

Memory Systems Interaction in the Pigeon: Working and Reference Memory

William A. Roberts, Caroline Strang, and Krista Macpherson
Western University

Pigeons' performance on a working memory task, symbolic delayed matching-to-sample, was used to examine the interaction between working memory and reference memory. Reference memory was established by training pigeons to discriminate between the comparison cues used in delayed matching as S+ and S- stimuli. Delayed matching retention tests then measured accuracy when working and reference memory were congruent and incongruent. In 4 experiments, it was shown that the interaction between working and reference memory is reciprocal: Strengthening either type of memory leads to a decrease in the influence of the other type of memory. A process dissociation procedure analysis of the data from Experiment 4 showed independence of working and reference memory, and a model of working memory and reference memory interaction was shown to predict the findings reported in the 4 experiments.

Keywords: memory systems, working memory, reference memory, delayed matching, pigeons

Evidence for multiple memory systems has been found in studies of nonhuman animals (hereafter referred to as animals). In an early study, [Olton and Papas \(1979\)](#) tested rats on a 16-arm radial maze in which a subset of arms was never baited and was defined as reference memory (RM; [Honig, 1978](#)) arms because rats had to learn to always avoid these arms. The complementary subset of arms was always baited and could be entered in any order. Because entrances into these arms had to be remembered within a trial to avoid repeat visits, they were defined as working memory (WM) arms. Thus, any visit to an RM arm was considered an RM error, and any revisit to a WM arm was considered a WM error. A dissociation between RM and WM was suggested by the finding that hippocampal lesions (fimbria-fornix) increased WM errors but had no effect on RM errors. In other research, [Shen, Barnes, Wenk, and McNaughton \(1996\)](#) found that injection of a cholinergic neurotoxin into the hippocampus impaired spatial WM but had no effect on the acquisition and retention of RM. [Packard, Hirsh, and White \(1989\)](#) found evidence of double dissociation between types of memory and brain structures. One group of rats that had received lesions of the fimbria fornix showed a large increase in WM errors relative to control rats but no increased difficulty in performing an RM task that involved entering arms containing a light cue for reward. Another group of rats that received caudate lesions showed the opposite effect, an increase in RM errors but not WM errors. In yet another study, [Levin, Kim, and Meray](#)

(1996) found that infusion of nicotine, a neurotransmitter stimulant, significantly lowered WM errors made by rats on the radial maze but had no effect on RM errors.

A particularly interesting question is how WM and RM may interact in the control of behavior when their contents are in disagreement. For example, a phenomenon familiar to most people is the loss of a recently formed WM and its replacement with memory for a well learned RM. Thus, a friend may tell you his new phone number, which you recite several times in WM. When needing to call your friend at a later time in the day, however, you may automatically dial his old number. This familiar scenario is an example of memory systems interaction. Had you called shortly after storing the number in WM, you would have dialed the correct number. After several hours, however, the WM has been lost and more permanent RM or habit takes over and guides you to call the now incorrect old number.

This type of competition between memory systems has been extensively examined in studies of human memory ([Squire, 2004](#)). Well learned memories or habits are described as implicit, automatic, and unconscious, whereas memories for more recent one-time events are described as explicit and conscious. [Jacoby \(1991\)](#) developed the *process dissociation procedure* (PDP) to examine the interaction between WM and RM by carrying out tests under two different conditions, one in which RM and WM indicate the same response on a retention test (congruent condition) and the other in which RM and WM indicate different responses and thus are placed in opposition to one another (incongruent condition). By using performance scores from these different conditions, it is possible to derive measures of each type of memory under varying test conditions.

On congruent tests, the same response stored in WM and RM is correct. Thus, the PDP analysis holds that performance obtained on congruent tests is the sum of two probabilities, the probability of correctly remembering items stored in WM and the probability of correctly remembering items stored in RM when they have been

This article was published Online First January 26, 2015.

William A. Roberts, Caroline Strang, and Krista Macpherson, Department of Psychology, Western University.

Support for the research reported was provided by a Discovery Grant to William A. Roberts from the Canadian Natural Sciences and Engineering Research Council.

