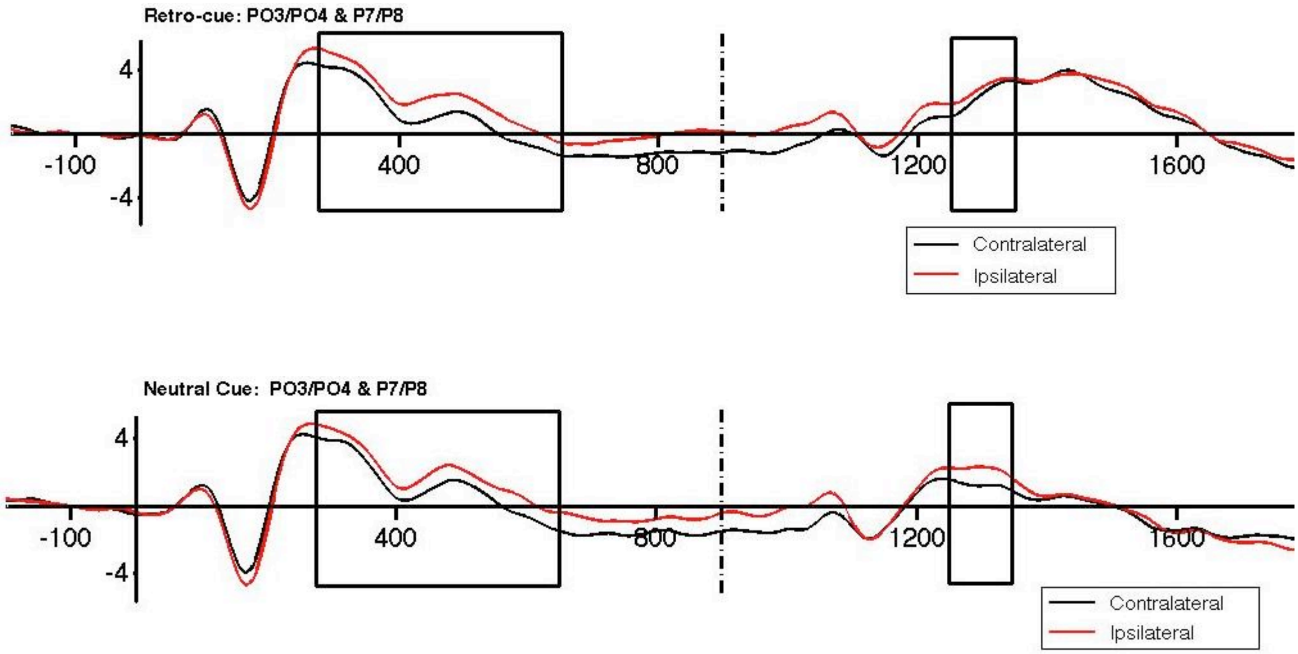


Figure 8. ERPs during the delay period for both retro-cue and neutral cue trials. The first rectangle indicates the time window for detecting the CDA prior to the cue. The dotted line indicates the presentation of the retro-cue or neutral cue. The second rectangle indicates the time window for investigating the CDA after the cue.

Slow-wave ERPs

Although we were unable to detect a CDA for so few participants in the previous, collapsing across hemifield allowed us to investigate slow-wave ERPs in 11 participants. Slow-wave ERPs are thought to reflect working memory maintenance and have been found to be modulated by subsequent long-term memory performance. Specifically, ERPs are more negative going for subsequently remembered trials compared to subsequently forgotten trials at occipital electrode sites when line-drawings of novel objects are used as stimuli (Khader et al., 2007).To assess slow-wave ERPs in the present study, mean amplitudes for hits at VWM that were subsequently remembered and those that were subsequently forgotten were calculated for a window 200-800ms after array presentation (see **Figure 9** for topographic map). These mean amplitudes were subjected to a Memory (remembered, forgotten) X Hemisphere (right, left) X Electrode Location (anterio-frontal (AF3 & AF4), central (C3 & C4), parietal (P3 & P4), parieto-occipital (PO3 & PO4)) repeated measures ANOVA. Results of this analysis revealed a main effect of Electrode Location [$F(1.98, 19.78) = 17.30$, $p < 0.001$] and a marginally significant Memory X Electrode Location interaction [$F(3, 30) = 2.53$, $p = 0.08$]. The main effect of Memory was not significant [$F(1,10) = 0.74$, $p = 0.41$] , and neither was the main effect of Hemisphere [$F(1,10) =0.63$, $p = 0.45$]. The Hemisphere X Location interaction was not significant [$F(3, 30) = 0.73$, $p = 0.54$] and neither was the Memory X Hemisphere X Location interaction [$F(2.94, 29.38) = 0.53$, $p = 0.66$]. Paired t-tests following up the marginal Memory X Electrode Location interaction resulted in a marginally significant difference in mean amplitude between subsequently remembered and forgotten trials at electrode PO3 [$t(1,10) = 1.97$ $p = .07$]. Specifically, mean amplitude for subsequently remembered trials was more negative than subsequently remembered trials (see **Figure 10**). There were no significant differences at electrodes AF3 [$t(1,10) = 0.25$ $p = 0.81$], AF4 [$t(1,10) = 0.62$ $p = 0.55$], C3 [$t(1,10) = 1.24$ $p = 0.24$], C4 [$t(1,10) = 1.25$ $p = 0.24$], P3 [$t(1,10) = 0.16$ $p = 0.87$], P4[$t(1,10) = 0.43$ $p = 0.68$], and PO4 [$t(1,10) = 1.33$ $p = .21$].

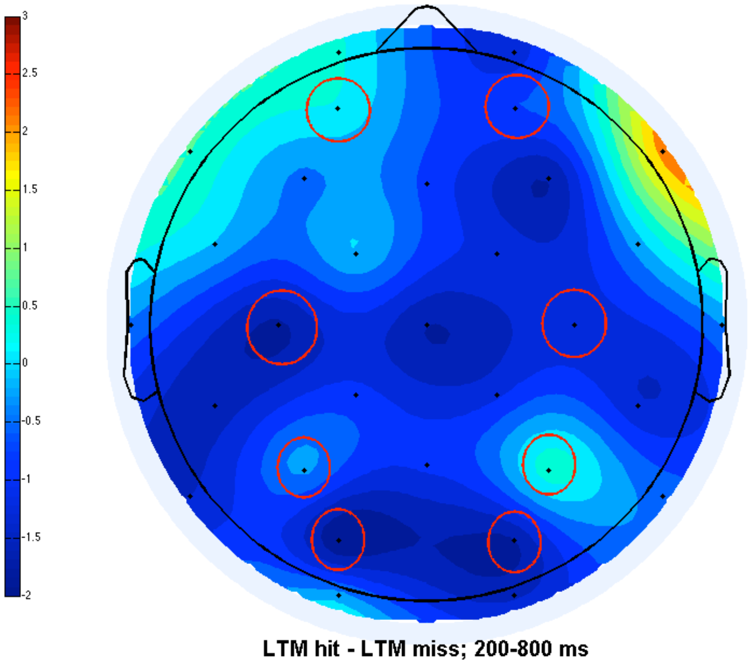


Figure 9. Slow-wave topography during the delay period. Electrodes used in the analysis are circled.

