

CONTEXT CONTROLS ACCESS TO WORKING AND REFERENCE MEMORY
IN THE PIGEON (*COLUMBA LIVIA*)

WILLIAM A. ROBERTS, KRISTA MACPHERSON, AND CAROLINE STRANG

WESTERN UNIVERSITY

The interaction between working and reference memory systems was examined under conditions in which salient contextual cues were presented during memory retrieval. Ambient colored lights (red or green) bathed the operant chamber during the presentation of comparison stimuli in delayed matching-to-sample training (working memory) and during the presentation of the comparison stimuli as S+ and S- cues in discrimination training (reference memory). Strong competition between memory systems appeared when the same contextual cue appeared during working and reference memory training. When different contextual cues were used, however, working memory was completely protected from reference memory interference.

Key words: working memory, reference memory, context, pigeons

A common phenomenon experienced by most people is replacement of short-term working memory (WM) by long-term reference memory (RM). Asked to pick up milk at the market on the way home from work, one may form an instruction in WM to carry out this responsibility. By the end of work, however, this instruction is lost from consciousness and the habit of driving straight home controls behavior. Competition between WM and RM becomes particularly acute in dementia and Alzheimer's disease, in which WM is particularly fleeting (Baddeley, Bressi, Della Sala, Logie, & Spinnler, 1991; Morris, 1986; Stopford, Thompson, Richardson, Neary, & Snowden, 2010;). An important question, then, is whether there may be ways in which WM could be protected from RM interference.

The experiments reported here concern the control of behavior by WM and RM in the pigeon. The term *working memory* was adopted from studies of WM in humans. Baddeley (Baddeley, 1992; Baddeley & Hitch, 1974) defined WM in humans as a processing center with a central executive, phonological loop, and visual spatial sketchpad. In pigeons, we define the content of WM as memory for visual fields or patterns (Gibson, Wasserman, & Luck, 2011; Magnotti et al., 2013). Its further functional properties are that it is short term

and involves information that changes from one trial to the next (Honig, 1978). The most commonly used procedure for studying WM in pigeons has been delayed matching-to-sample. After seeing a sample stimulus, a pigeon is required to choose a matching stimulus from two or more comparison stimuli for reinforcement. Although the sample and correct comparison stimulus are often identical, their relationship may be arbitrary or symbolic. The symbolic matching-to-sample procedure was used in the current experiments. On each trial, the sample stimulus is first seen as one of two colored fields on the center key of an intelligence panel in an operant chamber. After the pigeon completes a fixed number of pecks on the sample stimulus key, the sample extinguishes and comparison stimuli are presented on right and left keys, consisting of vertical stripes on one key and a horizontal stripes on the other key. The relationship between the sample stimulus and the correct (reinforced) comparison key is arbitrary. For example, choice of the vertical stripes is correct after seeing one color and choice of the horizontal stripes is correct after seeing the other color. The pigeon then must learn to choose the correct comparison stimulus based on its WM of the sample stimulus.

The term *reference memory* was adopted by Honig (1978) and refers to an association or habit that is established by repeated reinforcement of response to the same stimulus. In contrast to WM, RM involves long-term retention and memory for a behavior that does not change from trial to trial.

Support for this research was provided by a discovery grant to the first author from the Natural Sciences and Engineering Research Council of Canada.

Address correspondence to William A. Roberts, Department of Psychology, Western University, London, Ontario N6A 5C2, Canada (email: roberts@uwo.ca).

doi: 10.1002/jeab.188

In a recently reported set of experiments, we demonstrated the competitive interaction between WM and RM in pigeons (Roberts, Strang, & Macpherson, 2015). Pigeons were trained to perform symbolic delayed matching-to-sample in an enclosed operant chamber. Each trial began with the presentation of a red or green center key (the sample) which the pigeon was required to peck 10 times in order to advance to the next stage of the trial. At the completion of 10 pecks, the center key was darkened and two side keys were illuminated, one with vertical black and white stripes and the other with horizontal black and white stripes. In order to obtain grain reinforcement from a food hopper in the wall of the chamber below the keys, a pigeon had to peck the key with vertical stripes after seeing the red sample stimulus and to peck the key with horizontal stripes after seeing the green sample stimulus. Thus, the pigeon had to learn the arbitrary or symbolic relationship between the sample color and the correct choice between the striped test stimuli. Importantly, in order to choose the correct test stimulus, the pigeon had to maintain a WM of the sample stimulus. After pigeons learned to match the sample at a high level of accuracy with the retention interval set at 0 s, tests occurred in which the delay between the termination of the sample stimulus and the presentation of the test stimuli was increased from 0 to 10 s. Matching accuracy dropped from around 90% at 0 s to near the chance level of 50% at 10 s, showing the forgetting of information from WM (Roberts, 1972; Roberts & Grant, 1976).

