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BS, University of North Carolina at Chapel Hill, 2014

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An abstract of a thesis submitted to the Faculty of the
James T. Laney School of Graduate Studies of Emory University
in partial fulfillment of the requirements for the degree of
Master of Arts
in Psychology
2016

Abstract

Rhesus monkeys *(Macaca mulatta)* shift working memory resources to prioritize the maintenance of relevant information

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Working memory is a system by which a limited number of representations are maintained in the absence of sustained sensory input. Because resources are limited, the ability to control working memory resources is critical to prioritize the maintenance of information relevant to the current task. While evidence exists that monkeys exhibit some control over working memory, the extent to which monkeys can select among multiple representations to prioritize maintenance of relevant information is not known. Using a post-sample cueing paradigm, we tested the extent to which monkeys can prioritize the maintenance of relevant information among competing representations held in working memory. Monkeys saw an array of multiple items. Shortly after its disappearance, they were visually cued to a location that predicted which item would be tested in a subsequent recognition test. If monkeys prioritize the maintenance of the cued item, then they will show better memory for cued items compared to non-cued items. The results of three experiments indicate that monkeys prioritize the cued item with a memory load of two items, but not three. Our results suggest that monkeys, similar to humans, shift working memory resources to prioritize the maintenance of relevant information. Future work will be aimed at understanding the relationship between cognitive load and working memory control.

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Figures and Tables

1. Introduction

Working memory is a system by which a limited number of representations are maintained in the absence of sustained sensory input (Baddeley & Hitch, 1974; Oberauer, 2013) Because working memory resources are limited, it is critical to prioritize the maintenance of information relevant to the current task (Chun, Golomb, & Turk-Browne, 2011; Cowan, 2010; Unsworth & Engle, 2007). For instance, when navigating to a destination you may encode directions comprised of several steps. Each step you complete then becomes irrelevant to reaching your destination and does not need to be further maintained. It is beneficial then, to control memory resources in order to prioritize the maintenance of the relevant directions still to be completed. In humans, memory maintenance and control is often accomplished through the aid of verbal rehearsal (Baddeley, 2000; Smith, Jonides, & Koeppe, 1996; Wright et al., 1990). Thus, it is unclear how nonverbal species may engage in similar memory maintenance and control.

Recent studies have provided evidence that monkeys, similar to humans, may engage in active memory control such as the rehearsal of visual stimuli (Basile & Hampton, 2013), and the maintenance of working memory contents when a cue predicts an upcoming memory test (Tu & Hampton, 2014). However, a critical component of working memory control that has not been addressed in monkeys is the ability to selectively prioritize the maintenance of relevant information. We investigated the extent to which monkeys can select among multiple representations in working memory to prioritize the maintenance of relevant information.

Directed forgetting paradigms in humans have been used to test how memory resources are actively controlled to maintain specific items in working memory. When shown one or many stimuli to encode, participants can control whether or not they allocate memory resources to maintain items when a cue instructs them to do so (MacLeod, 1998). Typically, participants encode a set of items and are given a cue that predicts either an upcoming memory test, or a test not related to the encoded items such as a visual discrimination task. Control of memory resources is inferred from superior memory performance for items participants encoded and were instructed to remember, compared to items participants were not instructed to remember. Particiapnts show a memory benefit items cued to remember whether the cue is presented before, during, or after presentation of the sample stimuli, demonstrating that humans have a high degree of control over how memory resources are directed in working memory (MacLeod, 1998; Sheard & MacLeod, 2005).

In order to investigate the control of working memory in nonhumans, directed forgetting paradigms can be modified by replacing verbal instructions with contingencies of reinforcement where some conditions benefit from the control of memory and others do not (Tu & Hampton, 2014). Initial work applying this paradigm to nonhumans was performed with pigeons and monkeys (Roberts, Mazmanian, & Kraemer, 1984; Roper & Zentall, 1993; Washburn & Astur, 1998), however these studies produced varying results. Recent evidence from applying the directed forgetting paradigm to monkeys suggests that nonhuman primates may engage in control of memory resources similar to humans (Tu & Hampton, 2014). Monkeys were trained in a visual matching-to-sample paradigm with a post-sample memory cue. The cue was either a *remember-cue*, indicating an upcoming matching test that required memory for the sample, or a *forget-cue*, that indicated an upcoming discrimination test that did not require memory of the sample. Accuracy for the sample was significantly less when the matching test unexpectedly came after a forget-cue compared to when the matching test came after a remember-cue. This performance decrement was not due to the surprise of the unexpected matching test, as performance was no different when the discrimination test unexpectedly came after the remember-cue. Thus, the inferior memory performance when unexpectedly tested after being cued to forget a sample, suggests that the memory cue controlled whether or not monkeys maintained the contents of working memory until the memory test (Tu & Hampton, 2014).

It is important to note that the remember-cue used in Tu & Hampton (2014) indicated that all sample items encoded, either one or a list of two, should be maintained until test. Thus, *all* items that were encoded should be remembered equally following a remember-cue, or *all* items encoded did not need to be remembered following a forget-cue. While this paradigm tested a broad degree of control within working memory, it did not address the ability to select among many representations in working memory to prioritize relevant information. This is a critical component of efficiently controlling working memory resources as the priority of which representations should be maintained in working memory is dynamic and dependent on the current goal. Thus, a more specific test of how monkeys control working memory resources would be to test if monkeys prioritize the maintenance of a single task-relevant item amongst other task-irrelevant items concurrently held in working memory.

The human ability to selectively shift memory resources between representations in working memory has traditionally been investigated through the retro-cue paradigm (Astle & Scerif, 2011; Berryhill, Richmond, Shay, & Olson, 2012; Griffin & Nobre, 2003; Lepsien, Griffin, Devlin, & Nobre, 2005; Matsukura, Luck, & Vecera, 2007; Sligte, Scholte, & Lamme, 2008). Typically, participants are presented with an array of stimuli to encode, and then provided a spatially informative cue presented up to <1-10 seconds *after* the offset of the array (Astle & Scerif, 2011; Griffin & Nobre, 2003). The cue indicates to participants which of the stimuli in the previously viewed array will be tested in an upcoming recognition test. Prioritization of the cued item is inferred when participants are more accurate or respond more quickly on trials for which the cue correctly predicts which item will be tested, compared to trials for which the cue incorrectly predicts which item will be tested, and to neutral trials that do not contain a cue (Griffin & Nobre, 2003). Because the cue is presented after the offset of the studied array of images, memory for the cued item benefits only if participants both 1) maintain the spatial layout of the items in the studied array, and then 2) prioritize the maintenance of the item that was previously in the cued location.

We applied the retro-cue paradigm to investigate the extent to which monkeys control memory resources to prioritize the maintenance of relevant over less relevant representations held in working memory. In Experiment 1, we trained monkeys to associate a spatial post-sample cue (retro-cue) with the expectation that the item previously in that location would be tested in an upcoming recognition test. We presented monkeys with a stimulus array of two items and tested whether or not monkeys would use a predictive retro-cue to prioritize the maintenance of the cued item in working memory. We hypothesized that if monkeys do control memory resources to prioritize relevant information, then memory performance for cued items would be significantly better than probe trials in which the un-cued irrelevant item was tested.