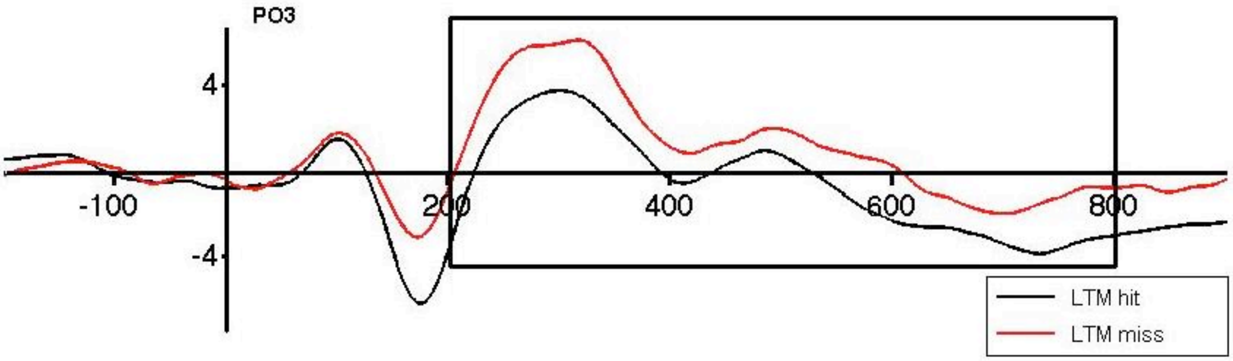
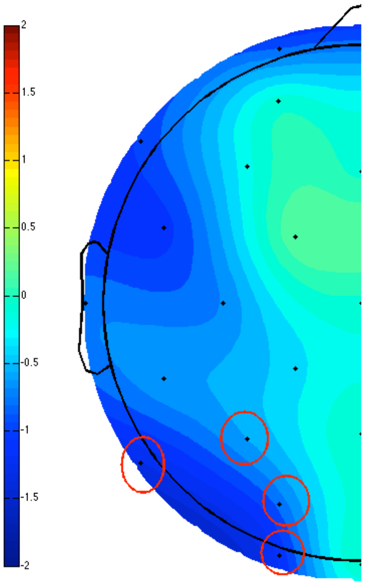


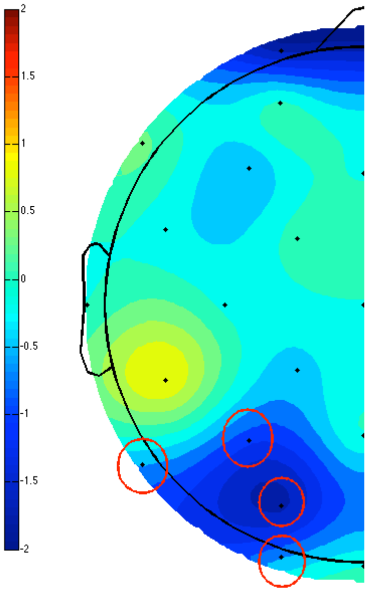
Figure 10. Slow-wave ERP during the delay period for electrode PO3. The rectangle indicates the analysis window.

N2pc

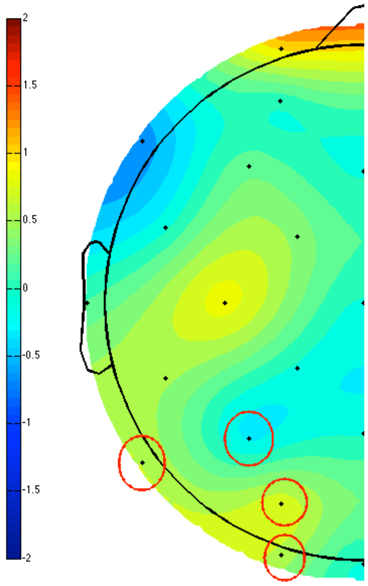
Due to low trial counts for 5 participants (< 10 trials in a condition) and excessive artifacts in the EEG data for 1 participant, N2pc analyses were conducted on 13 participants. In order to assess the contents of visual working memory, we sought to compare N2pc activity during a visual search task with possible N2pc activity to the probe at working memory. To this end, mean amplitudes measured 240-300ms after the array for hits in the visual search task and after the probe for hits in the VWM task were subjected to a Task (visual search, VWM retro-cue, VWM neutral-cue) X Hemifield (contralateral, ipsilateral) X Electrode Pair (P7P8, P3/P4, PO3/PO4, O1/O2) repeated measures ANOVA (see **Figure 11** for topographical maps of each task; see **Figure 12** for waveforms at each electrode pair in the analysis) . This analysis revealed main effects of Hemifield [$F(1,12) = 8.32, p = .01$] and Electrode Pair [$F(2.15,25.79) = 4.69, p = 0.02$], and significant Task X Hemifield [$F(1.82, 21.90) = 4.10, p = 0.03$], and Task X Electrode Pair [$F(4.76, 57.12) = 8.67, p < .001$] interactions. The main effect of Task was not significant [$F(1.65, 19.77) = 0.12, p = 0.85$] and neither was the Hemifield X Electrode Pair interaction [$F(3, 36) = 0.18, p = .91$]. The three-way Task X Hemifield X Electrode Pair interaction also was not significant [$F(4.71, 56.66) = 1.44, p = 0.23$]. Subsidiary ANOVAs tested for the N2pc (main effect of Hemifield) in each task separately. For the visual search task, a Hemifield (contralateral, ipsilateral) X Electrode Pair (P7P8, P3/P4, PO3/PO4, O1/O2) repeated measures ANOVA led to significant main effects of Hemifield [$F(1, 12) = 5.45, p = 0.04$] and Electrode Pair [$F(2.55, 30.57) = 14.82, p < 0.001$], but no Hemifield X Electrode Pair interaction [$F(2.94, 35.34) = 0.87, p = 0.47$]. The same ANOVA For the neutral cue trials at VWM led to a significant main effect of Hemifield [$F(1, 12) = 4.55, p = 0.05$], no main effect of Electrode Pair [$F(1.90, 22.79) = 1.64, p = 0.22$], and no Hemifield X Electrode Pair interaction [$F(2.47, 29.65) = 1.21, p = 0.32$]. The same ANOVA for the retro-cue trials at VWM led to a marginally significant main effect of Hemifield [$F(1, 12) = 4.23$, $p = 0.06$], no main effect of Electrode Pair [$F(2.09, 25.05) = 1.16$, $p = 0.33$], and no Hemifield X Electrode Pair interaction [$F(2.76, 33.12) = 0.76$, $p = 0.52$]. In the visual search task ANOVA and the VWM neutral cue task ANOVA, the main effect of Hemifield reflects contralateral activity being more negative than ipsilateral activity typical of the N2pc. The marginal main effect of Hemifield in the VWM retro-cue task ANOVA however, reflects ipsilateral activity being more negative gong than contralateral activity.