After pigeons had learned to perform delayed matching, Roberts et al. (2015) established an RM or habit by training pigeons to always choose one of the test stimuli for reinforcement. In these training sessions, just vertical and horizontal stripes appeared on the side keys (equally often on right and left keys) on each of 64 trials, and only one pattern was reinforced when chosen. For example, if the vertical stripes pattern was the reinforced choice, pigeons came to choose it on nearly 100% of the trials within five sessions of training.

The WM and RM training given pigeons provided the opportunity to carry out an *oppositional analysis* to examine the effects of RM on WM as the retention interval was increased.

The oppositional analysis was developed by Jacoby and his colleagues (Jacoby, 1991; Jacoby, Lindsay, & Toth, 1992) to examine the interaction between memory systems in humans. In our application of this analysis to pigeons, we examined pigeons' accuracy of delayed matching at retention intervals of 0, 3, 6, and 10 s on trials when WM and RM were *congruent* or in agreement and on trials when they were *incongruent* or in opposition to one another. For example, on a trial when the sample was red, the matching choice was vertical stripes and this stimulus was also congruent with the correct choice in RM training. On trials when the sample was green, however, the matching choice was horizontal stripes, which was incongruent with the correct choice in RM training. This experiment revealed a clear interaction between congruency and retention interval. At short retention intervals when WM was strong, there was little difference in matching accuracy on congruent and incongruent tests. As the retention interval increased, performance on congruent trials remained high but performance on incongruent trials dropped dramatically, showing that RM or habit came to control choice as WM was lost.

Further experiments by Roberts et al. (2015) showed that this competition could be manipulated by strengthening or weakening either WM or RM. Thus, strengthening WM by extending exposure to the sample stimulus led to a much smaller difference between congruent and incongruent conditions than seen when the sample was exposed for a shorter duration. The strength of RM was altered by RM training in which the probability of reinforcing one stimulus over the other was varied from .5:.5 to .75:.25 to 1.0:0. Working memory tests carried out after RM training at different probabilities showed that the difference between congruent and incongruent retention curves declined as the probability dropped from 1.0:0 to .5:.5. Finally, a *process dissociation procedure* (PDP) analysis developed by Jacoby (1991) provided derived measures of WM and RM under different conditions. This analysis suggested independent memory systems because retention interval affected WM PDP scores but had no effect on RM PDP scores and probability of reinforcement affected RM PDP scores but had no effect on WM PDP scores. Similar findings have been reported

from studies of memory systems interaction in rhesus monkeys (*Macaca mulatta*; Tu & Hampton, 2013; Tu, Hampton, & Murray, 2011).

Although substantially foreshortened in time, these experiments provided a pigeon model of the common competition between WM and RM experienced by humans. In the experiments reported here, we turned to the question of whether WM could be protected from the effects of RM in pigeons. Although neurological or pharmacological procedures might be possible, we used a procedure commonly used in the human memory and associative learning literatures, the manipulation of environmental context. Reinstatement of the context in which a memory was encoded has been shown to improve human retention (Murnane, Phelps, & Malmberg, 1999; Smith & Vela, 2001). A number of rodent experiments have shown that Pavlovian conditioning established in Context A and then extinguished in Context B will reappear when animals are tested in Context A (the renewal effect; Bouton, 1993, 2004). The context in these animal experiments is often thought of as a retrieval cue or an occasion setter. The question asked here was whether the competition between WM and RM systems could be reduced by associating each memory system with a different context. The first experiment demonstrates that the memory systems interaction effect found by Roberts *et al.* (2015) can be found when the same visual context is associated with WM and RM. The second experiment shows that WM can be protected from RM interference when different visual contexts are associated with each type of memory.

Experiment 1

Because color is a highly salient dimension for pigeons, we used it as a context cue. Red and green lights mounted in the ceiling of the operant chamber served as context cues that could be instantly turned on and off. Pigeons were trained to symbolically match vertical and horizontal striped patterns to working memories of blue and white sample stimuli. Reference memory training required a pigeon to choose vertical or horizontal stripes on every trial of a session for reinforcement. In these procedures, however, a context was associated with WM and RM tests. During delayed matching training, the chamber was bathed in

red or green light for 1 s before presentation of the test patterns and remained on until a choice was made. On RM training sessions, the chamber also was bathed in colored light for 1 s before and during choice between the test stimuli. The same color was presented on WM delayed matching tests and on RM tests. Delayed matching was then tested at retention intervals of 1, 3, 6, and 10 s, and retention curves were examined separately for trials when the correct WM choice was congruent and incongruent with RM.

Method

Subjects. Eight adult White King pigeons were tested. These birds had been used previously in studies of timing and midsession reversal. In those studies, they were reinforced for pecking at colors and patterns on the keys of the operant chamber, but they were never exposed to red or green houselights. The birds were maintained at approximately 85% of their free-feeding weights throughout the experiment, with constant access to water and health grit. They were individually housed in cages in a room environmentally controlled at 22 degrees C. Fluorescent lights were turned on at 7:00 a.m. and off at 7 p.m. each day. Testing was performed between 9 a.m. and 4 p.m. for 5 days each week.