2. Experiment 1

We were first interested if monkeys would appreciate the predictive value of a retro-cue and what effect it would have on memory performance. In a yes/no recognition paradigm, monkeys were presented with an array of two items to remember, and would later have to decide whether a probe stimulus had been present in the previous array. Between the sample array and test, monkeys were given a spatially informative retro-cue that appeared in the location of the item (see Fig. 1). The retro-cue validly predicted which item would be tested 88 percent of the time. Importantly, because the retro-cue appeared after the offset of the stimulus array, monkeys had to remember which sample was in the cued location in order to associate the cue with the sample that would be tested. To test if monkeys were in fact prioritizing the cued item within working memory, performance for *congruent* trials, in which a cued item was tested, was compared with *incongruent* probe trials, in which the non-cued item was unexpectedly tested (Fig. 1). We hypothesized that if monkeys shifted memory resources within working memory to prioritize the maintenance of the cued item, then performance for congruent trials would be significantly higher than incongruent trials.

2.1 Methods

2.1.1 Subjects and apparatus

Eight adult male rhesus monkeys (*Macaca mulatta*) were used. Monkeys were pair-housed, received a full daily food ration, and had ad libitum access to water. Monkeys had prior experience with automated cognitive testing using a touch-screen computer. Each portable testing rig contained a 15-inch color LCD touch-sensitive screen (Elo TouchSystems, Menlo Park, CA) operating with a resolution of 1024 X 768 pixels, and two automatic food dispensers (Med Associates, Inc., Stl. Albans, VT) that delivered nutritionally balanced primate pellets

(Bio-Serv, Frenchtown, NJ) into food cups below the screen. A screen was mounted on the front of each monkeys' cage. Testing was controlled by a personal computer with a custom program written in Visual Studio 2013 (Microsoft Corporation).

2.1.2 Stimuli

During each session, a black screen contained five 218 X 196 pixel square frames with a white border. They were arranged in a cross pattern, so that a square was in the center with the other four squares arranged on each side of the middle square. The square frames never went away during a test session, and served as the locations in which stimuli appeared (see Fig. 1). Test stimuli consisted of a small set of nine 146 X 139 pixel color photographs of nature scenes that were used throughout all experiments. During a recognition test, a white circle with an *M* crossed out in the middle was used for monkeys to indicate a *not-there* response.

2.2 Procedure

Experiments were conducted in the monkeys' home cages. During testing the pair-housed monkeys were separated by dividers that allowed limited visual and physical contact, but prevented access to one another's testing equipment. Each subject received multiple sessions per day, six days a week.

2.2.1 Initial Training

Monkeys were first trained on a yes/no recognition paradigm. All trials began by touching a green square (100 X 91) presented in the middle of the center square frame. Monkeys had to touch the square twice (FR2) to enter the study phase. During the study phase, the green square disappeared and two picture samples were presented simultaneously for two seconds. After the two seconds, the samples disappeared and were followed by a 1.8 second delay in which only the square frames were on screen. After the delay period, the recognition test began. During the recognition test, a test image would appear in the middle square frame, in addition to a *not-there* response that appeared below the right most square frame (See Fig 1). Touching (FR2) the image in the middle box frame was correct when one of the samples had been previously seen during study for that trial. Touching (FR2) the not-there response was correct when the test image was not one of the two samples that had been previously seen during study for that trial. Correct responses were rewarded with one banana pellet as well as an "Excellent!" sound. Incorrect responses resulted in a "D'oh!" sound and a seven second time-out in which only the square frames were on screen. Correct trials were separated by an inter-trial interval of 5 seconds.

Training sessions consisted of 120 trials, 60 match trials, and 60 non-match trials. All trials were broken into blocks of 24 so that each session contained five blocks. Within each block, each of the four study locations contained sample items equally, and each location was paired with the other three study locations an equal number of times. Each sample appeared four times per block during the study phase, with the exception of six samples, which were used once. The six samples used once per block were randomly selected at the beginning of each block. The pairing of samples during study never repeated within a block. Of the 60 match trials, a sample from each location was used as a test image three times. Of the 60 non-match trials, samples were randomly selected per block to serve as the test image. Monkeys completed a minimum of six sessions and moved to the next phase if they reached a criterion of 75 percent accuracy for two sessions in a row. All monkeys reached criterion between six and fifteen sessions.

2.2.2 Concurrent Cue Training 100 % predictive

The monkeys were then introduced to an attentional cue that was presented concurrently with the sample stimuli. The cue was a larger frame that bordered one of the box frames, and the original box frame changed from a solid border to a dashed line border (see Fig. 1). This cue appeared for 150 ms, disappeared for 150 ms, and appeared again for 150 ms to create the perception of a blinking square frame that captured the monkeys attention. The first blink began 150 ms before the onset of the sample, and the second blink began 150 ms after the onset. Because the cue appeared before and during the presentation of the stimuli, it served as both a pre-cue and a concurrent cue. The cue was 100 percent predictive so that on all match trials, the cued picture would be the sample image during test. In concurrent training, monkeys can perceptually identify the stimulus to remember because the cue appears concurrently with the stimulus. The purpose of this training was to 1) ensure that adding an attentional cue would not disrupt performance on the overall task, and 2) to train monkeys to associate the cue with the sample image that they had to remember. On all 60 non-match trials, the cued image would not be the sample image at test. All monkeys were tested on this phase until they reached a criterion of 80 percent accuracy in two consecutive sessions. Once reaching criterion, they were moved to retro-cue training.

2.2.3 Retro-cue training 100 % predictive

We ran monkeys on a retro-cue training phase before inserting probe trials to ensure that they could perform the task accurately, since the attentional cue would now be occurring after the offset of the sample array rather than concurrently with the samples. Monkeys were trained on the same paradigm as concurrent cue training, except with the cue appearing during the delay period between study and test. After initiating a green ready square (FR2), monkeys saw two sample stimuli for two seconds. The stimuli disappeared and 700 ms later the cue occurred. The cue was the same as in concurrent cue training. It appeared as a larger square frame outlining one of the spatial locations in the array, and flashed twice for 150 ms with a 150 ms pause in between. Following the cue, the test image appeared 650 ms later (see Fig. 1). The total time from stimulus offset to test was 1.8 seconds.

Training sessions were the same number of trials and were counterbalanced the same as in initial training. To meet criterion, monkeys had to run at least six sessions and obtain 80 percent accuracy on two consecutive sessions. All but two monkeys met this criterion in less than 15 sessions. For these two monkeys, the delay after the cue was shortened from 1.8 seconds to 1.5 seconds in order to improve accuracy. With this adjustment, the two monkeys met criterion within 15 additional sessions.

2.2.4 Test of retro-cue probe trials

Once monkeys met criterion, probe trials were administered. The paradigm was the same as retro-cue training, with the exception that five of the 60 match trials (8%) were probe trials. In a probe trial, the sample that was presented during study but not cued was used as the test image. Across each session, an image from each location served as the probe image. Choosing the test image was reinforced appropriately as a correct answer. Monkeys ran eight sessions of this phase, which summated to 40 total probe trials.