Visual Search: Contralateral - Ipsilateral; 240-300ms after the array



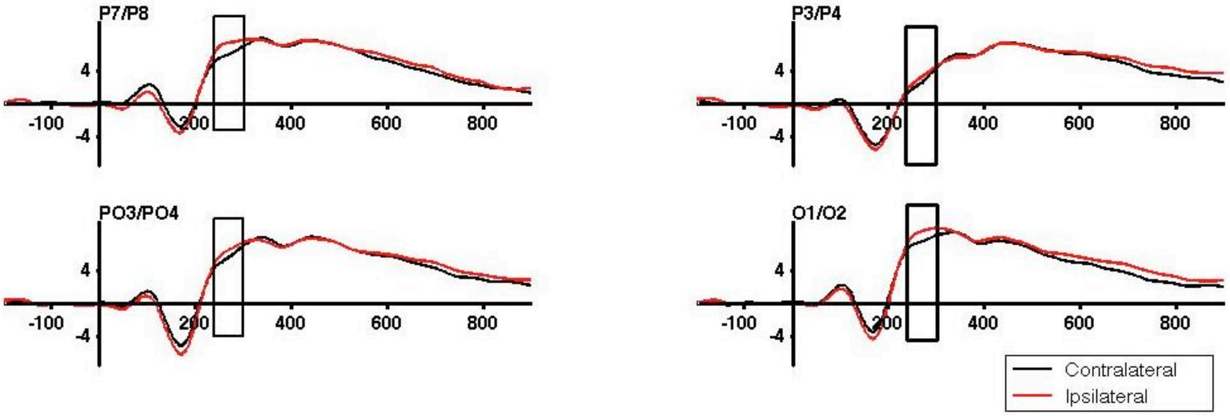
Neutral Cue: Contralateral - Ipsilateral; 240-300ms after the probe



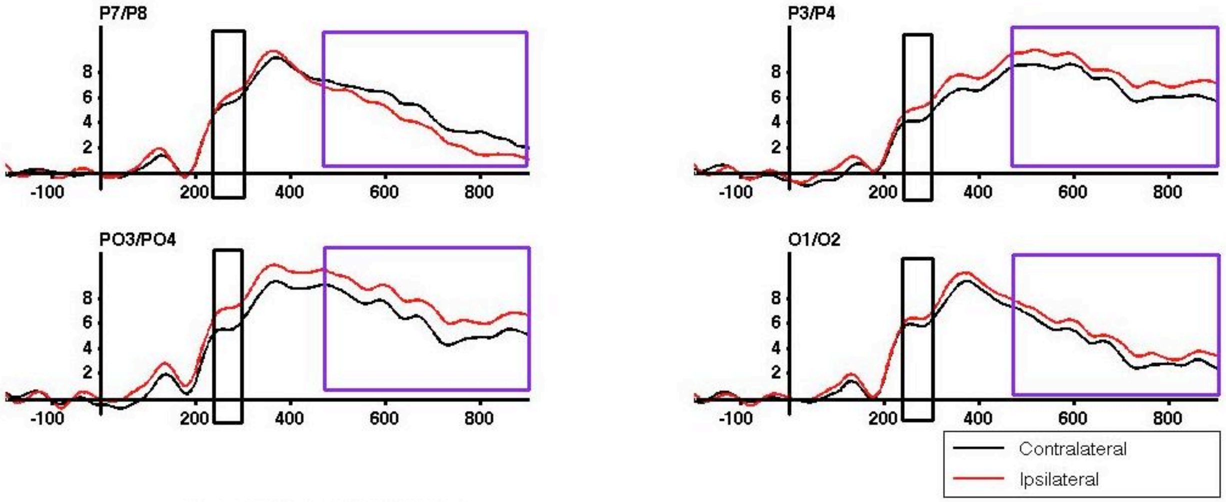
Retro-cue: Contralateral - Ipsilateral; 240-300ms after the probe

Figure 11. Scalp topographies of the N2pc for the visual search task, neutral-cue trials in the VWM task, and retro-cue trials in the VWM task. Electrodes used in the analysis are circled. Only one side of the scalp is shown since activity was averaged across hemispheres.

Visual Search ERPs:



Neutral Cue at VWM ERPs:



Retro-Cue at VWM ERPs:

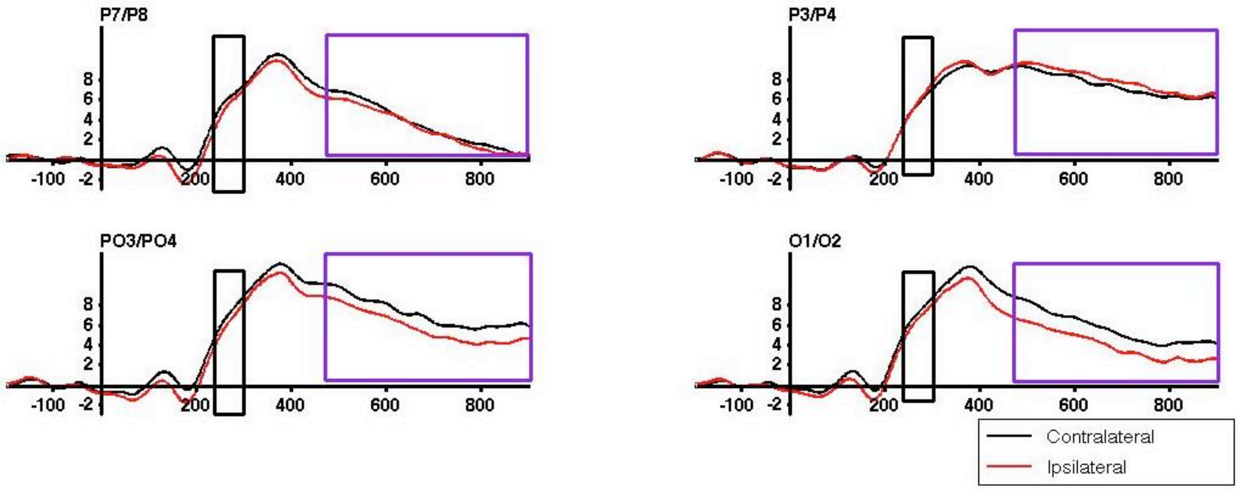


Figure 12. ERPs to the array in the visual search task and to the probe in the VWM component for both retro-cue and neutral-cue trials. The first rectangle indicates the time window for detecting an N2pc. The second rectangle indicates the time window for investigating the hemifield differences in the P3b.