Apparatus. Two enclosed, sound-attenuating operant chambers measuring 31 x 35.5 (floor) x 35.3 cm (height) were used. The front wall of each chamber held three pecking keys, 2.5 cm in diameter and level with the pigeon's head, in a row, spaced 8 cm apart. Projectors behind each key projected filtered light, presenting different colors or patterns on the keys. Mixed grain reinforcement was delivered by an electromechanical hopper through a 6 x 6 cm opening in the front wall located near the floor, directly below the center key. A rectangular box measuring 10.5 x 5 x 2.5 cm was positioned on the center of the ceiling. It contained two 6-w light bulbs, one covered with a red lens and other with a green lens. These lights were used to bathe the chamber in red or green light as a contextual cue. Presentation of stimuli, reinforcement, and recording of responses were carried out by microcomputers, in another room, interfaced to the operant chambers. A white noise generator was

played during sessions to mask extraneous sounds.

Procedure. Pigeons were initially trained on a symbolic delayed matching-to-sample task in which the samples were blue and white fields presented on the center key and the comparison stimuli were vertical and horizontal striped patterns presented on the side keys. Each trial began with the presentation of either a white or blue center key. A pigeon had to complete a fixed ratio (FR) of 10 pecks on the sample stimulus. The sample was then turned off and a red or green ambient context cue appeared for 1 s. The context cue was red for four pigeons and green for the other four pigeons. The comparison stimuli then appeared on the side keys while the context cue remained lit. Three alternating black and white stripes appeared on each side key as comparison stimuli, with the stripes oriented vertically on one side key and horizontally on the other side key. The left-right positions of the vertical and horizontal striped stimuli were counterbalanced across trials. The reinforcement contingencies were programmed so that a peck on vertical stripes was required for reinforcement after pecking a blue sample stimulus and a peck on horizontal stripes was required for reinforcement after pecking a white sample stimulus. A correct matching response turned off the comparison stimuli and the context cue and illuminated the food hopper, providing 2.5 s of access to mixed grain as reinforcement. A response to the incorrect or nonmatching comparison stimulus turned off the comparison stimuli and context cue without reinforcement. Following either reinforcement or an incorrect choice, the pigeon spent an intertrial interval in the darkened chamber that varied randomly between 10 and 30 s. The intertrial intervals were sampled from a rectangular distribution. There were 64 trials in each session, and pigeons were trained until the mean matching accuracy was over 85% on two consecutive sessions (34 sessions, 86.91% correct).

All eight pigeons then were tested over 10 sessions in which varying delays or retention intervals were inserted in random order between the sample and comparison stimuli. The retention intervals were 1 s (the training interval) and 3, 6, and 10 s. Before the presentation of the comparison stimuli at each interval, the context cue was presented for 1 s and

remained on until a choice was made between the comparison stimuli. The purpose of testing the birds with extended delays was to give them experience with longer retention intervals and to generate a preliminary forgetting curve.

The pigeons then were given five sessions of reference memory training. This training consisted of sessions containing 64 visual discrimination trials. On each trial, vertical and horizontal stripes patterns appeared on the left and right side keys, with positions counterbalanced over trials. For four pigeons, a peck on vertical stripes always yielded 2.5 s of grain reinforcement. For the other four pigeons, a peck on horizontal stripes led to reinforcement. The same overhead context cue light the pigeon had experienced in delayed matching training was lit for 1 s before the appearance of the striped patterns and remained on until a choice was made. For the four birds experiencing the red context, the vertical stripes pattern was reinforced for two birds and the horizontal stripes pattern was reinforced for the other two birds. For the four birds experiencing the green context, two were reinforced for choosing vertical stripes and two were reinforced for choosing horizontal stripes. The intertrial intervals were spent in darkness and lasted for 10–30 s.

In the final phase of the experiment, visual discrimination training and experimental testing were carried out over five daily sessions, with 64 trials in each session. On sessions 1, 3 and 5, the pigeons were returned to delayed matching testing with retention intervals of 1, 3, 6 and 10 s. On sessions 2 and 4, they received visual discrimination training between vertical and horizontal striped patterns. In both types of sessions, the same color context cue appeared for 1 s before presentation of the striped test stimuli and remained on until a choice response was made. The data of primary interest were the pigeons' performance on delayed matching trials when the correct matching comparison stimulus was the same as the correct stimulus in visual discrimination training (congruent test) and on delayed matching trials when the matching choice was opposite to the correct choice in visual discrimination training (incongruent test). On congruent tests, WM and RM indicated the same response, but on incongruent tests, WM and RM dictated different responses.

Results and Discussion

Over the 34 sessions of delayed matching-to-sample training, pigeons showed steady improvement in matching accuracy at a 1-s retention interval. On sessions 1–5, pigeons were only at chance, making 49.04% correct choices ($SE = 1.21$). Over the final five sessions (30–34), mean accuracy was 86.34% ($SE = 3.01$). Over the subsequent 10 sessions of testing at retention intervals of 1, 3, 6 and 10 s, the percentages of correct choices were 86.17, 73.12, 69.14, and 63.59, respectively ($SEs = 3.13, 4.98, 4.49, \text{ and } 3.42$). Thus, birds showed clear forgetting of WM content over increasing retention intervals, $F(3, 21) = 31.47$, $p < .01$, $\eta_p^2 = .82$.