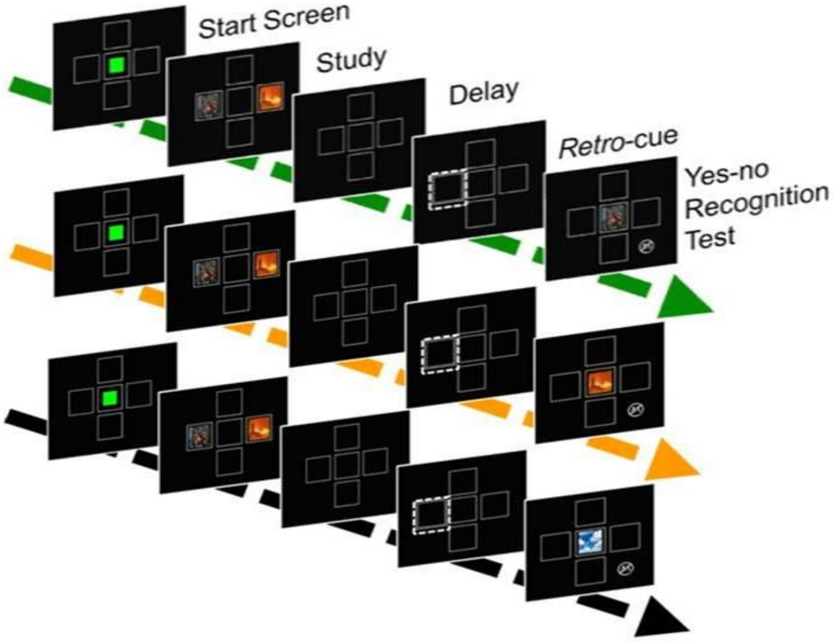

Figure 1: Example of retro-cue trials. **Top)** Example of congruent trial. **Middle)** Example of incongruent probe trial. **Bottom)** Example of non-match trial. Touching the image was rewarded when it was one of the items in the sample array. Touching the "not-there" symbol was rewarded when the test image was not present in the array.

2.3 Results and Discussion

The aim of Experiment 1 was to investigate whether or not monkeys would use a predictive retro-cue to prioritize the maintenance of the cued sample. Monkeys performed well on the task as the average overall proportion correct for all monkeys was (M = .79, SD = .014). Additionally, monkeys performed well on both non-match (M = .86, SD =.03) and match trials (M = .72, SD = .02), indicating that both sample stimuli were being encoded into working memory during study. The critical comparison was between congruent and incongruent probe trials. Monkeys were significantly more accurate on congruent trials, when the cue correctly predicted the test item, than on incongruent probe trials, when the un-cued item was tested, t(5) = 3.39, p = 0.02, (see Fig 2a).

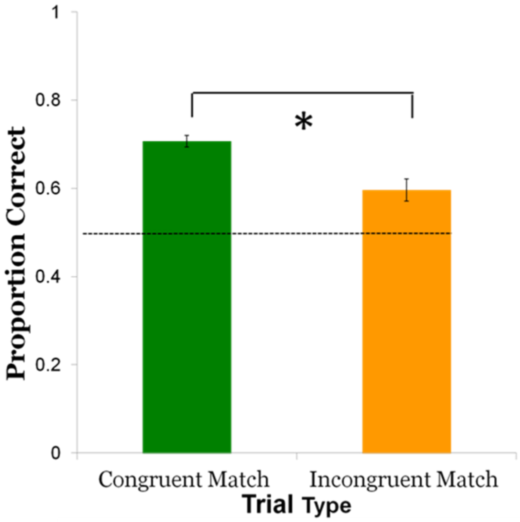

Figure 1b: Mean proportion correct for all monkeys in Experiment 1.

Repeated measures ANOVA was performed on mean median correct reaction times per session with errors excluded. Results indicated a main effect of trial type, F(2,5) = 8.23, p = .008 as monkeys were fastest on match trials (M = 942ms , SD =145ms ,) and slowest on non-match trials (M = 1314ms, SD =151ms). This suggests that monkeys performed an exhaustive memory retrieval strategy when judging the test image such that monkeys compared each item held in working memory with the test image, before choosing the *not-there* response. The slower reaction time for non-match trials was not due to task difficulty, as accuracy performance was highest for non-match trials. Pair-wise comparisons indicated that monkeys were significantly faster to respond on congruent match trials compared to incongruent match trials or non-match trials, t(10) = -3.12 , p = .026, suggesting that monkeys began their memory search with the cued item.

This behavioral pattern of higher memory performance and faster responses to cued items suggests that after encoding, monkeys used the cue to prioritize the maintenance of cued items compared to un-cued items. The results obtained here are similar to those obtained by Griffin & Nobre (2003), suggesting that monkeys, similar to humans, can shift memory resources to prioritize

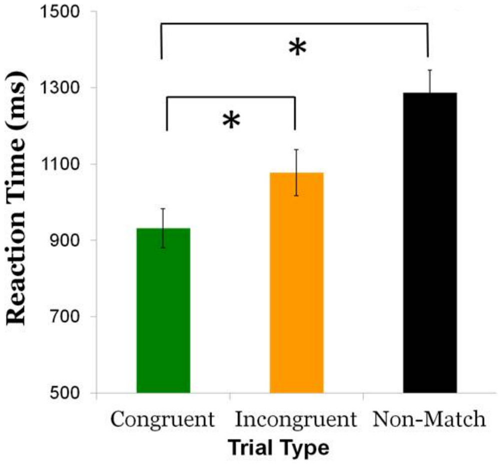

Figure 1c: Mean median correct reaction time for all monkeys in Experiment 1

the maintenance of relevant information.

3. Experiment 2

Experiment 1 established that monkeys use a predictive retro-cue to prioritize the maintenance of the cued sample when working memory load was two items. If the prioritization of memory resources is an adaptation for maximizing the effectiveness of limited memory resources, then we should observe even more powerful effects of the retro-cue when memory load is increased and resources are under greater demand. In Experiment 2a, monkeys performed the same experimental procedure as Experiment 1 with the exception that they were presented with three items in the stimulus array rather than two (see Fig. 2a). We hypothesized that if the retro-cue focuses processing on the cued item, then the difference between congruent and incongruent trials would be larger when cognitive load was increased.

3.1 Experiment 2a

3.1.1 Methods

3.1.1.1 Subjects and apparatus

All six subjects used in Experiment 1 were also used in Experiment 2. Additionally, all testing apparatuses were identical to those described in Experiment 1.

3.1.1.2 Stimuli

All stimuli used in Experiment 1 were used in Experiment 2.

3.1.2 Procedure

3.1.2.1 Training

Monkeys were trained with the same paradigm as Experiment 1 with the exception that three stimuli were presented during study phase instead of two (Fig. 3a). To meet criterion and move on to probe trials, monkeys had to run at least six sessions and obtain 70 percent accuracy on two consecutive sessions. The criterion for this phase was 10 percent less than Experiment 1because the task was more difficult overall.

3.1.2.2 Probe Trials

The proportion of probe trials was the same as Experiment 1. Monkeys ran eight sessions of 120 trials, resulting in 40 total probe trials.

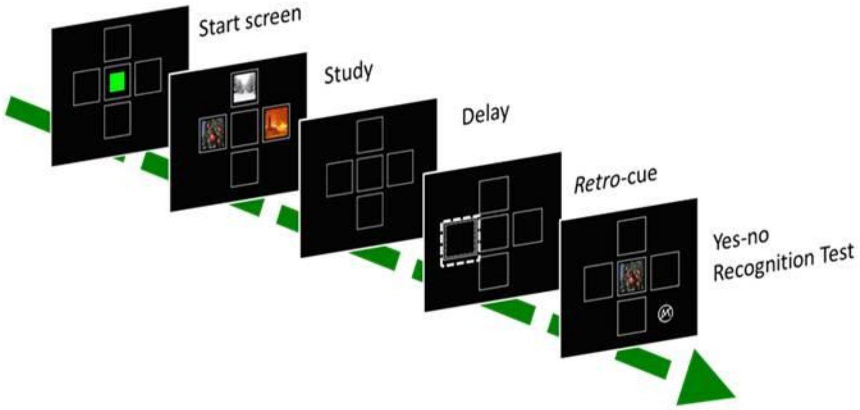

Figure 2a: Example of congruent retro-cue trial with memory load of three items.