Correspondence concerning this article should be addressed to William A. Roberts, Department of Psychology, Western University, London, Ontario, Canada, N6A 5C2. E-mail: roberts@uwo.ca

forgotten in WM, $RM(1 - WM)$. The obtained score then equals $WM + RM(1 - WM)$. On incongruent tests, however, the response stored in RM is incorrect and different from the correct response stored in WM. Thus, an error in memory recall will occur if WM is forgotten. The PDP analysis holds that the probability of incorrectly recalling RM items is $RM(1 - WM)$. The derived WM score is then calculated by subtracting probability of incorrectly remembering RM items on incongruent tests from the probability of correctly remembering WM and RM items on congruent tests (Equation 1).

$$WM = \text{Congruent Score} - \text{Incongruent Score} \quad (1)$$

If the incongruent score is equal to $RM(1 - WM)$, then through algebraic manipulation, a derived RM score is obtained as shown in Equation 2.

$$RM = \text{Incongruent Score} / (1 - WM) \quad (2)$$

Hay and Jacoby (1996) applied the PDP analysis to people's memory for word pairs that had been previously established as strong or weak habits (RM) and then more recently presented on a single occasion (WM). More important, PDP scores suggested that the memory systems under study were independent of one another. That is, manipulations designed to affect strength of RM affected only RM PDP scores and not WM scores, and manipulations designed to affect WM affected only WM PDP scores and not RM scores.

Recently, Tu and Hampton (2013) extended the PDP procedure to the study of memory in rhesus monkeys. Using a delayed matching-to-sample procedure to test WM, monkeys were shown a clip-art sample stimulus on a screen. Four images (quads) were then shown after a delay, with only one image identical to the sample and the correct matching choice. Habit or RM was manipulated by presenting different quads in which a given image matched the sample on 100%, 75%, 50%, or 25% of the training trials. Thus, on different tests, the correct image that matched the sample corresponded to a relatively strong habit image (congruent condition) or corresponded to a relatively weak habit image (incongruent condition). An interesting find was that they obtained results similar to those reported with human subjects. When the delay or retention interval was increased, WM one-trial memory PDP scores dropped but RM habit PDP scores were unaffected. When the probability of a sample-match pair was varied between 25% and 100% within sets of four images, RM PDP scores increased but WM PDP scores remained unchanged.

Recent findings suggest that the dissociation found in PDP analysis of memory scores may be associated with different brain structures. Tu, Hampton, and Murray (2011) found evidence for dissociation of memory systems based on brain lesions. Monkeys with perirhinal cortex removal showed a marked reduction in one-trial memory scores (WM) relative to normal monkeys but no difference from controls in habit scores (RM).

In the experiments reported here, we extended the study of memory systems to a nonmammalian species, the pigeon. Extensive past research has developed tasks that are clearly operationally defined as tests of WM and RM in pigeons. The delayed matching-to-sample procedure has long been recognized as a test of WM in pigeons (Honig, 1978; Roberts, 1972). After a single presentation of a sample cue, a pigeon is reinforced only for

choosing between two comparison stimuli the one that matches the sample. The other type of memory, RM, is readily established through discrimination training in which two stimuli are repeatedly shown to a bird, with response to one stimulus reinforced and response to the other stimulus nonreinforced. We were interested in examining the interaction between WM and RM under different conditions that are known to affect the strength of each kind of memory. The interaction of these types of memory was observed by using the opposition procedure developed by Jacoby (Hay & Jacoby, 1996; Jacoby, 1991). Basically, pigeons were required to match a sample stimulus under conditions in which the correct comparison stimulus was congruent or incongruent with the correct stimulus from a visual discrimination task learned on previous training sessions. The basic interaction of WM and RM was shown in Experiment 1 when WM strength was varied by increasing the delayed matching retention interval. In Experiments 2 and 3, this effect was replicated along with a demonstration of the effect of manipulating the initial strength of WM through sample presentation time. In Experiment 4, the strength of RM was manipulated by training pigeons with probability matching schedules that varied from 50:50 to 100:0 and examining their effect on WM performance under congruent and incongruent conditions.