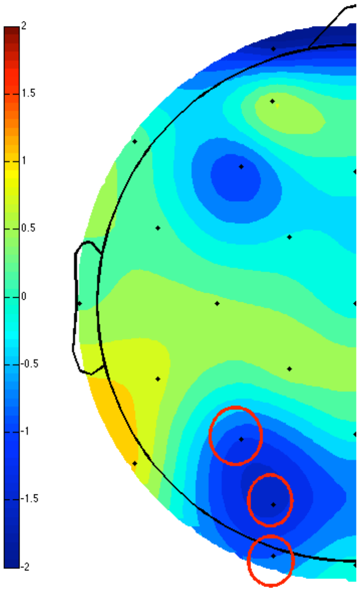
P3b: Sustained Hemifield Differences

Hemifield differences continued to persist 470-900ms after the onset of the probe for both retro-cue and neutral-cue trials at occipital electrodes (see **Figure 13** for topographical maps and **Figure 12** for waveforms at occipital electrodes). This positive deflection at occipital electrodes occurring 470-900ms after the test probe is characteristic of the P3b ERP, which reflects working memory updating (Donchin & Coles, 1988). Mean amplitudes measured 470-900ms after the test probe onset were subjected to a Cue (retro, neutral) X Hemifield (contralateral, ipsilateral) X Electrode Pair (P3/P4, PO3/PO4, O1/O2) repeated measures ANOVA. This analysis revealed a main effect of Electrode Pair [$F(2, 24) = 20.09$, $p < 0.001$] and a significant Cue X Hemifield interaction [$F(1, 12) = 28.08$, $p < 0.001$]. The main effect of Cue was not significant [$F(1, 12) = 0.005$, $p = 0.95$] and neither was the main effect of Hemifield [$F(1, 12) =$

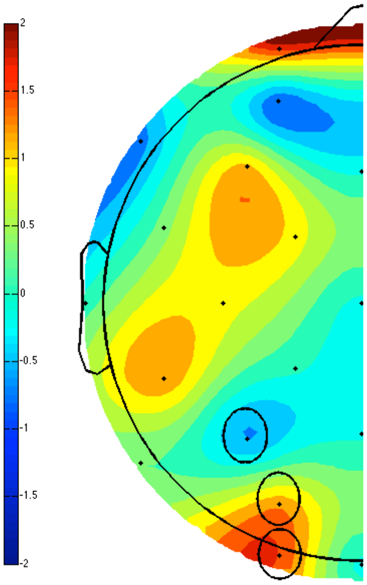
0.09, $p = 0.77$]. The Cue X Electrode Pair interaction was not significant [$F(1.86, 22.33) = 0.85$, $p = 0.43$] and neither was the Hemifield X Electrode Pair interaction [$F(1.58, 18.97) = 1.13$, $p = 0.33$], nor the Cue X Hemifield X Electrode Pair interaction [$F(1.98, 23.75) = 2.23$, $p = 0.13$].

We followed up the Cue X Hemifield interaction with subsidiary ANOVAs for each cue-type. For retro-cue trials, a Hemifield (contralateral, ipsilateral) X Electrode Pair (P3/P4, PO3/PO4, O1/O2) repeated measures ANOVA revealed a significant main effect of Hemifield [$F(1, 12) = 5.37$, $p = 0.04$], a main effect of Electrode Pair [$F(1.97, 23.67) = 13.68$, $p < 0.001$], and a marginally significant Hemifield X Electrode Pair interaction [$F(1.57, 18.86) = 3.26$, $p = 0.07$]. Paired t-tests were used to determine the source of the marginal Hemifield X Electrode Pair interaction. These tests revealed that for retro-cue trials, contralateral mean amplitudes were more positive than ipsilateral amplitudes at electrode pairs PO3/PO4 [$t(1,12) = 3.21$ $p = 0.01$] and O1/O2 [$t(1,12) = 4.82$ $p < 0.001$]. There were no significant differences at pair P3/P4 [$t(1,12) = 0.51$ $p = .62$].

For neutral cue-trials, a Hemifield (contralateral, ipsilateral) X Electrode Pair (P3/P4, PO3/PO4, O1/O2) repeated measures ANOVA revealed a significant main effect of Hemifield [$F(1, 12) = 9.40$, $p = 0.01$] and a main effect of Electrode Pair [$F(1.80, 21.61) = 14.74$, $p < 0.001$]. The Hemifield X Electrode Pair interaction was not significant [$F(1.573\ 18.32) = 0.19$, $p = 0.77$]. The main effect of Hemifield reflects ipsilateral activity being more positive than contralateral activity.



Neutral Cue: Contralateral - Ipsilateral ; 470-900ms



Retro-Cue Contralateral - Ipsilateral; 470-900ms

Figure 13. P3b topographical maps for neutral-cue trials and retro-cue trials in the VWM task. Electrodes used in the analysis are circled. Only one side of the scalp is shown since activity was averaged across hemispheres.

Old/New Effects at Long-term Memory

Due to low trial counts in 9 participants (< 13 trials in a condition) and excessive EEG artifacts in 1 participant, the following analyses are based on 9 participants. To investigate potential lateralized differences, mean amplitudes measured 550-800ms after the presentation of the test probe for items that were hits at both VWM and long-term memory (VWM/LTM hit) were subjected to a Hemifield (contralateral, ipsilateral) X Electrode Pair (AF3/AF4, F7/F8, CP1/CP2, P3/P4, PO3/PO4) repeated measures ANOVA (see **Figure 14** for waveforms at electrodes used in this analysis). This analysis revealed a main effect of electrode pair [$F(2.74, 21.95) = 26.16, p < 0.001$] but no main effect of Hemifield [$F(1, 8) = 0.99, p = 0.35$], and no Hemifield X Electrode Pair interaction [$F(2.86, 22.88) = 0.49, p = 0.68$].

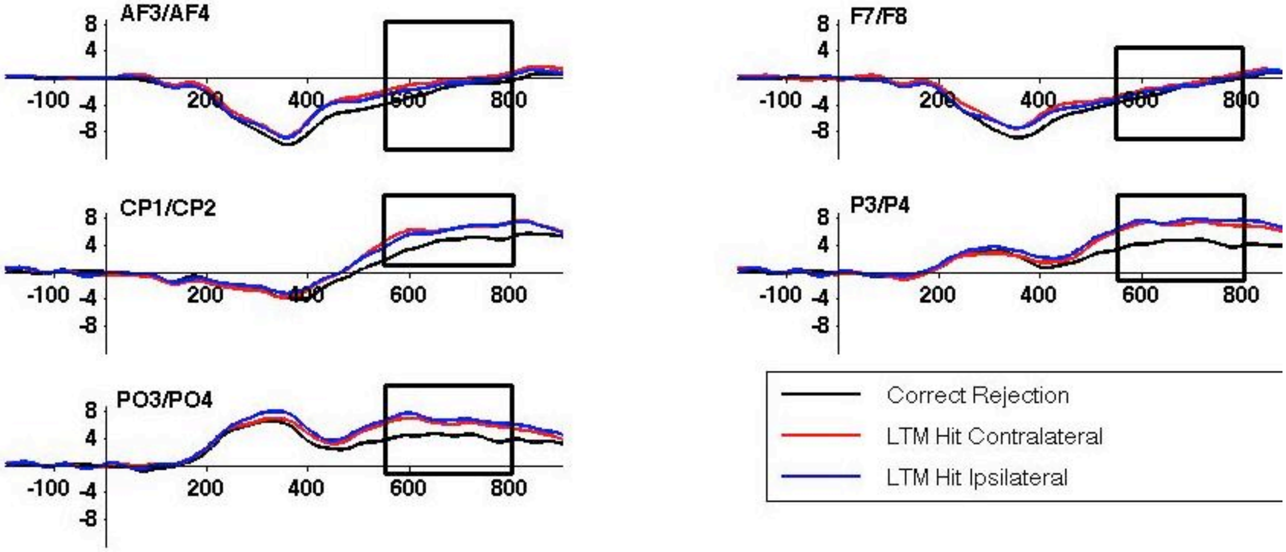


Figure 14. Waveforms during the long-term memory component. The rectangle indicates the analysis window.