Pigeons rapidly learned to choose the reinforced stimulus over the five sessions of visual discrimination training. Over sessions 1–5, mean percentages of correct choices were 67.19, 89.26, 96.88, 98.24, and 99.22, respectively ($SEs = 4.93, 2.96, 1.45, .62, \text{ and } .51$). On sessions 2 and 4 of discrimination training that alternated between delayed matching sessions in the final testing phase, accurate choices were made on 90.82 and 97.07 percent of the trials, respectively, ($SEs = 4.18 \text{ and } 1.12$).

Mean performance over the three sessions of delayed matching testing is shown in Figure 1 as retention curves obtained on trials when the matching choice was congruent and incongruent with discrimination training. These curves show a clear interaction between congruency and retention interval. Only a slight difference in performance is apparent at the 1-s retention interval. As the retention interval increases, however, the congruent curve drops only slightly while the incongruent curve drops sharply, showing progressively larger superiority of performance on congruent trials over incongruent trials.

An analysis of variance (ANOVA) was performed on these data, with the factors being congruency and retention interval. It revealed significant effects of congruency, $F(1, 7) = 57.00$, $p < .01$, $\eta_p^2 = .89$, retention interval, $F(3, 21) = 38.85$, $p < .01$, $\eta_p^2 = .85$, and the congruency \times retention interval interaction, $F(3, 21) = 6.29$, $p < .01$, $\eta_p^2 = .47$. Comparisons of matching accuracy at each retention interval using paired t -tests showed no significant effect of congruency at 1 s, $t(7) = 1.23$, $p > .05$, but significant effects of congruency at retention intervals of 3, 6, and

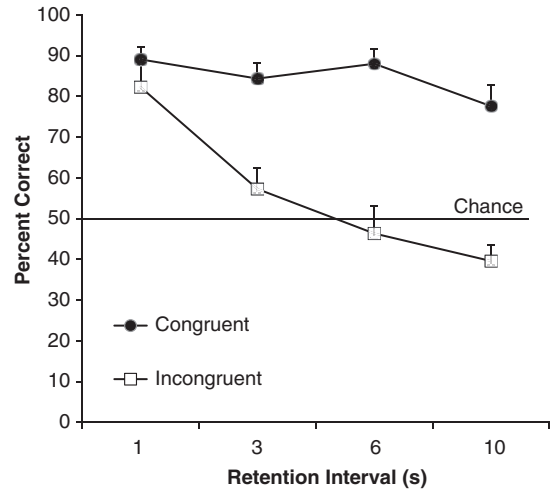


Fig. 1. Retention curves for congruent and incongruent trials from Experiment 1. Error bars represent SEM.

10 s, $t(7) \geq 4.66$, $p < .01$. Pigeons' matching accuracy on incongruent trials was below chance (50%) at the 6-s retention interval (46.35%) and at the 10-s retention interval (39.58%). Matching performance was significantly below chance at the 10-s interval, $t(7) = 2.59$, $p < .05$, but not at the 6-s interval.

These findings largely replicate those reported by Roberts *et al.* (2015) by showing that WM controls performance at short retention intervals and that the effect of RM becomes more dominant as the retention interval increases and WM weakens. The Roberts *et al.* experiments were carried out in a darkened chamber with no specific contextual cue provided during either WM or RM training. The findings of Experiment 1 importantly show that the same interaction between memory systems can be found when the same contextual cue is paired with WM and RM. This finding then sets the stage for the following experiment.

Experiment 2

Having shown that RM progressively comes to control choice performance as the retention interval becomes longer, we now address the question of whether WM could be protected or insulated from the effects of RM. Given the strong effects of context on human memory retrieval and on renewal of an acquired response after extinction in

Pavlovian experiments, we associated different visual contexts with WM and RM training. On delayed matching trials, red or green light bathed the test chamber for 1 s before comparison stimuli were presented and remained on during presentation of the comparison stimuli. During RM visual discrimination learning, the opposite color from that used during delayed matching trials was presented before and during a choice between stimuli. Once birds were performing at a high level of accuracy in both contexts, delayed matching sessions were carried out in which either the WM or RM contextual cue was presented on each trial. If context came to control access to different memory systems, it should be seen that the effect of congruity would be weakened when the WM context is tested and should be strengthened when the RM context is tested.

Method

Subject and apparatus. The same eight pigeons and apparatus used in Experiment 1 were used in Experiment 2.

Procedure. These birds continued to be trained on delayed matching-to-sample for five sessions, using the contextual cue they experienced in Experiment 1. Thus, the overhead red or green light was turned on for 1 s before the comparison stimuli were presented and remained on during their presentation. Performance on these trials remained comparable to that seen in Experiment 1.