Experiment 1

Pigeons were initially trained with a symbolic delayed matching-to-sample procedure in which the samples were colors (red and green) and the comparison stimuli were line orientations (vertical and horizontal). Once pigeons had learned to match samples with comparison stimuli at a high level of accuracy on immediate (0-s delay) tests, they were tested at several delays to establish a retention curve. After delayed matching testing, they were given sessions of visual discrimination training that alternated with sessions of delayed matching. On visual discrimination training sessions, vertical and horizontal lines were presented on left and right keys, with either vertical lines or horizontal lines always reinforced when pecked. To examine the development of memory interaction, a delayed matching session followed on the day after each visual discrimination training session. The observations of interest were the extent to which congruency between comparison test stimuli and visual discrimination training stimuli would affect performance at different retention intervals.

Method

Subjects. Six adult White King pigeons (*Columba livia*) were used. These subjects had previously been used in a midsession reversal experiment. Birds were maintained at ~85% of free-feeding weight throughout the experiment, with constant access to water and health grit. They were individually housed in cages in a room kept environmentally controlled at 22 °C. Fluorescent lights were turned on at 7:00 a.m. and off at 7:00 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 × 35.5 cm (floor) × 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. Grain reinforce-

ment was delivered by an electromechanical hopper through a 6 × 6 cm opening in the front wall located near the floor, directly below the center key. 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 testing to mask extraneous sounds.

Procedure. The pigeons initially were trained on a symbolic delayed matching-to-sample task. The symbolic procedure involves arbitrary matching between sample and comparison stimuli from different dimensions. Each trial began with the presentation of either a red or a green field on the center key as a sample stimulus, with each color appearing on half the trials in random order. To advance beyond the sample stimulus, a pigeon had to complete a fixed ratio of 10 pecks on the sample stimulus (FR 10). Immediately after the tenth peck, the center key was darkened and patterns of three white stripes on a black background appeared on the left and right side keys. The stripes were vertically oriented on one side key and horizontally oriented on the other side key. The left-right positions of vertical and horizontal stripes were balanced across trials for each sample stimulus. Reinforcement contingencies were programmed so that a peck on the key containing vertical stripes was reinforced after a red sample stimulus and a peck on the key containing horizontal stripes was reinforced after a green sample stimulus. Reinforcement was 2.5 s of access to mixed grain in the central hopper. Pecks on the key containing horizontal stripes after the red sample or to the key containing vertical stripes after the green sample darkened the chamber with no delivery of grain reinforcement. An intertrial interval spent in darkness began after an incorrect choice or delivery of reinforcement and lasted for a period that varied randomly between 10 and 20 s. There were 64 trials in each session, and pigeons were tested for 37 sessions, at the end of which they were choosing the matching comparison stimulus at a high level of accuracy.

All six pigeons then were tested over 10 sessions in which varying delays or retention intervals were inserted between the sample and comparison stimuli. These retention intervals were 0, 3, 6, and 10 s, and each interval occurred equally often after each sample stimulus. 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.

Visual discrimination training and experimental testing then were carried out over the next 10 sessions, with 64 trials in each session. In the first session, pigeons were trained to peck one of two visual stimuli for 2.5 s of grain reinforcement. On each trial, three vertical and horizontal stripes, identical to those used in the delayed matching task, appeared on the left and right side keys, with the left-right positioning of these cues balanced across trials. For three pigeons, a peck on vertical stripes was always reinforced and a peck on horizontal stripes was always nonreinforced. These contingencies were reversed for the other three pigeons. There was a darkened intertrial interval between successive trials that varied randomly in duration between 10 and 20 s. In the second session, pigeons were tested on delayed matching to sample with retention intervals of 0, 3, 6, and 10 s. For the three pigeons trained to peck vertical stripes for reinforcement, the correct vertical stripes pattern on trials with a red sample stimulus was congruent with discrimination training. Thus, WM and RM were congruent. On trials with a green sample stimulus, however, the correct horizontal stripes pattern was incongruent with discrimination training, and

therefore, WM and RM were incongruent. The reversed relationships were the case for the other three pigeons trained to peck horizontal stripes for reinforcement.

Discrimination training and delayed matching sessions continued to alternate in this fashion until 10 sessions were completed. These different types of sessions were alternated in this way to allow us to examine the development of congruency effects as the visual discrimination was acquired.