While lateralized effects were not evident given the lack of a Hemifield main effect, the typical parietal old/new effect whereby previously presented stimuli elicit greater positive activity than new items was still apparent. To investigate parietal old/new effects, mean amplitudes measured 550-800 after the presentation of the test probe for VWM/LTM hit trials were subjected to an Accuracy (WM/LTM hit, previously presented on the left; WM/LTM hit, previously presented on the right; correct rejection) X Electrode Location (anterio-frontal (AF3 & AF4), frontal (F7 & F8), parieto-central (CP1 & CP2), parietal (P3 & P4), parieto-occipital (PO3 & PO4)) X Hemisphere (right, left) repeated measures ANOVA. Results of this analysis indicated a marginally significant main effect of Accuracy [$F(1.65, 13.20) = 3.75$ $p = 0.06$], a main effect of Electrode Location [$F(2.81, 22.52) = 24.19$, $p < 0.001$], and a significant Accuracy X Electrode Location interaction [$F(8, 64) = 2.22$, $p = 0.04$]. The main effect of Hemisphere was not significant [$F(1, 8) = 2.51$, $p = 0.15$], and neither was the Accuracy X Hemisphere interaction [$F(1.79, 14.30) = 0.52$, $p = 0.58$], the Electrode Location X Hemisphere interaction [$F(4, 32) = 2.15$, $p = 0.10$], nor the Accuracy X Electrode Location X Hemisphere interaction [$F(4.46, 35.65) = 0.52$, $p = 0.74$].

The Accuracy X Electrode Location interaction was followed up with subsidiary ANOVAs comparing 2 levels of accuracy at a time to determine the source of the interaction (i.e. old/new effects). The first Accuracy X Electrode Location X Hemisphere ANOVA compared VWM/LTM hits presented on the left and VWM/LTM hits presented on the right. This analysis revealed a significant main effect of Electrode Location [$F(2.79, 22.30) = 25.48$, $p < 0.001$]. The main effect of Accuracy was not significant [$F(1, 8) = 0.48$, $p = 0.51$] and neither was the Main effect of Hemisphere [$F(1, 8) = 2.41$, $p = 0.16$]. The Accuracy X Electrode Location interaction was not significant [$F(4, 32) = 1.27$, $p = 0.30$], and neither was the Accuracy X Hemisphere interaction [$F(1, 8) = 0.769$, $p = 0.43$], the Electrode Location X Hemisphere interaction [$F(3.98, 31.82) = 1.95$, $p =$

0.13], nor the Accuracy X Electrode Location X Hemisphere interaction [$F(3.33, 26.63) = 0.53$, $p = 0.68$].

The same ANOVA was conducted with the 2 levels of Accuracy as VWM/LTM hits presented on the left and correct rejections. This analysis revealed a significant main effect of Electrode Location [$F(2.64, 21.14) = 18.53$, $p < 0.001$]. The main effect of Accuracy was not significant [$F(1, 8) = 2.95$, $p = 0.12$] and neither was the Main effect of Hemisphere [$F(1, 8) = 1.25$, $p = 0.29$]. The Accuracy X Electrode Location interaction was marginally significant [$F(3.16, 25.26) = 2.46$, $p = 0.08$]. The Accuracy X Hemisphere interaction was not significant [$F(1, 8) = 0.04$, $p = 0.84$], and neither was the Electrode Location X Hemisphere interaction [$F(4, 32) = 1.95$, $p = 0.13$], nor the Accuracy X Electrode Location X Hemisphere interaction [$F(4, 32) = 0.80$, $p = 0.53$]. Pared samples t-tests were used to investigate the marginal Accuracy X Electrode interaction. Mean amplitude for VWM/LTM hits presented on the left was significantly more positive than mean amplitude for correct rejections (i.e. old/new effect) at electrode PO3 [$t(1,8) = 2.42$, $p = 0.04$] and marginally significant at electrode P3 [$t(1,8) = 2.21$, $p = 0.06$] and P4 [$t(1,8) = 1.97$, $p = 0.08$]. There were no significant differences at electrodes AF3 [$t(1,8) = 1.03$, $p = 0.33$], AF4 [$t(1,8) = 1.61$, $p = 0.15$], F7 [$t(1,8)= 0.36$, $p = 0.72$], F8 [$t(1,8) = 0.45$, $p = 0.67$], CP1 [$t(1,8) = 1.01$, $p = 0.34$], CP2 [$t(1,8) = 0.89$, $p = 0.40$], and PO4 [$t(1,8) = 1.43$, $p = 0.19$].

The final Accuracy X Electrode Location X Hemisphere ANOVA compared VWM/LTM hits presented on the right and correct rejections. This analysis revealed a significant main effect of Accuracy [$F(1, 8) = 18.20$, $p = 0.003$] and Electrode Location [$F(3.35, 26.78) = 25.78$, $p < 0.001$]. The main effect of Hemisphere was not significant

[$F(1, 8) = 3.25$, $p = 0.11$. The Accuracy X Electrode Location interaction was significant [$F(3.88, 31.08) = 2.89$, $p = 0.04$]. The Accuracy X Hemisphere interaction was not significant [$F(1, 8) = 1.45$, $p = 0.27$], and neither was the Electrode Location X Hemisphere interaction [$F(4, 32) = 0.54$, $p = 0.71$], nor the Accuracy X Electrode Location X Hemisphere interaction [$F(3.06, 24.49) = 0.15$, $p = 0.93$]. Pared samples t-tests were used to investigate the Accuracy X Electrode interaction. Mean amplitude for VWM/LTM hits presented on the right was significantly more positive than mean amplitude for correct rejections (i.e. old/new effect) at electrode CP1 [$t(1,8) = 3.94$, $p = 0.004$], CP2 [$t(1,8) = 2.28$, $p = 0.05$], P3 [$t(1,8) = 4.19$, $p = 0.003$], P4 [$t(1,8) = 4.41$, $p = 0.002$], PO3 [$t(1,8) = 4.75$, $p = 0.001$], PO4 [$t(1,8) = 2.32$, $p = 0.05$], and marginally at F8 [$t(1,8) = 2.17$, $p = 0.06$]. There were no significant differences at electrodes AF3 [$t(1,8) = 1.24$, $p = 0.25$], AF4 [$t(1,8) = 0.47$, $p = 0.65$], and F7 [$t(1,8)= 1.00$, $p = 0.34$].