To establish a new reference memory in a new context, pigeons learned the reversal of the visual discrimination learned in Experiment 1. If the vertical stripes pattern had been correct in Experiment 1, only pecks to the horizontal stripes pattern now yielded reinforcement in Experiment 2 training. In addition, the contextual cue experienced during reversal training was new. The four birds that had seen a red context on all trials in Experiment 1 now saw a green context 1 s before and during presentation of the striped patterns on every trial during discrimination learning. Thus, these pigeons experienced a red context during delayed matching and a green context during discrimination training. The other four pigeons experienced the opposite combination, a green context during delayed matching and a red context during discrimination training. Pigeons completed

nine sessions of reversal training under these conditions, with 64 trials in each session.

Following visual discrimination training, pigeons were tested over nine sessions. These sessions were subdivided into three sets of three sessions each. On the first session of a set of three, pigeons were tested on delayed matching for 64 trials with the WM context always presented on every trial. Each trial involved presentation of a blue or white sample and completion of 10 pecks on the sample, followed by a retention interval of 1, 3, 6, or 10 s before the comparison stimuli appeared. The appropriate WM contextual cue appeared for 1 s before and during the presentation of the comparison stimuli. Another 64 trials of delayed matching testing was given on the second session, but the contextual cue that appeared before and during comparison stimuli was the RM context used in discrimination training. On the third session of training, pigeons received a refresher day of 64 trials of training on the visual discrimination in the RM context. This pattern of testing was repeated over the subsequent two sets of three sessions.

Results and Discussion

Pigeons quickly learned the reversed visual discrimination over the nine sessions of training. Performance on the first session of training was 56.06% correct choices ($SE = 2.30$) and reached 96.29% correct choices ($SE = 1.69$) on the final session of training. On the five delayed matching training sessions with a 1-s retention interval, the mean accuracy of matching was 85.20% ($SE = 3.37$).

Delayed matching performance on congruent and incongruent trials is shown in Figure 2 for trials in which the WM context was presented and for trials in which the RM context was presented. When the WM context was presented, typical delayed matching forgetting curves are seen that show no evidence of a congruity effect. In fact, the incongruent curve is a little higher than the congruent curve. When the RM context was presented, however, pigeons showed almost total preference for the stimulus reinforced during discrimination training, with no decline in choice percentage as a function of retention interval.

An ANOVA was carried out to analyze these data which included the factors of context,

congruency, and retention interval. The analysis revealed significant main effects of context, $F(1, 7) = 35.27, p < .01, \eta_p^2 = .83$, congruency, $F(1, 7) = 160.57, p < .01, \eta_p^2 = .96$, and retention interval, $F(3, 21) = 12.02, p < .01, \eta_p^2 = .63$. Significant interactions were found between context and congruency, $F(1, 7) = 123.46, p < .01, \eta_p^2 = .95$, and between context and retention interval, $F(3, 21) = 4.44, p < .05, \eta_p^2 = .39$. Separate congruency by retention interval ANOVAs were performed on the WM context and RM context curves. The analysis of the WM context curves yielded a significant effect of retention interval, $F(3, 21) = 9.86, p < .01, \eta_p^2 = .58$, but nonsignificant effects of congruency and the congruency by retention interval interaction. The analysis of the RM context curves found a significant effect of congruency, $F(1, 7) = 165.39, p < .01, \eta_p^2 = .96$, but nonsignificant effects of retention interval and the congruency by retention interval interaction.

These findings show that associating different visual contexts with retention of information from WM and RM eliminated competition between these memory systems. When delayed matching tests were given in the RM context, pigeons chose the S+ stimulus from discrimination training with no effect of retention interval. Delayed matching tests given in the WM context yielded typical

forgetting curves that overlapped and showed no effect of congruency. It is important to note that context did not simply cue a particular response. When the WM context cue appeared, pigeons had to use memory of the sample stimulus to choose between the vertical and horizontal stripes patterns, with the sample and correct choice changing between trials. Thus, red and green contexts accessed different memory systems.

The effect of protecting WM by associating it with its own context is shown in Figure 3. This figure plots retention curves for incongruent delayed matching tests from Experiment 1 in which the same context was present on WM and RM tests and from Experiment 2 in which different contexts were present on WM and RM tests. The curves show little difference at the 1-s retention interval but progressively separate as the retention interval increases to 10 s. As WM weakens over the retention interval, the interfering effect of RM becomes more prominent when the same context cues WM and RM. Working memory is protected, however, even at longer retention intervals, when different contexts cue WM and RM. A context (same versus different) \times retention interval ANOVA performed on the curves in Figure 3 produced significant effects of context, $F(1, 7) = 49.05, p < .01, \eta_p^2 = .88$, retention interval, $F(3, 21) = 42.92, p < .01,$