3.1.3 Results and Discussion

Results indicated that overall accuracy decreased when an additional item was added to working memory, (M = .74, SD = .04), indicating that as expected, higher cognitive load made the task more difficult. Monkeys' performance on non-match trials (M = .81, SD = .05) and match trials (M = .67, SD = .06) indicated that all three items were encoded into working memory. Critically however, there was no significant difference between congruent and incongruent match trials, t(5) = -2.52, $p > 0.05$, as monkeys performed better on incongruent match trials (see Fig. 2b). These results suggest that when working memory load was increased to three items, monkeys were able to perform above chance on the task, but did not use the retro-cue to prioritize the maintenance of the cued item.

Repeated measures ANOVA was performed on mean median correct reaction times per session with errors excluded. Results indicated a main effect of trial type, F(2,5) = 4.92, p = .03 as monkeys were fastest on match trials (M = 960ms , SD =198ms ,) and slowest on non-match trials (M = 1221ms, SD =163ms) (see Fig. 2c). This suggests that monkeys performed an exhaustive memory search retrieval strategy similar to in Experiment 1, however, pair-wise comparisons indicated that monkeys were not significantly faster to respond on congruent match trials compared to incongruent match trials, t(10) = -.94 , $p >.05$, suggesting that they did not begin their memory search with the cued item.

The aim of experiment 2a was to investigate the effectiveness of the retro-cue when memory load was increased to three items. Our hypothesis was that if the retro-cue focuses processing on the cued item, then the difference between congruent and incongruent trials will be larger when cognitive load is increased. Interestingly however, monkeys showed no behavioral advantage from the retro-cue in accuracy or reaction time. It is possible however, that the absence of the effect found here is due to practice effects. Although we predicted that it would be more beneficial to use the cue with a higher cognitive load, the monkeys may have learned to adopt the strategy of ignoring the cue and attempting to remember all items. Thus, to confirm that the absence of the effect was particular to a working memory load of three items, and not due to monkeys adopting a new strategy, we tested monkeys with a working memory load of two items again in Experiment 2b, and then with three items in Experiment 2c ultimately arranging an A-B-A design.

3.2 Experiment 2b

3.2.1 Methods

3.2.1.1 Subjects and apparatus

All six subjects used in Experiment 1 were also used in Experiment 2. In addition, all testing apparatuses were identical to those described in Experiment 1.

3.2.1.2 Stimuli

All stimuli used in Experiment 1 were used in Experiment 2.

3.2.2 Procedure

3.2.2.1 Training

Monkeys were trained with the same paradigm as Experiment 1. To meet criterion, monkeys had to run at least six sessions and obtain 80 percent accuracy on two consecutive sessions.

3.2.2.2 Probe Trials

The proportion of probe trials was the same as Experiment 1. Monkeys ran eight sessions of 120 trials, resulting in 40 total probe trials.

3.2.3 Results and Discussion

The aim of Experiment 2 was to investigate if monkeys had learned an alternative strategy through extensive practice with this paradigm, or if the absence of the effect found in Experiment 2a was particular to a working memory load of three items. Monkeys performed well on the task as the average overall proportion correct for all monkeys was (M = .83, SD = .04). Additionally, monkeys performed well on both non-match (M = .86, SD = .04) and match trials (M = .80, SD = .06), indicating that both sample stimuli were being encoded into working memory during study. The critical comparison was between congruent and incongruent probe trials. Monkeys were significantly more accurate on congruent match trials, when the cue correctly predicted the test item, than they were on incongruent probe trials, t(5) = 5.02, p = 0.004 (see Figure 2b).

Repeated measures ANOVA was performed on mean median correct reaction times per session with errors excluded. Results indicated main effect of trial type, F(2,5) = 22.3, p = .000, as monkeys were fastest on match trials (M = 914ms , SD =172ms), and slowest on non-match trials (M = 1132ms, SD =135ms) (see Fig. 2c). This suggests that monkeys performed an exhaustive memory retrieval strategy when judging the test image, such that monkeys compared each item held in working memory with the test image before choosing the *not-there* response. The slower reaction time for non-match trials was not due to task difficulty, as accuracy performance was highest for non-match trials. Pair-wise comparisons indicated that monkeys were significantly faster to respond on congruent match trials compared to incongruent match trials or non-match trials, t(10) = -4.25, p = .008, suggesting that monkeys began their memory search with the cued item.

The results of experiment 2b show a successful replication of the primary findings in Experiment 1. Again, the retro-cue affected monkeys' performance as they showed prioritization of maintenance for the cued item, as well as an exhaustive memory search retrieval process beginning with the cued item. We then tested monkeys with a memory load of three items, to assess if the absence of cue effect found in Experiment 2a was particular to a memory load of three items, or if monkeys would now demonstrate a cue effect after extensive practice.

3.3 Experiment 2c

3.3.1 Methods

3.3.1.1 Subjects and apparatus

All six subjects used in Experiment 1 were also used in Experiment 2. In addition, all testing apparatuses were identical to those described in Experiment 1.

3.3.1.2 Stimuli

All stimuli used in Experiment 1 were used in Experiment 2.

3.3.2 Procedure

3.3.2.1 Training

Monkeys were trained with the same paradigm and to the same criterion as Experiment 2a (see Fig. 3a).

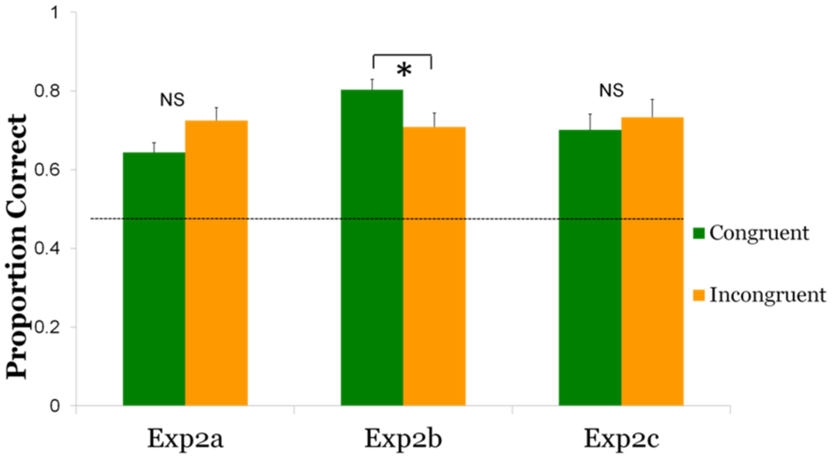

Figure 2b: Average proportion correct comparing congruent and incongruent trials. Exp2a and Exp2c contained a memory load of three items. Exp 2b contained a memory load of two items. Monkeys only showed evidence of a cue effect in Exp 2b.

3.3.2.2 Probe Trials

The proportion of probe trials was the same as Experiment 1. Monkeys ran eight sessions of 120 trials, resulting in 40 total probe trials.

3.3.3 Result and Discussion

Results indicated that, again, overall accuracy decreased when an additional item was added to working memory. The average overall proportion correct for all monkeys was (M = .76, SD = .06). Monkeys performance on non-match trials (M = .80, SD = .06) and match trials (M =72 , SD =.09) indicated that all three items were encoded into working memory. Critically however, there was no significant difference between congruent and incongruent match trials, t(5) = -.724, p > 0.05, as monkeys performed better on incongruent match trials (see Fig. 2b). These results suggest that when visual working memory load is increased to three items, monkeys did not use the retro-cue to prioritize maintenance of the cued item.