The same Accuracy (WM/LTM hit, previously presented on the left; WM/LTM hit, previously presented on the right; correct rejection) X Electrode Location (anterio-frontal, frontal, parieto-central, parietal, parieto-occipital) X Hemisphere (right, left) repeated measures ANOVA was conducted on a time window 250-450ms after presentation of the test probe to investigate frontal old/new effects. This analysis revealed a main effect of Electrode Location [$F(1.86, 14.86) = 45.95$, $p < .001$], no main effect of Accuracy [$F(1.93, 15.46) = 1.80$, $p = 0.20$], and no main effect of Hemisphere [$F(1, 8) = 0.89$, $p = 0.37$]. The Accuracy X Electrode Location interaction was not significant [$F(8, 64) = 1.15$, $p = 0.34$] and neither was the Accuracy X Hemisphere interaction [$F(2, 16) = 0.60$, $p = 0.56$], the Electrode Location X Hemisphere interaction [$F(3.97, 31.80) = 0.71$, $p = 0.59$], nor the Accuracy X Electrode Location X Hemisphere interaction [$F(5.21, 41.71) = 0.92, $p = 0.48$]. The lack interactions involving Accuracy and Electrode Location indicate that we did not detect a significant frontal old/new effect.

CHAPTER 5

DISCUSSION

Behavior

Item Memory

This is the first study to our knowledge to assess retrospective attention benefits at long-term memory. Results from the VWM task revealed a typical retro-cue benefit whereby item accuracy and reaction time improved following retro-cue trials compared to neutral cue trials. In agreement with an interactive systems account of memory, the item accuracy benefit afforded by the retro-cue continued to be reflected in long-term memory performance. These results suggest that attentional processes like retrospective attention can influence later long-term memory, which is consistent with a less discrete model of memory than previous models have proposed (i.e. Atkinson & Shiffrin, 1968). We do note, however, that there was statistically significant memory decay for both cue types at long-term memory and that effect size (Cohen's d) was larger for the VWM task compared to the long-term memory task. This may indicate that whatever protective features the retro-cue offers at working memory (reducing effective memory load, refreshing the representation of the cued item, or some combination) does not offer complete protection from memory decay at later delays.

Location Memory

It was also novel to test for retrospective attention benefits for location memory. The present study did not find accuracy differences for location memory at long-term memory between the two cue types. As a reminder, we couldn't probe location memory at working memory because we couldn't be certain that participants were remembering the location of the object and not the recently presented retro-cue. The long-term memory results suggest that retro-cues selectively enhance item memory and not location memory. It is interesting to note that while retro-cues selectively enhance item memory, that benefit isn't to the detriment of location memory. It would be reasonable to think that a cue enhancing item identity might cause participants to purge the currently irrelevant location information, which should lead to decreased location memory performance. That is not what we found here. Instead, location accuracy for both the hemifield and specific vertical location were nearly identical for previously neutral cued and retro-cued trials. However, participants did complete a practice block of both the VWM component and long-term memory component, so participants were aware that location information would be probed at a later test. This may have lead participants to maintain location-information for retro-cue trials during working memory, which may not represent how retrospective attention facilitates memory when future memory demands are unknown.

ERPs Measured During Working Memory Maintenance

Contralateral Delay Activity and Working Memory Maintenance

This was the first study to use real-world objects as a stimulus class for detecting the CDA. Previous studies have used simple stimuli like colored squares (for example, Kuo et al., 2012), so it was an open question whether or not the CDA would reflect maintenance of more complex stimuli. We did detect a significant CDA during the delay period using real-world objects, so it seems that the CDA can reflect maintenance of complex stimuli. However, the present study was not designed to assess the vividness/complexity of the representations being maintained. A set of experiments by Gao and colleagues did manipulate the complexity of stimuli (simple, nameable shapes versus complex symbols) and found amplitude differences in the CDA for memory loads of 2 and 4 (higher amplitudes for load of 4 compared to 2) when using simple but not complex shapes in a change detection task. The authors conclude that the CDA indexes coarse information entering VWM and not more detailed information. Based on this research, the CDA found here may reflect maintenance of the low-level features of the complex stimuli and not necessarily a vivid or detailed representation of the complex stimuli. More research manipulating stimuli complexity and resolution within an experiment in necessary for determining the nature of the representation held in VWM and what aspects of that representation influence the CDA.

Based on previous research (Duarte et al., 2013), we expected the CDA to persist following spatially uninformative neutral cues, which would indicate the continued maintenance of both items in the array, and attenuate following retro-cues, which would indicate a change from maintaining both items in the array to maintaining the cued item. However, we did not find significant differences in the CDA after the cue depending on cue type. More specifically, the CDA continued following both retro-cues and neutral cues. This may be due to the nature of the stimuli and the set-size used in the present study. That is, the cognitive demand of maintaining one complex item in working memory following a retro-cue isn't significantly different from continuing to maintain two complex items following a neutral cue. Previous research does indicate that reductions in the CDA following retro-cues are less evident for smaller set-sizes (Kuo et al., 2012), so it may be the case that a larger set size in the array would have lead to larger differences in amplitude between retro-cue and neutral cue trials.

Contralateral Delay Activity as a Function of Subsequent Long-term Memory Performance

We predicted that CDA magnitude observed at working memory would reflect accurate maintenance at both working memory and long-term memory delays. Previous studies have found that CDA amplitude is reduced for incorrect trials compared to correct trials at working memory (McCollough et al., 2007), so it seemed reasonable to think that reduced amplitude would also be associated with subsequently forgotten trials at long-term memory; the idea being that greater magnitude reflected more information about the stimulus being maintained. However, we were severely underpowered for this analysis. Long-term item accuracy was quite good, which left a small number of participants (6) with enough subsequently forgotten trials to examine ERPs. A CDA was not detectable with so few participants.

Slow-wave ERPs During Maintenance

While we couldn’t determine from this data whether or not the CDA was modulated by subsequent long-term memory performance, we were able to assess another marker of working memory maintenance: slow-wave ERPs. Previous research by Khader and colleagues (Khader et al., 2007) has shown that negative-going, slow-wave ERPs are modulated by subsequent performance on a surprise long-term memory task for both strings of letters and line drawings of novel objects. Topographies of the 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 distinctions and differences depending on subsequent long-term memory performance, these researchers conclude that working memory maintenance in stimulus-specific brain areas is conducive to long-term memory formation. Results of the present study corroborate Khader and colleagues work (Khader et al., 2007) while using real-world objects as stimuli. In the present data, we observed significant differences in slow-wave ERPs at occipital locations for VWM hits that were subsequently remembered and those that were forgotten. These results support the idea that working memory maintenance impacts long-term memory performance, which is consistent with a less discrete model of memory.