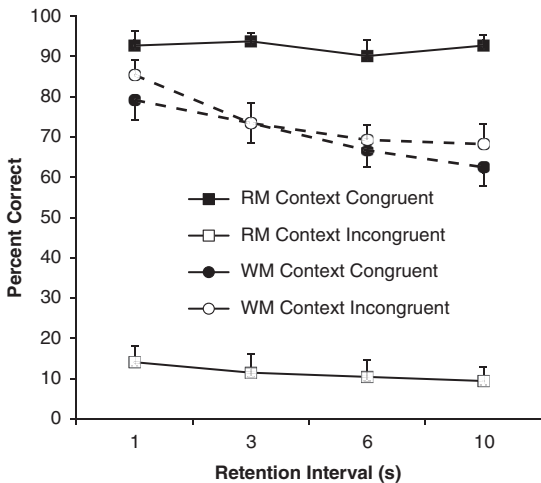


Fig. 2. Retention curves for congruent and incongruent trials are shown for delayed matching tests when working memory (WM) and reference memory (RM) contexts were presented before and during the presentation of comparison stimuli in Experiment 2. Error bars are *SEM*.

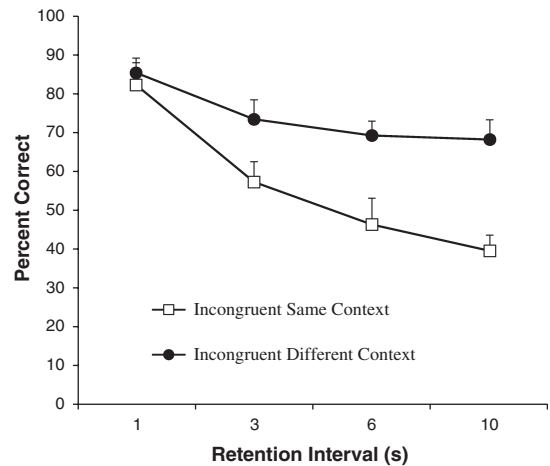


Fig. 3. Retention curves for incongruent trials when the same context was present on working and reference memory training trials (Experiment 1) and when different contexts were present on working and reference memory training trials (Experiment 2). Error bars are *SEM*.

$\eta_p^2 = .86$, and the context by retention interval interaction, $F(3, 21) = 3.08$, $p = .05$, $\eta_p^2 = .31$.

General Discussion

Pigeons showed competition between WM and RM when the same context was associated with both memory systems in Experiment 1. This was shown by comparing delayed matching retention curves between trials when the correct comparison stimulus was congruent and incongruent with RM training. Little effect of congruity was seen at a short 1-s retention interval, but, as the retention interval grew to 10 s, the retention curves separated as the incongruent curve dropped precipitously and the congruent curve remained relatively flat. Working memory largely controlled performance on the immediate test, but as WM weakened at longer retention intervals RM more and more dominated choice behavior. This was shown when the same contextual color cue (red or green) appeared during the presentation of vertically and horizontally striped stimuli in both WM and RM training. The same context cue accessed both memory systems, leading to competition between them and the interacting retention curves.

Similar findings were reported by Roberts et al. (2015) when no contextual cue was presented with comparison stimuli. However, it may be argued that the darkened chamber acted as a contextual cue that accessed WM and RM in those experiments. The Roberts et al. experiments also showed that the relative effects of WM and RM on retention performance can be modified by strengthening or weakening either type of memory. Increasing sample exposure led to continued dominance of WM over RM throughout the retention interval. Increasing the probability of S+ reinforcement in discrimination training led to more pronounced influence of RM on retention curves. A process dissociation analysis (Jacoby, 1991) of data from these experiments showed that WM and RM were independent systems, a conclusion similar to that reached from analysis of human (Hay & Jacoby, 1996; Jacoby et al., 1992) and monkey (Tu & Hampton, 2013; Tu et al., 2011) data.

In Experiment 2, separate contexts were associated with WM and RM. For each pigeon, all presentations of the lines comparison

stimuli during delayed matching training involved the presentation of an overhead light that bathed the chamber in red or green illumination. During RM discrimination training, the alternate color bathed the chamber during presentation of the choice stimuli for each pigeon. Pigeons were then tested for delayed matching accuracy at different retention intervals on sessions when the WM context appeared with the comparison stimuli and on sessions when the RM context appeared with the comparison stimuli. The curves shown in Figure 2 revealed that context totally controlled access to WM and RM systems. When the WM context was presented, typical delayed matching-to-sample curves were found on trials when the matching correct choice was both congruent and incongruent with RM. No effect of congruity was observed. When the RM context was presented, pigeons performed as if no sample stimulus had been presented and they were making a choice based only on RM discrimination training. That is, the reinforced S+ stimulus was chosen on most trials and this choice was not influenced by the retention interval since the sample stimulus had been presented.

It might be argued that the results seen in Experiment 2 represent only contextual control of discrimination learning. For example, the red houselight became an occasion setter for pecking the key with horizontal stripes for reinforcement. In the absence of the red context, pigeons matched to sample unaffected by discrimination training. It should be remembered, however, that these pigeons had learned to peck the key with vertical stripes for reinforcement in the presence of the green houselight in Experiment 1. If houselight context only controlled discrimination performance in these experiments, we would then expect to see congruity effects on delayed matching tests performed in the WM context in Experiment 2. That is, pigeons should be biased toward choosing vertical stripes at longer retention intervals in the green context. Figure 2 shows no evidence of such bias. Rather, the findings suggest that discrimination training in the red context eliminated discriminative responding controlled by the green context. However, the green context continued to direct control by WM, yielding delayed matching retention curves with no effect of congruity.