Repeated measures ANOVA was performed on mean median correct reaction times per session with errors excluded.

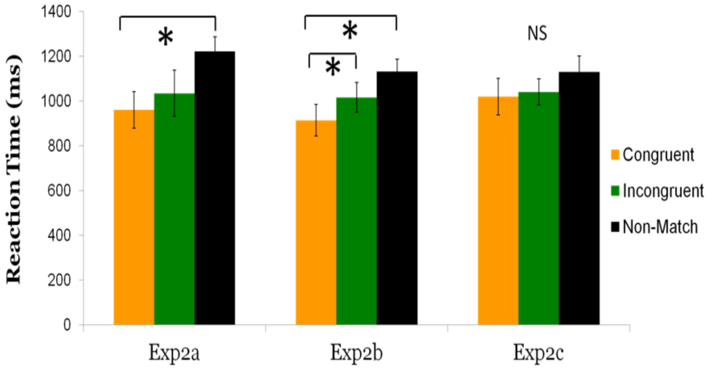

Figure 2c: Mean median reaction time for correct trials comparing congruent, incongruent, and non-match trials for Experiment 2. With a memory load of three items (Exp2a,2c), no effect of cue was found. With a memory load of two items (Exp2b), there was an effect of cue on reaction time.

Results indicated no main effect of trial type, F(2,5) = 2.7, p > .05. Although monkeys were fastest on match trials, (M = 960ms , SD =198ms ,) and slowest on non-match trials (M = 1221ms, SD =163ms), the lack of a main effect is further evidence that the retro-cue did not affect memory.

The original purpose of Experiment 2 was to investigate the effect of the retro-cue when memory load was increased. We hypothesized that the need to prioritize the cued item would be greater as memory load increases, indicated by a larger difference between congruent and incongruent trials. However, results from Experiment 2a and 2c indicated that the retro-cue did not have an effect on memory performance when working memory load is increased. Performance on congruent and incongruent trials was similar indicating that the relevant items were not prioritized. Additionally, there was no difference in reaction time for responding to cued vs. non-cued items, further suggesting that the retro-cue did not have an effect.

Why did monkeys not show the control of memory resources when memory load was increased? The lack of effect cannot be explained by practice, as monkeys demonstrate the effect again when tested with a memory load of two items, and then fail to do so when tested with three items for a second time. We suggest that the absence of memory control found with a memory load of three items may be because the representations were too weak in working memory.

4. Experiment 3

In Experiment 3, we tested if the memory strength of representations in working memory determines whether or not the retro-cue is effective. In Experiment 3a we presented monkeys with three items to encode and shortened the pre-cue delay (see Fig. 3a), so that the retro-cue would appear earlier when representations are stronger. We hypothesized that by presenting the retro-cue earlier with a memory load of three items, the retro-cue would have an effect on memory performance. Conversely, in Experiment 3b, monkeys encoded two items and the retro-cue was presented later. We hypothesized that lengthening the pre-cue delay would attenuate the effect of the retro-cue with a memory load of two items.

4.1 Experiment 3a

4.1.1 Methods

4.1.1.1 Subjects and apparatus

All six subjects used in Experiment 1 were also used in Experiment 2. In addition, all testing apparatuses were identical to those described in Experiment 1.

4.1.1.2 Stimuli

All stimuli used in Experiment 1 were used in Experiment 2.

4.1.2 Procedure

4.1.2.1 Training

Monkeys were trained with the same paradigm as Experiment 2a, with the retro-cue being shortened by 400 ms. In Experiment 2a, the retro-cue appeared 700 ms after stimulus offset, while in Experiment 3a, the retro-cue appeared 300 ms after stimulus offset (see Fig. 3a.). Monkeys were trained with a 100 percent predictive cue until reaching a criterion of 70 percent overall accuracy or higher in two consecutive sessions. All monkeys reached criterion within 15 sessions.

4.1.2.2 Probe Trials

The proportion of probe trials was the same as Experiment 1. Monkeys ran eight sessions of 120 trials, resulting in 40 total probe trials.

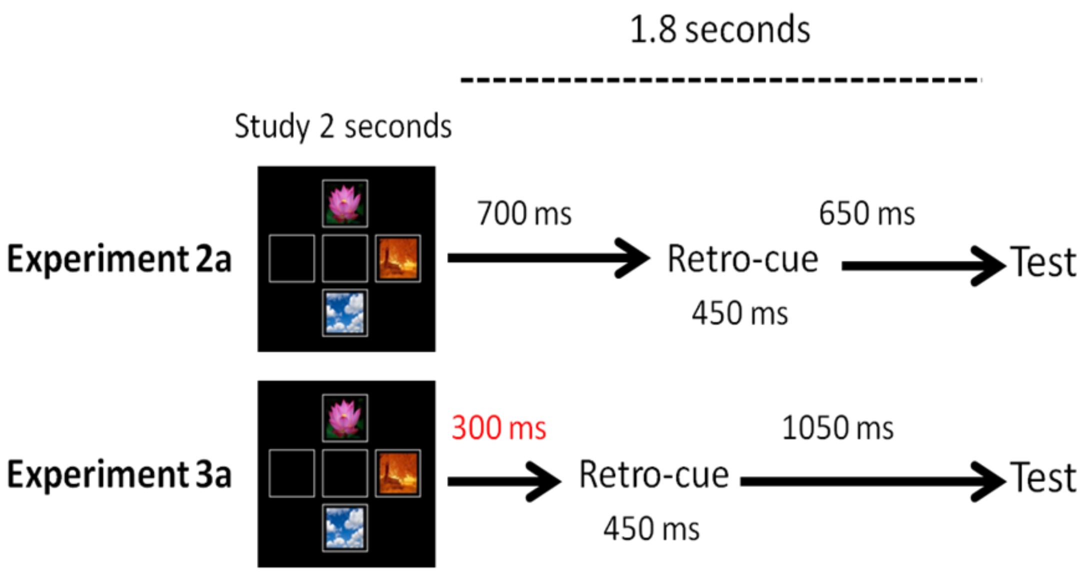

Figure 3a: Comparison of Experiment 2a and Experiment 3a. The pre-cue delay (red) was shortened by 400ms in Exp 3a. The total time between study and test is the same.

4.1.3 Results and Discussion

The average overall proportion correct for all monkeys was (M = .78, SD = .05). Monkeys' performance on non-match trials (M = .83, SD = .055) and match trials (M =.72 , SD =.08) indicated that all three items were encoded into working memory. Critically however, there was no significant difference between congruent and incongruent match trials, $t(5) = .914$, $p > 0.05$, (see Fig. 3a.), indicating that the retro-cue did not affect memory performance. These results suggest that with a memory load of three items, presenting the retro-cue 400 ms earlier did not affect how monkeys used the cue compared to Experiment 2a or 2c.

A repeated measures ANOVA was performed on mean median correct reaction times per session with errors excluded. Results indicated a main effect of trial type, F(2,5) = 22.6, p = .000, as monkeys were fastest on match trials (M = 968ms , SD =190ms), and slowest on non-match trials (M = 1172ms, SD =193ms). This suggests that monkeys performed an exhaustive memory retrieval strategy when judging the test image, such that monkeys compared each item held in working memory with the test image before choosing the *not-there* response. The slower reaction time for non-match trials was not due to task difficulty, as accuracy performance was highest for non-match trials. Pair-wise comparisons indicated that monkeys were significantly faster to respond on congruent match trials compared to incongruent match trials or non-match trials, t(10) = -2.61, p = .048, suggesting that monkeys began their memory search with the cued item.