Results and Discussion

Pigeons showed steady improvement in delayed matching-to-sample performance over the 37 sessions of training at a 0-s delay. On the first five sessions, pigeons made 49.79% ($SE = 1.75$) correct choices. Over the final five sessions, they made 90.67% ($SE = 2.71$) correct choices. On tests carried out for 10 sessions at varying retention intervals, the mean percentage of correct matches at 0, 3, 6, and 10-s retention intervals was 92.81, 74.48, 68.64, and 66.56, respectively ($SEs = 3.33, 5.49, 5.31, \text{ and } 2.70$). Birds showed the standard forgetting function often seen in delayed matching experiments with pigeons (Roberts, 1972; Roberts & Grant, 1976).

Over the five sessions of visual discrimination training, pigeons showed fairly rapid acquisition of the correct choice. The mean percentage of correct choices over Sessions 1–5 was 64.32, 82.03, 83.33, 90.62, and 93.75, respectively ($SEs = 5.43, 6.06, 6.41, 2.88, \text{ and } 1.98$).

The effect of congruency on retention functions is shown in Figure 1. Percentage of correct matching choices is plotted as a function of retention interval separately for congruent and incongruent trials. The curves show a clear interaction of congruency with retention interval. The increasing separation between congruent and incongruent tests as the retention interval becomes longer suggests control of choice by WM at short intervals and increasing control of choice by RM at longer intervals. Separate panels for Session 1 and all sessions combined are presented to show how

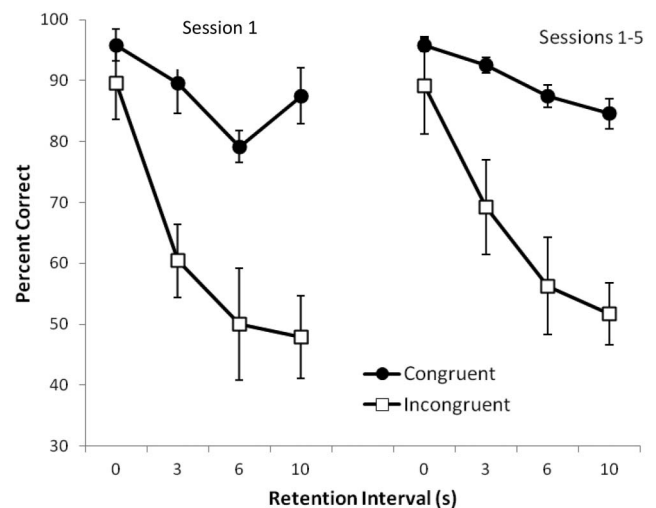


Figure 1. Retention curves for congruent and incongruent trials plotted for Session 1 and all five sessions in Experiment 1. Error bars represent SEM.

rapidly discrimination training had an effect on congruency on WM tests. That is, after only one session of visual discrimination training (mean correct choices = 64.32%), the pigeons' retention functions for congruent and incongruent trials look much like the functions for all five sessions.

These observations were confirmed by Congruity \times Retention Interval analyses of variance (ANOVA). The data from Session 1 yielded significant effects of congruency, $F(1, 5) = 48.08$, $p < .001$, $\eta_p^2 = .91$, 95% CI [.50, .94], retention interval, $F(3, 15) = 10.43$, $p < .001$, $\eta_p^2 = .68$, 95% CI [.31, .76], and the Congruity \times Retention Interval interaction, $F(3, 15) = 3.55$, $p < .05$, $\eta_p^2 = .42$, 95% CI [.01, .56]. An analysis of data from Sessions 1–5 also yielded significant effects of congruency, $F(1, 5) = 10.15$, $p < .05$, $\eta_p^2 = .67$, 95% CI [.06, .81], retention interval, $F(3, 15) = 98.90$, $p < .001$, $\eta_p^2 = .95$, 95% CI [.88, .96], and the Congruity \times Retention Interval interaction, $F(3, 15) = 17.48$, $p < .001$, $\eta_p^2 = .78$, 95% CI [.49, .83].