Two further important points should be made about the findings from Experiment 2. First, they do not just show that a response learned in Context A is cued by Context A and a response learned in Context B is cued by Context B. One might argue this for the effects of presentation of the RM context. When the WM context was presented, however, pigeons had to respond on the basis of memory of the sample stimulus, and that memory changed from trial to trial. The second point is that these findings cannot be explained as typical memory retrieval reinstatement effects. In many human and animal experiments, it has been shown that memories formed in one context are then remembered better when that context is reinstated than when it is not. A process of *encoding specificity* accounts for these effects (Tulving & Thomson, 1973). Again, encoding specificity might account for the effect of presentation of the reference memory context because it was present during the presentation of the stripes stimuli during both discrimination training and delayed matching testing. During delayed matching training and testing, however, the WM context was never presented during a pigeon's exposure to the sample stimulus. The contextual cue appeared only at the test for working memory of the sample stimulus. For these reasons, we argue that the contextual cues of color of chamber illumination accessed independent memory systems and that memories taken from the cued system then controlled choice behavior.

The use of ambient colored light as a contextual cue in these experiments with pigeons may have been fortuitous. Pigeons are known to have excellent color vision; in fact, the pigeon retina contains four or five different photopigments (Waldvogel, 1990). Thus, a particularly salient context appeared to provide access to WM and RM systems in pigeons. Although pigeons are evolutionarily distant from humans, and these findings occur over relatively short retention intervals, the use of salient contextual cues might provide access to different memory systems in humans. If strikingly different visual environments were repeatedly associated with the retrieval of WM information and RM information, could these visual contexts then access each memory system for the retrieval of newly formed memories?

Evidence for independent WM and RM memory systems has been found in rodents on the radial maze. Olton and Papas (1979) trained rats on a 16-arm radial maze to enter eight randomly chosen arms for reward and to avoid entrance into the other 16 nonrewarded arms. Entrance into a nonrewarded arm was considered an RM error, and repetition of a visit to a rewarded arm was considered a WM error. When rats received hippocampal lesions, WM errors increased, but RM errors were unaffected. Packard, Hirsh, and White (1989) showed double dissociation between memory systems and locus of brain lesions. Hippocampal lesions caused a large increase in WM errors but had no effect on RM errors. Caudate lesions had the opposite effect, increasing RM errors but having no effect on WM errors.

A possible comparable neural system responsible for WM may be found in pigeons. Lesions of the pigeon neostriatum caudolaterale (NCL), an analogue of the mammalian prefrontal cortex, significantly reduce WM on a visual delayed matching-to-sample task (Diekamp, Gagliardo, & Gunturkun, 2002). Diekamp, Kalt, and Gunturkun (2002) found that firing of NCL cells was directly related to accuracy of performance in a delayed go-no-go task, and Rose and Colombo (2005) found greater firing of NCL neurons when a sample stimulus was followed by a remember cue than when it was followed by a forget cue.

The Roberts *et al.* (2015) experiments showed that WM and RM systems compete for control of memory performance in pigeons. A model was suggested in which the relative strengths of WM and RM would yield weak or strong congruency effects (See Figs. 7 and 8 in Roberts *et al.*, 2015). The neural systems responsible for WM and RM may then be coactive during delayed matching tests and vary in their relative influence depending on the length of the retention interval. The current experiments suggest that these neural systems may be selectively activated. When delayed matching and discrimination learning are trained in the same context (Experiment 1), both WM and RM systems may operate. However, when delayed matching and discrimination training take place in different contexts, context may selectively activate one neural system and not the other. Experiments that record neural firing from different neural

systems related to WM and RM would be of considerable interest when same and different contexts are associated with delayed matching and discrimination learning.

In pursuit of a mammalian model of memory systems interaction, Guitar and Roberts (2015) have shown interaction between WM and RM in the rat on the radial maze. Rats also show an interaction of congruity between WM and RM with retention interval. However, the retention intervals used with rats were substantially longer than those used with pigeons, extending up to an hour. Thus, it will be of considerable interest to see if context can overcome congruity and provide access to different memory systems in the rat, as it does in the pigeon. A rodent model of these effects would be particularly valuable for examining the effects of selective lesions in and recording from neural areas thought to be responsible for WM and RM (hippocampus and caudate nucleus).