These results suggest that, while providing the retro-cue did not have an effect on accuracy, it did have an effect on reaction time similar to the pattern found in Experiment 1. This is indicative of a cue-based retrieval strategy and was not observed in Experiment 2a or 2c, suggesting that providing the cue earlier may have allowed monkeys to associate the cue with stronger memory representations. In Experiment 3b, we further tested the hypothesis that using the retro-cue requires representations of a certain memory strength, by presenting two items with a delayed retro-cue, when representations may be weakened.

4.2 Experiment 3b

4.2.1 Methods

4.2.1.1 Subjects and apparatus

After Experiment 3a, two monkeys left the lab and were transferred to a different lab. to maintain the sample size of six, four of the monkeys used in the previous experiments were still tested and an two new monkeys were added to the sample. The new monkeys were trained through all training phases described in Experiment 1, including probe trials. After completing all phases, the monkey began Experiment 3b training with the other four monkeys. All testing apparatuses were identical to those described in Experiment 1.

4.2.1.2 Stimuli

All stimuli used in Experiment 1 were used in Experiment 3.

4.2.2 Procedure

4.2.2.1 Training

Monkeys were trained with the same paradigm as Experiment 1, with the exception that the retro-cue appeared 400 ms later. In Experiment 1, the retro-cue appeared 700 ms after stimulus offset, while in Experiment 3b, the retro-cue appeared 1100 ms after stimulus offset (see Fig. 3b). Monkeys were trained with a 100 percent predictive cue until reaching a criterion of 80 percent overall accuracy or higher in two consecutive sessions. All monkeys reached criterion within 15 sessions.

4.2.2.2 Probe Trials:

The proportion of probe trials was the same as Experiment 1. Monkeys ran eight sessions of 120 trials, resulting in 40 total probe trials.

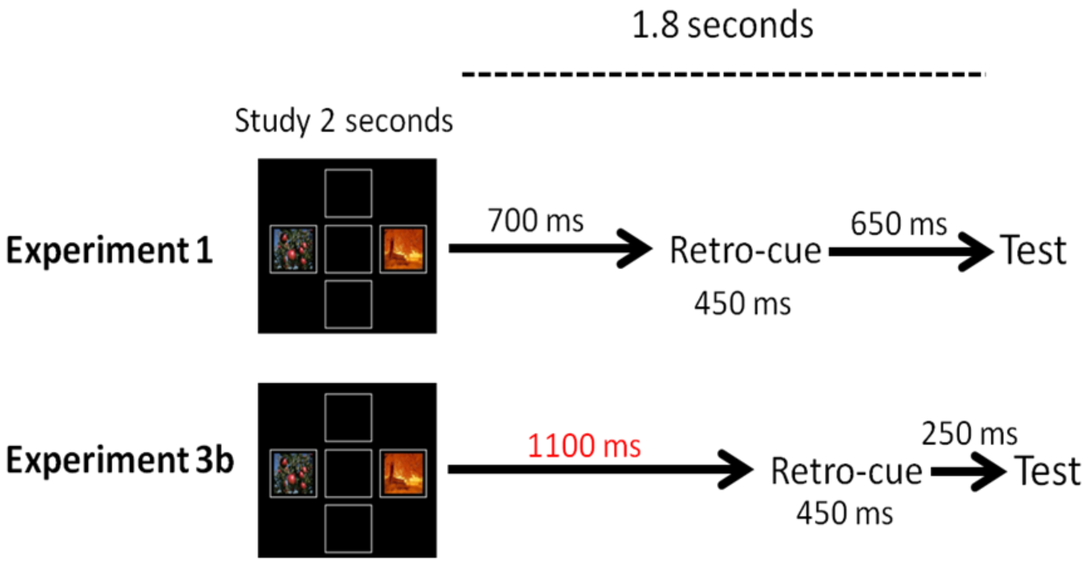

Figure 3b: Comparison of Experiment 1 and Experiment 3b. The pre-cue delay (red) was lengthened by 400ms in Exp3b. The total time between study and test is the same.

4.2.3 Results and Discussion

The average overall proportion correct for all monkeys was (M = .80, SD = .05). Monkeys' performance on non-match trials (M = .86, SD = .02) and match trials (M =.73 , SD =.11) indicated that all three items were encoded into working memory. Critically however, there was no significant difference between congruent and incongruent match trials, $t(5) = 1.27$, $p > 0.05$, (see Fig. 3c), indicating that the retro-cue did not affect memory performance. These results suggest that, with a memory load of two items, presentation of the retro-cue 400 ms later did not change the retro-cue's effect on memory representations.

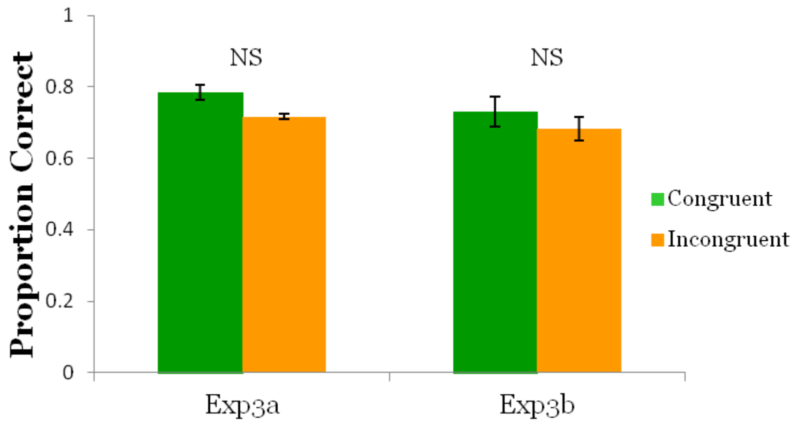

Figure 3c: Average proportion correct comparing congruent and incongruent trials. In Exp3a, monkeys had a memory load of three items and were given the retro-cue earlier. In Exp 3b, monkeys had a memory load of two items and were given the retro-cue later. There was no effect of cue on proportion correct in either experiment.

Repeated measures ANOVA was performed on mean median correct reaction times per session with errors excluded. Results indicated a main effect of trial type, F(2,10) = 52.8, p = .000 , as monkeys were fastest on match trials (M = 934ms , SD =78ms), and slowest on non-match trials (M = 1174ms, SD =102ms) (see Fig. 3d). This suggests that monkeys performed an exhaustive memory retrieval strategy when judging the test image. Just as in Experiment 1, the slower reaction time for non-match trials was not due to task difficulty as accuracy was highest for non-match trials. Pair-wise comparisons indicated that monkeys were significantly faster to respond on congruent match trials compared to incongruent match trials or non-match trials, t(10) = -4.37 , p = .007, suggesting that monkeys began their memory search with the cued item.