ERPs to the Probe

N2pc at Visual Working Memory Compared to Visual Search

The present study also sought to investigate the nature of visual working memory representations. We were particularly interested in whether or not item identity and location information were maintained as a bound representation within working memory. In order to assess whether or not location information was part of the representation held in working memory, we monitored N2pc activity to the probe, which represents attentional selection in visual search. Previous research has shown that both visual search tasks and VWM tasks can elicit N2pc activity with the same time-course and topographic distribution (Kuo et al., 2009). These results suggested that participants search through a visual display held in VWM in the same manner as they search a physically present display in a visual search task. That is, location information and item identity are bound in the array held in memory as they are in a physical array. We tested for similar effects here using complex, real world objects instead of simple colored squares and random line shapes as stimuli, as the previous study had. As expected, we observed a significant N2pc during the visual search task. More interestingly, we also observed a significant N2pc following neutral-cue trials during the VWM task at the same time window and scalp location. This suggests that participants were searching the array held in visual working memory for the probe in the same way they searched for a target in the physically present array. These results corroborate previous research and support the idea that item identity and item location are bound representations in visual working memory.

We did not observe an N2pc following retro-cue trials, which is not surprising given the evidence that retro-cues improve VWM by reducing effective memory load (Kuo et al., 2009). That is, following the retro-cue, participants stopped maintaining the irrelevant items and, at the time of the probe, the only necessary comparison was between the remaining item held in working memory and the probe.

P3b and Hemifield Differences

As discussed in the introduction, a previous study by Duarte and colleagues (Duarte et al., 2013) monitored the P3b to examine any effects retro-cuing had on working memory updating. In that study, the P3b did not differ between contralateral and ipsilateral hemifield so mean amplitudes of the P3b were collapsed across hemifield. In the present study however, there were hemifield differences in the P3b. An important difference between the present study and the previous study by Duarte and colleagues (Duarte et al., 2013) is that the present study assess item location at a subsequent long-term memory test, which participants are aware of. The hemifield differences observed in the present study may indicate the updating of location information in anticipation of the future location probe at long-term memoy. If so, this updating process doesn't appear to be identical across cue-type. For neutral cue trials, ipsilateral activity was greater than contralateral activity. In contrast, contralateral activity was greater than ipsilateral activity for retro-cue trials. This may indicate that the way the retro-cue isolates the to-be probed item changes the way location information is updated and maintained. It is apparent from behavioral long-term memory performance that location information is maintained to a similar degree for both cue-types, but these differences in the P3b by cue-type suggest that the processes that support later location memory may not be the same for both cues.

ERPs at Long-term Memory

In addition to VWM representations, we were also curious about the content of long-term memory representations. To this end, we monitored lateralized old/new potentials to determine if traces of previous hemifield location were evident at long-term memory (as found in Gratton et al., 1997). Unfortunately, we were underpowered for this analysis with only 9 participants having a sufficient number of trials to examine ERPs. Specifically, dividing subsequent long-term memory hits by hemifield presentation led to too few trials in 9 participants. An additional participant was excluded for excessive EEG noise. The analysis of the remaining 9 participants did not reveal any lateralized old/new effects, tentatively suggesting that spatial traces were not evident at long-term memory. However, behavioral evidence from the present study demonstrates that location information was remembered above chance for both cue types. The potential discrepancy between preserved location information demonstrated behaviorally and a lack of hemisphere organization may be due in part to the nature of the present task. To elaborate, the present study required participants to attend to half of an array with 3 distinct positions while the Gratton et al. (1997) study presented one item to the left or right of a central fixation. It could be the case that the more complex visual array here required a different kind of maintinence at working memory (potentially demonstrated here in the P3b hemifield differences) which led to a different kind of long-term memory representation compared to the more discrete positions used in the Gratton et al. study (1997). Although lateralized old/new effects were not apparent in so few participants, we were able to detect a typical parietal old/new effect, which discriminated recollection of previously presented stimuli from correct rejections.

CHAPTER 6

CONCLUSION

To summarize, the present study offers support for an interactive systems account of memory. Retrospective attention improved item accuracy at both working-memory and long-term memory delays, which challenges previous models of memory that suggest working-memory and long-term memory are discrete systems. Additionally, ERP measures of working-memory maintenance in the form of slow-waves differentiated depending on later long-term memory performance, which also suggests that working memory and long-term memory are interactive. More specifically, slow-wave differences depending on subsequent long-term memory performance may suggest that working-memory maintenance in stimuli-specific cortical areas (occipital sites for objects, in the case of the present study) helps strengthen long-term memory traces (see Khader et al., 2007).

Regarding VWM representations, results from the present study corroborate previous evidence that location information and item identity are bound in VWM representations. Here, the N2pc elicited during the visual search task and the N2pc elicited during the VWM task for neutral cue trials occurred over the same time course and topography, suggesting that participants were searching an array held in VWM for a target in the same manner they searched a physically present array for a target.

REFERENCES

Anderson, D. E., Vogel, E. K., & Awh, E. (2011). 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, 31*(3), 1128-1138. doi: 10.1523/JNEUROSCI.4125-10.2011

Atkinson, R. C., & Shiffrin, R. M. (1968). Human memory: A proposed system and its control processes. In K. W. Spence & J. T. Spence (Eds.), *The psychology of learning and motivation: Advances in research and theory* (Vol. 2). New York: Academic Press.

Bahcall, D. O., & Kowler, E. (1999). Attentional interference at small spatial separations. *Vision Research, 39*(1), 71-86.

Benton, A. L., Hamsher, K., Sivan, A.B. (1994). Multilingual Aphasia Examination. Bleckley, M. K., Durso, F. T., Crutchfield, J. M., Engle, R. W., & Khanna, M. M. (2003). Individual differences in working memory capacity predict visual attention allocation. *Psychon Bull Rev, 10*(4), 884-889.

Brady, T. F., Konkle, T., Alvarez, G. A., & Oliva, A. (2008). Visual long-term mmemory has a massive storage capacity for object details. *Proceedings of the National Academy of Sciences, 105*(38), 14325-14329.

Brisson, B., & Jolicoeur, P. (2007). The N2pc component and stimulus duration. *Neuroreport, 18*(11), 1163-1166. doi: 10.1097/WNR.0b013e3281e72d1b

Brodeur, M. B., Dionne-Dostie, E., Montreuil, T., & Lepage, M. (2010). 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, 5*(5), e10773.

Cohen, J. (1988). *Statistical power analysis for the behavioral sciences* (2 ed.). Hillsdale, NJ: Lawrence Earlbaum Associates.

Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics. . *Journal of Neuroscience Methods, 134*, 9-21.

Donchin, E., & Coles, M. G. H. (1988). Is the P300 component a manifestation of context updating. *Behavioral and Brain Sciences, 11*, 357-374.

Duarte, A., Hearons, P., Jiang, Y., Delvin, M. C., Newsome, R. N., & Verhaeghen, P. (2013). Retrospective attention enhances visual working memory in the young but not the old: an ERP study. *Psychophysiology, 50*(5), 465-476. doi: 10.1111/psyp.12034

Eimer, M. (1996). The N2pc component as an indicator of attentional selectivity. *Electroencephalography and Clinical Neurophysiology, 99*(3), 225-234.