Experiment 2

The control of performance on congruent and incongruent trials by WM in Experiment 1 was based on pigeons pecking the sample key on an FR 10 schedule. This schedule yielded curves for congruent and incongruent conditions that showed little difference at the 0-s retention interval but increasing separation and control by RM at longer retention intervals. If RM competes with WM for the control of response to the comparison stimuli, it should be possible to manipulate the degree of separation between congruent and incongruent curves by varying the strength of WM. WM can be controlled by varying the length of presentation time (PT) of the sample stimulus. Thus, accuracy of delayed matching increases as PT increases on standard delayed matching-to-sample tests (Grant, 1976; Roberts & Grant, 1974).

In Experiment 2, we tested pigeons on congruent and incongruent trials over retention intervals of 0, 3, 6, and 10 s, as in Experiment 1, but we varied the PT of the sample stimulus. Instead of having to complete an FR on the sample key, pigeons were now exposed to the sample stimulus for 1, 3, or 6 s before the retention interval. If the interaction between WM and RM depends on the relative strengths of each type of memory, we should expect to see the greatest separation between congruent and incongruent trials at the shortest PT, with decreasing separation as PT increases.

Method

Subjects and apparatus. The same six pigeons and apparatus used in Experiment 1 were used in Experiment 2.

Procedure

Pigeons continued to be tested on 64 trials of delayed matching-to-sample on alternate daily sessions, with retention intervals of 0, 3, 6, and 10 s occurring in random order over trials. On different sessions, the sample stimulus was presented for a PT duration of 1, 3, or 6 s over all trials within the session. Each pigeon was tested at each PT within a block of three delayed matching sessions. The order in which the PTs were tested varied for pairs of pigeons across three blocks. Two pigeons were tested in the order 1–3–6, two in the order 3–6–1, and two in the order 6–1–3. On sessions

that alternated with delayed matching sessions, pigeons continued to receive visual discrimination training for 64 trials, with the reinforced choice (vertical or horizontal stripes) being the same as the reinforced stimulus in Experiment 1. The experiment began with a session of visual discrimination training and lasted for 18 sessions in total.

Results and Discussion

On the visual discrimination sessions, pigeons continued to choose the correct stimulus at a high degree of accuracy. The mean percentage of choice of the correct stimulus over nine sessions of testing was 95.05 ($SE = 1.40$).

Delayed matching performance on congruent and incongruent trials is shown as a function of retention interval in Figure 2, with separate panels for each PT. The data support the hypothesis of a larger separation of congruent and incongruent curves at the short PT of 1 s, with the curves drawing together as the PT increases to 3 and 6 s. The curves at PT = 1 and 3 s also show increasing separation as the retention interval becomes longer, but the curves at PT = 6 s show little separation at any retention interval. The curves for PT = 3 s look quite similar to the data obtained in Experiment 1 with an FR 10 schedule for pecking the sample key. That is, the curves are very close at the 0-s retention interval and show considerable separation by retention intervals of 6 and 10 s.

A three-way ANOVA was performed on percentage of correct choices, with the factors being congruency, PT, and retention interval. Significant one-way effects were found for congruency, $F(1, 5) = 271.57$, $p < .01$, $\eta_p^2 = .98$, 95% CI [.87, .99], PT, $F(2, 10) = 24.38$, $p < .01$, $\eta_p^2 = .83$, 95% CI [.50, .88], and retention interval, $F(3, 15) = 43.19$, $p < .01$, $\eta_p^2 = .90$, 95% CI [.74, .92]. Significant interactions were found of Congruency \times PT, $F(2, 10) = 70.52$, $p < .01$, $\eta_p^2 = .93$, 95% CI [.78, .95], and Congruency \times Retention Interval, $F(3, 15) = 8.51$, $p < .01$, $\eta_p^2 = .63$, 95% CI [.24, .72], but