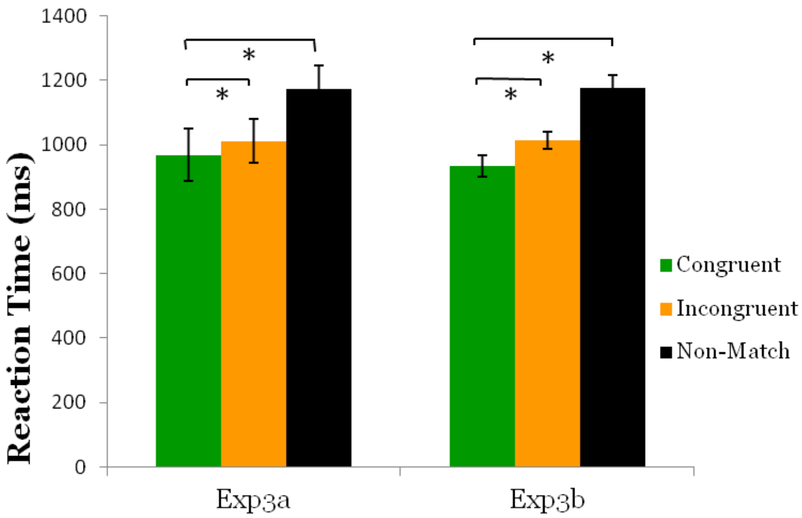

Figure 3d: Mean median reaction time for correct trials comparing congruent, incongruent, and non-match trials for Experiment 3a and 3b. In both experiments, there was an effect of cue on reaction time.

In Experiment 3, we tested the notion that working memory representations must be of a certain strength in order for the retro-cue to have an effect. In Experiment 3a, we hypothesized that if representations were too weak with a working memory load of three items, then providing the cue earlier, when representations are stronger, may cause an effect of the retro-cue. In Experiment 2, there was neither an effect on accuracy nor reaction time. In comparison, Experiment 3a showed that when the retro-cue was presented earlier, a reaction time effect was evident as monkeys responded more quickly to the presence of cued items compared to un-cued items. Compared with absence of a retro-cue effect in Experiment 2, the presence of an effect in Experiment 3a where the only condition changed was presenting the retro-cue earlier, supports our hypothesis that memory representations must be a certain strength for the cue to have an effect. Conversely, in Experiment 3b, we predicted that with a memory load of two items, where we previously do show a retro-cue effect, providing the cue later when representations are weaker should attenuate the effect of the retro-cue. We found that the retro-cue's effect on accuracy but not reaction time was attenuated. Taken together, the results of Experiment 3 suggest that the ability for a retro-cue to affect the maintenance and/or retrieval of working memory representations relies on an interaction between memory load and memory strength.

5. General Discussion

We observed significantly higher accuracy and faster reaction times for cued items compared to un-cued items, with a memory load of two items. This effect was consistent across Experiment 1 and Experiment 2b. As the encoding conditions were the same for both cued and un-cued probe trials, the difference in memory performance indicates that the retro-cue caused a difference in working memory maintenance, or retrieval prioritization, following the cue. The results found in Experiment 1 and 2b, are in parallel with the behavioral pattern that has been found in human memory research using the retro-cue paradigm (Griffin & Nobre, 2003; Makovski & Jiang, 2007; Astle, Summerfield, Griffin, & Nobre, 2012). This suggests that monkeys, like humans, shift working memory resources to prioritize the maintenance of relevant information.

In Experiment 2, we hypothesized that if prioritization of memory maintenance is an adaptation for maximizing the effectiveness of limited memory resources, we should observe even more powerful effects of the retro-cue when memory load is increased. However, we did not observe an effect of the retro-cue on working memory maintenance or retrieval prioritization when memory load was increased to three items. The absence of the effect was not due to failure to encode all three images, as performance remained above chance. Nor was the absence of memory control due to practice effects, as monkeys showed memory control when memory load was decreased back to two items (Exp 2b), and then failed to show memory control when tested again with a memory load of three items (Exp 2c). We suggest that the limitation on memory control may be due to an interaction with the capacity limits of visual working memory.

One model in humans suggests that visual working memory (VWM) consists of three or four independent memory “slots” that each store information about a single visual item (Cowan, 2010; Luck & Vogel, 1997; Pashler, 1988; Schmidt, Vogel, Woodman, & Luck, 2002). In the *slot model*, as you increase the number of items to hold in VWM, the resolution, or strength, of each item should not be affected by memory load until the capacity limit is exceeded. Because performance was above chance in Experiment 2, suggesting that all three items were available for retrieval at test, we maintain that a memory load of three items is within the capacity limits of visual working memory in monkeys. Thus, according to the slot model, representations in VWM whether holding three items, or two items, should be equivalent in resolution or strength. Therefore, the slot model cannot explain why monkeys were not able to associate the cue with the representations in working memory when memory load was three.

The view that working memory consists of a fixed number of independent slots has recently been challenged by studies suggesting that the resolution with which items are maintained depends *critically* on how many other items are concurrently held in memory (Alvarez & Cavanagh, 2004; Awh, Barton, & Vogel, 2007). This *resource model* of VWM proposes that a single memory resource is shared between items concurrently held in working memory. According to this model, the precision with which an item is stored is determined by the fraction of total resources allocated to it (Bays, Catalao, & Husain, 2009). In contrast to the slot model, this view predicts that even when operating within VWM capacity, as more items are added to maintain, the resolution of each item decreases as less resources are available to maintain details of each item.

The resource model, then, may explain why there was no effect of the retro-cue on monkeys performance when memory load was increased to three items. In the retro-cue paradigm, correctly identifying the relevant item from VWM via the spatial post-sample cue critically requires that the spatial information in VWM regarding each sample's previous location in the array is maintained. According to the resource model, if the precision with which an item is stored decreases as the number of items held in VWM increases, then representations with a memory load of two items will be stronger than representations with a memory load of three items. Therefore, a viable explanation of why there was no effect of the retro-cue when three items were held in working memory VWM may be that the precision with which each item was stored was such that the spatial information was not maintained or could not be retrieved. In comparison, when two items were held in VWM, the spatial information was maintained as more resources were allocated to each representation, thus allowing monkeys to associate the cue with the item in VWM. Future studies will investigate how spatial versus visual information is lost during maintenance and/or retrieval when working memory load is increased.

Along these lines, another factor that might affect memory strength/resolution is time. In Experiment 3, we tested the hypothesis that if representations decay as a function of time, and if memory representations have to a certain strength for the cue to have an effect, then providing the retro-cue earlier for representations that are weak would make it more likely that the cue would affect memory performance. Conversely, if representations are strong, then providing the retro-cue later would make it less likely for the cue to have an effect on memory performance. In Experiment 3a, monkeys were presented with three items to encode, similar to Experiment 2, but the retro-cue appeared earlier. Although there was no effect of the cue on accuracy, results indicated that monkeys began their memory search with the cued item, a result not evident when previously tested with three items in Experiment 2. This suggests that providing the cue earlier allowed monkeys to associate the cue with the item in VWM, at least during retrieval. In Experiment 3b, monkeys were presented with two items to encode, similar to Experiment 1, but the retro-cue appeared later. In Experiment 1 the cue affected accuracy and reaction time, though when the cue was presented later in Experiment 3b, the retro-cue's affect on accuracy was attenuated. This suggests that providing the cue later lessened the affect of the cue on representations in VWM, perhaps as it was more difficult for the cue to be associated with representations in VWM. Taken together, the results of Experiment 3 suggest that the control over memory resources is confined to properties by which resources are allocated to each item. It may be that because monkeys operate with more limited VWM resources, limited control is available. Thus, differences in memory control between humans and monkeys may be due to differences in VWM resources available.