References

- Baddeley, A. (1992). Working memory. *Science*, 255, 556–559.
- Baddeley, A. D., & Hitch, G. (1974). Working memory. In G. H. Bower (Ed.), *The psychology of learning and motivation: Advances in research and theory* (pp. 47–89). New York: Academic Press.
- Baddeley, A. D., Bressi, S., Della Sala, S., Logie, R., & Spinnler, H. (1991). The decline of working memory in Alzheimer's disease. A longitudinal study. *Brain*, 114, 2521–2542.
- Bouton, M. E. (1993). Context, time, and memory retrieval in the interference paradigms of Pavlovian learning. *Psychological Bulletin*, 114, 80–99.
- Bouton, M. E. (2004). Context and behavioral processes in extinction. *Learning & Memory*, 11, 485–494.
- Diekamp, B., Gagliardo, A., & Güntürkün, O. (2002). Non-spatial and subdivision-specific working memory deficits after selective lesions in the avian prefrontal cortex. *The Journal of Neuroscience*, 22, 9573–9580.
- Diekamp, B., Kalt, T., & Güntürkün, O. (2002). Working memory neurons in pigeons. *The Journal of Neuroscience*, 22, RC210, 1–5.
- Gibson, B., Wasserman, E., & Luck, S. J. (2011). Qualitative similarities in the visual short-term memory of pigeons and people. *Psychonomic Bulletin & Review*, 5, 979–984.
- Guitar, N. A., & Roberts, W. A. (2015). The interaction between working and reference spatial memories in rats on a radial maze. *Behavioural Processes*, 112, 100–107.
- Hay, J. F., & Jacoby, L. L. (1996). Separating habit and recollection: Memory slips, process dissociations, and probability matching. *Journal of Experimental Psychology: Learning Memory, and Cognition*, 22, 1323–1335.
- Honig, W. K. (1978). Studies of working memory in the pigeon. In S. Hulse, H. Fowler, & W. K. Honig (Eds.), *Cognitive processes in animal behavior* (pp. 211–248). Hillsdale, NJ: Erlbaum.
- Jacoby, L. L. (1991). A process dissociation framework: Separating automatic from intentional uses of memory. *Journal of Memory and Language*, 30, 513–541.
- Jacoby, L. L., Lindsay, D. S., & Toth, J. P. (1992). Unconscious influences revealed. Attention, awareness, and control. *American Psychologist*, 47, 802–809.
- Magnotti, J. F., Goodman, A. M., Daniel, T. A., Elmore, L. C., Wright, A. A., & Katz, J. S. (2013). Visual object complexity limits pigeon short-term memory. *Behavioural Processes*, 93, 31–38.
- Morris, R. G. (1986). Short term forgetting in senile dementia of the Alzheimer's type. *Cognitive Neuropsychology*, 3, 77–97.
- Murnane, K., Phelps, M. P., & Malmberg, K. (1999). Context-dependent recognition memory: The ICE theory. *Journal of Experimental Psychology: General*, 128, 403–415.
- Olton, D. S., & Papas, B. C. (1979). Spatial memory and hippocampal function. *Neuropsychology*, 17, 669–682.
- Packard, M. G., Hirsh, R., & White, N. M. (1989). Differential effects of fornix and caudate nucleus lesions on two radial maze tasks: Evidence for multiple memory systems. *Journal of Neuroscience*, 9, 1465–1472.
- Roberts, W. A. (1972). Short-term memory in the pigeon: Effects of repetition and spacing. *Journal of Experimental Psychology*, 94, 74–83.
- Roberts, W. A., & Grant, D. S. (1976). Studies of short-term memory in the pigeon using the delayed matching to sample procedure. In D. L. Medin, W. A. Roberts, & R. T. Davis (Eds.), *Processes of animal memory* (pp. 79–112). Hillsdale, NJ: Erlbaum.
- Roberts, W. A., Strang, C., & Macpherson, K. (2015). Memory systems interaction in the pigeon: Working and reference memory. *Journal of Experimental Psychology: Animal Learning and Cognition*, 41, 152–162.
- Rose, J., & Colombo, M. (2005). Neural correlates of executive control in avian brain. *PLoS, Biology*, 3, e190.
- Smith, S. M., & Vela, E. (2001). Environmental context-dependent memory: A review and Meta-analysis. *Psychonomic Bulletin & Review*, 8, 203–220.
- Stopford, C. L., Thompson, J. C., Richardson, A. M. T., Neary, D., & Snowden, J. S. (2010). Working memory in Alzheimer's disease and frontotemporal dementia. *Behavioural Neurology*, 23, 177–179.
- Tu, H.-W., & Hampton, R. R. (2013). One-trial memory and habit contribute independently to matching-to-sample performance in rhesus monkeys (*Macaca mulatta*). *Journal of Comparative Psychology*, 127, 319–328.
- Tu, H.-W., Hampton, R. R., & Murray, E. A. (2011). Perirhinal cortex removal dissociates two memory systems in matching-to-sample performance in rhesus monkeys. *Journal of Neuroscience*, 31, 16336–16343.
- Tulving, E., & Thomson, D. M. (1973). Encoding specificity and retrieval processes in episodic memory. *Psychological Review*, 80, 352–373.
- Waldvogel, J. A. (1990). The bird's eye view. *American Scientist*, 78, 342–353.

Received: August 4, 2015

Final Acceptance: November 16, 2015