Ester, E. F., Serences, J. T., & Awh, E. (2009). Spatially global representations in human primary visual cortex during working memory maintenance. *The Journal of neuroscience : the official journal of the Society for Neuroscience, 29*(48), 15258-15265. doi: 10.1523/JNEUROSCI.4388-09.2009

Gazzaley, A., Rissman, J., & D'Esposito, M. (2004). Functional connectivity during working memory maintenance. *Cogn Affect Behav Neurosci, 4*(4), 580-599.

Gratton, G., Corbalis, P. M., & Jain, S. (1997). Hemispheric organization of visual memories. *Journal of Cognitive Neuroscience, 9*(1), 92-104.

Hickey, C., Di Lollo, V., & McDonald, J. J. (2009). Electrophysiological indices of target and distractor processing in visual search. *Journal of Cognitive Neuroscience, 21*(4), 760-775. doi: 10.1162/jocn.2009.21039

Jost, K., Bryck, R. L., Vogel, E. K., & Mayr, U. (2011). Are old adults just like low working memory young adults? Filtering efficiency and age differences in visual working memory. *Cerebral Cortex, 21*(5), 1147-1154. doi: 10.1093/cercor/bhq185

Khader, P., Ranganath, C., Seemüller, A., & Rösler, F. (2007). Working memory maintenance contriubutes to long-term memory formation: Evidence from slow-event-related brain potentials. *Cognitive, Affective, & Behavioral Neuroscience, 7*(3), 212-224.

Kiss, M., Van Velzen, J., & Eimer, M. (2008). The N2pc component and its links to attention shifts and spatially selective visual processing. *Psychophysiology, 45*(2), 240-249. doi: 10.1111/j.1469-8986.2007.00611.x

Kuo, B. C., Rao, A., Lepsien, J., & Nobre, A. C. (2009). Searching for targets within the spatial layout of visual short-term memory. *Journal of Neuroscience, 29*(25), 8032-8038. doi: 29/25/8032 [pii]
10.1523/JNEUROSCI.0952-09.2009

Kuo, B. C., Stokes, M. G., & Nobre, A. C. (2012). Attention modulates maintenance of representations in visual short-term memory. *Journal of Cognitive Neuroscience, 24*(1), 51-60. doi: 10.1162/jocn_a_00087

Lepsien, J., & Nobre, A. C. (2007). Attentional modulation of object representations in working memory. *Cerebral Cortex, 17*(9), 2072-2083. doi: 10.1093/cercor/bhl116

Luck, S. J., & Hillyard, S. A. (1994). Spatial filtering during visual search: evidence from human electrophysiology. *Journal of Experimental Psychology: Human Perception and Performance, 20*(5), 1000-1014.

Makovski, T., & Jiang, Y. V. (2007). Distributing versus focusing attention in visual short-term memory. *Psychon Bull Rev, 14*(6), 1072-1078.

Makovski, T., Sussman, R., & Jiang, Y. V. (2008). Orienting attention in visual working memory reduces interference from memory probes. *Journal of Experimental Psychology. Learning, Memory, and Cognition, 34*(2), 369-380. doi: 10.1037/0278-7393.34.2.369

Matsukura, M., Luck, S. J., & Vecera, S. P. (2007). Attention effects during visual short-term memory maintenance: protection or prioritization? *Perception and Psychophysics, 69*(8), 1422-1434.

McCollough, A. W., Machizawa, M. G., & Vogel, E. K. (2007). Electrophysiological measures of maintaining representations in visual working memory. *Cortex; a journal devoted to the study of the nervous system and behavior, 43*(1), 77-94.

Murdock, B. B., Jr. (1962). The serial position effect of free recall. *Journal of Experimental Psychology, 64*(5), 482-488. doi: 10.1037/h0045106

Oberauer, K., Schulze, R., Wilhelm, O., & Suss, H. M. (2005). Working memory and intelligence--their correlation and their relation: comment on Ackerman, Beier, and Boyle (2005). *Psychological Bulletin, 131*(1), 61-65; author reply 72-65. doi: 10.1037/0033-2909.131.1.61

Öztekin, I., McElree, B., Staresina, B. P., & Davachi, L. (2009). Working memory retrieval: Contributions of the left prefrontal cortex, the left posterior parietal cortex, and the hippocampus. *Journal of Cognitive Neuroscience, 21*(3), 581-593. doi: 10.1162/jocn.2008.21016

Polich, J. (2007). Updating P300: an integrative theory of P3a and P3b. *Clinical Neurophysiology, 118*(10), 2128-2148. doi: S1388-2457(07)00189-7 [pii] 10.1016/j.clinph.2007.04.019

Postle, B. R., & D'Esposito, M. (1999). "What"-Then-Where" in visual working memory: an event-related fMRI study. *Journal of Cognitive Neuroscience, 11*(6), 585-597.

Ranganath, C., Cohen, M. X., & Brozinsky, C. J. (2005). Working Memory Maintenance Contributes to Long-term Memory Formation: Neural and Behavioral Evidence. *Journal of Cognitive Neuroscience, 17*(7), 994-1010. doi: 10.1162/0898929054475118

Reitan, R., & Wolfson, D. (1985). The Halstead-Reitan Neuropsychological Test Battery: Therapy and clinical assessment. *Tucson, AZ, Neuropsychological Press*.

Snodgrass, J., & Corwin, J. (1988). Pragmatics of measuring recognition memory: applications to dementia and amnesia. *Journal of Experimental Psychology, 116*, 34-50.

Squire, L. R. (2009). The legacy of patient H.M. for neuroscience. *Neuron, 61*(1), 6-9. doi: 10.1016/j.neuron.2008.12.023

Stokes, M., Thompson, R., Cusack, R., & Duncan, J. (2009). Top-down activation of shape-specific population codes in visual cortex during mental imagery. *The Journal of neuroscience : the official journal of the Society for Neuroscience, 29*(5), 1565-1572. doi: 10.1523/JNEUROSCI.4657-08.2009

Talmi, D., Grady, C. L., Goshen-Gottstein, Y., & Moscovitch, M. (2005). Neuroimaging the serial position curve. A test of single-store versus dual-store models. *Psychol Sci, 16*(9), 716-723. doi: 10.1111/j.1467-9280.2005.01601.x

Unsworth, N., & Engle, R. W. (2008). Speed and accuracy of accessing information in working memory: an individual differences investigation of focus switching. *Journal of Experimental Psychology. Learning, Memory, and Cognition, 34*(3), 616-630. doi: 10.1037/0278-7393.34.3.616

Unsworth, N., Heitz, R. P., Schrock, J. C., & Engle, R. W. (2005). An automated verson of the operation span task. . *Behavior Research Methods, 37*, 498-505.

Unsworth, N., & Spillers, G. J. (2010). Variation in working memory capacity and episodic recall: the contributions of strategic encoding and contextual retrieval. *Psychon Bull Rev, 17*(2), 200-205. doi: 10.3758/PBR.17.2.200

Vogel, E. K., & Machizawa, M. G. (2004). Neural activity predicts individual differences in visual working memory capacity. *Nature, 428*(6984), 748-751. doi: 10.1038/nature02447

Wechsler, D. (1997). *Wechsler memory scale*. San Antonio: Psychological corporation.

Williams, J. (1991). Memory assessment scales professional manual.