In sum, because working memory resources are limited, it is critical to prioritize the maintenance of information relevant to the task at hand (Chun et al., 2011; Cowan, 2000; Unsworth & Engle, 2007). The results of the current study extend the findings of Tu & Hampton (2014) and provide evidence that monkeys, similar to humans, will shift working memory resources to prioritize the maintenance of relevant information. Taken together, these results suggest that the ability to maximize the effectiveness of memory resources was an adaptation as early as 20 million years ago, when old world monkeys and humans shared a common ancestor. The observed effect in the current study, however, was limited to a memory load of two items presented simultaneously. When more than two items were presented, monkeys could still maintain the items in working memory, but the retro-cue had no effect on the prioritization of memory resources. In humans, the retro-cue has an effect on memory performance for sample arrays from two to eight items (Astle et al.,2012; Griffin & Nobre, 2003; Matsukura et al., 2007). Future studies should be aimed at better understanding the relationship between cognitive load and the ability to control memory resources.

References

Alvarez, G. a, & Cavanagh, P. (2004). The capacity of visual short-term memory is set both by visual information load and by number of objects. *Psychological Science : A Journal of the American Psychological Society / APS*, *15*(2), 106–111. http://doi.org/10.1167/2.7.273

Astle, D. E., & Scerif, G. (2011). Interactions between attention and visual short-term memory (VSTM): What can be learnt from individual and developmental differences? *Neuropsychologia*, *49*(6), 1435–1445. http://doi.org/10.1016/j.neuropsychologia.2010.12.001

Astle, D. E., Summerfield, J., Griffin, I., & Nobre, A. C. (2012). Orienting attention to locations in mental representations. *Attention, Perception, & Psychophysics*, *74*(1), 146–162. http://doi.org/10.3758/s13414-011-0218-3

Awh, E., Barton, B., & Vogel, E. K. (2007). Visual working memory represents a fixed number of items regardless of complexity. *Psychological Science*, *18*(7), 622–628. http://doi.org/10.1111/j.1467-9280.2007.01949.x

Baddeley, A. (2000). The episodic buffer: A new component of working memory? *Trends in Cognitive Sciences*, *4*(11), 417–423. http://doi.org/10.1016/S1364-6613(00)01538-2

Baddeley, A. D., & Hitch, G. (1974). Working memory. *The Psychology of Learning and Motivation Advances in Research and Theory*. http://doi.org/10.1016/S0079-7421(08)60452-1

Basile, B. M., & Hampton, R. R. (2013). Dissociation of active working memory and passive recognition in rhesus monkeys. *Cognition*, *126*(3), 391–396. http://doi.org/10.1016/j.cognition.2012.10.012

Bays, P. M., Catalao, R. F. G., & Husain, M. (2009). The precision of visual working memory is set by allocation of a shared resource. *Journal of Vision, 9*(10), 7.1–11. http://doi.org/10.1167/9.10.7

Berryhill, M. E., Richmond, L. L., Shay, C. S., & Olson, I. R. (2012). Shifting attention among working memory representations: Testing cue type, awareness, and strategic control. *The Quarterly Journal of Experimental Psychology*, *65*(3), 426–438. http://doi.org/10.1080/17470218.2011.604786

Chun, M. M., Golomb, J. D., & Turk-Browne, N. B. (2011). A taxonomy of external and internal attention. *Annual Review of Psychology*, *62*, 73–101. http://doi.org/10.1146/annurev.psych.093008.100427

Cowan, N. (2000). The magical number 4 in short-term memory: A reconsideration of mental storage capacity. *Behavioral and Brain Sciences*, *24*(1), 87–185. http://doi.org/10.1017/S0140525X01003922

Cowan, N. (2010). The Magical Mystery Four: How Is Working Memory Capacity Limited, and Why? *Current Directions in Psychological Science*, *19*(1), 51–57. http://doi.org/10.1177/0963721409359277

Griffin, I. C., & Nobre, A. C. (2003). Orienting attention to locations in internal representations. *Journal of Cognitive Neuroscience*, *15*(8), 1176–1194. http://doi.org/10.1162/089892903322598139

Lepsien, J., Griffin, I. C., Devlin, J. T., & Nobre, A. C. (2005). Directing spatial attention in mental representations: Interactions between attentional orienting and working-memory load. *NeuroImage*, *26*(3), 733–743. http://doi.org/10.1016/j.neuroimage.2005.02.026

Luck, S. J., & Vogel, E. K. (1997). Luck 1997- Nature- VWM, *193*(1996), 1996–1998. http://doi.org/10.1038/36846

MacLeod, C. (1998). Directed forgetting. *Intentional Forgetting: Interdisciplinary Approaches*. Retrieved from http://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:Directed+forgetting#2

Matsukura, M., Luck, S. J., & Vecera, S. P. (2007). Attention effects during visual short-term memory maintenance: protection or prioritization? *Perception & Psychophysics*, *69*(8), 1422–34. http://doi.org/10.3758/BF03192957

Oberauer, K. (2013). The focus of attention in working memory-from metaphors to mechanisms. *Frontiers in Human Neuroscience*, *7*(October), 673. http://doi.org/10.3389/fnhum.2013.00673

Pashler, H. (1988). Familiarity and visual change detection. *Perception & Psychophysics*, *44*(4), 369–378. http://doi.org/10.3758/BF03210419

Roberts, W. A., Mazmanian, D. S., & Kraemer, P. J. (1984). Directed forgetting in monkeys. *Animal Learning & Behavior*, *12*(1), 29–40. http://doi.org/10.3758/BF03199810

Roper, K. L., & Zentall, T. R. (1993). Directed forgetting in animals. *Psychological Bulletin*. http://doi.org/10.1037/0033-2909.113.3.513

Schmidt, B. K., Vogel, E. K., Woodman, G. F., & Luck, S. J. (2002). Voluntary and automatic attentional control of visual working memory. *Perception and Psychophysics*, *64*(5), 754–763. http://doi.org/10.3758/BF03194742

Sheard, E. D., & MacLeod, C. M. (2005). List method directed forgetting: Return of the selective rehearsal account. *Dynamic Cognitive Processes*, 219–248. http://doi.org/10.1007/4-431-

27431-6_10

Sligte, I. G., Scholte, H. S., & Lamme, V. A. F. (2008). Are there multiple visual short-term memory stores? *PLoS ONE*, *3*(2), 2–10. http://doi.org/10.1371/journal.pone.0001699

Smith, E. E., Jonides, J., & Koeppe, R. a. (1996). Dissociating Verbal and Spatial Working. *Cerebral Cortex*, *6*, 11–20. http://doi.org/10.1093/cercor/6.1.11

Tu, H., & Hampton, R. R. (2014). Control of Working Memory in Rhesus Monkeys (Macaca mulatta). *Journal of Experimental Psychology: Animal Learning and Cognition*, *40*(4), 467–476.

Unsworth, N., & Engle, R. W. (2007). The nature of individual differences in working memory capacity: Active maintenance in primary memory and controlled search from secondary memory. *Psychological Review*, *114*(1), 104–132. http://doi.org/10.1037/0033-295X.114.1.104

Washburn, D. a, & Astur, R. S. (1998). Nonverbal working memory of humans and monkeys: rehearsal in the sketchpad? *Memory & Cognition*, *26*(2), 277–286. http://doi.org/10.3758/BF03201139

Wright, a a, Cook, R. G., Rivera, J. J., Shyan, M. R., Neiworth, J. J., & Jitsumori, M. (1990). Naming, rehearsal, and interstimulus interval effects in memory processing. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, *16*(6), 1043–1059. http://doi.org/10.1037/0278-7393.16.6.1043