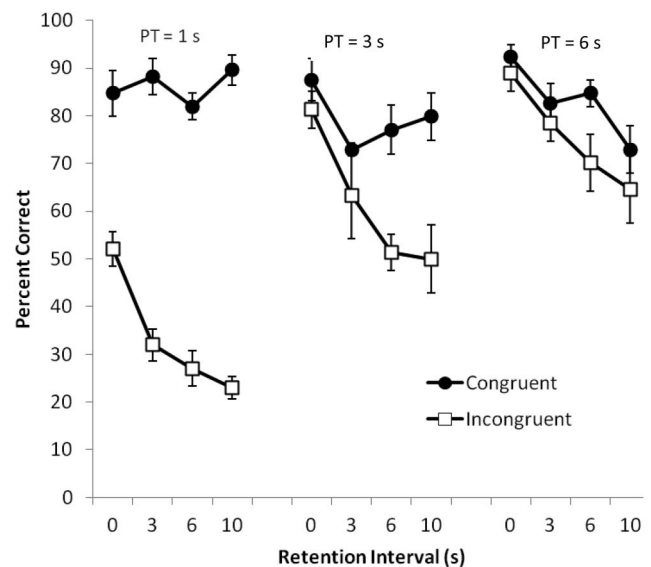


Figure 2. Retention curves for congruent and incongruent trials, with separate panels for presentation time (PT) = 1, 3, and 6 s, in Experiment 2. Error bars represent SEM.

not of $PT \times$ Retention Interval, $F(6, 30) = 1.89$, $p > .05$, or Congruity \times $PT \times$ Retention Interval, $F(6, 30) = 2.09$, $p > .05$.

Separate Congruity \times Retention Interval ANOVAs were performed on the data at each PT. Significant effects of congruity were found at $PT = 1$ s, $F(1, 5) = 511.67$, $p < .01$, $\eta_p^2 = .99$, 95% CI [.93, .99], and at $PT = 3$ s, $F(1, 5) = 49.41$, $p < .01$, $\eta_p^2 = .91$, 95% CI [.50, .94], but not at $PT = 6$ s, $F(1, 5) = 5.61$, $p > .05$. Retention interval was a significant factor at $PT = 1$ s, $F(3, 15) = 4.84$, $p < .05$, $\eta_p^2 = .49$, 95% CI [.08, .62], 3 s, $F(3, 15) = 22.83$, $p < .01$, $\eta_p^2 = .82$, 95% CI [.57, .87], and 6 s, $F(3, 15) = 16.52$, $p < .01$, $\eta_p^2 = .77$, 95% CI [.47, .83]. The Congruity \times Retention Interval interaction was significant at $PT = 1$ s, $F(3, 15) = 13.31$, $p < .01$, $\eta_p^2 = .73$, 95% CI [.39, .80] but not at $PT = 3$ s, $F(3, 15) = 2.48$, $p > .05$, or $PT = 6$ s, $F(3, 15) = 2.16$, $p > .05$.

Experiment 3

The findings from Experiment 2 clearly suggest that the interaction between WM and RM can be strongly affected by the initial strength of WM. When WM was weak because exposure to the sample stimulus lasted for only 1 s, a strong effect of RM was seen in the wide separation between congruent and incongruent trial curves. When WM was strong, however, because the sample stimulus was viewed for 6 s, the effect of congruency was minimal, even at a retention interval of 10 s.

In Experiment 3, we examined the effect of WM strength in a different way. We asked if a similar effect on the WM/RM interaction would occur if a well-established WM was then weakened or erased before the retention test. Instead of manipulating the initial strength of WM, as in Experiment 2, we allowed a strong WM to be formed and then introduced an interfering stimulus before the retention test. The interfering stimulus was simply the presentation of house light in the operant chamber for 3 s. It has been well established that the introduction of a light stimulus during the retention interval leads to substantial forgetting in delayed matching-to-sample experiments with pigeons (Grant & Roberts, 1976; Roberts & Grant, 1978). Pigeons were tested on congruent and incongruent trials after seeing the sample stimulus for 3 s. The retention interval was 0 or 3 s on different trials. On trials when the retention interval was 3 s, the retention interval was spent in darkness on half of the trials and in light on the other half of the trials. Because light during the retention interval weakens WM accuracy, we predicted that the effect of congruency would be stronger on light trials than on dark trials. That is, a bigger difference between congruent and incongruent trials should appear on trials with light during the retention interval than on trials with darkness during the retention interval.

Method

The apparatus used was the same as that used in Experiments 1 and 2. The six pigeons used in Experiments 1 and 2 continued to be trained on the visual discrimination on sessions that alternated with sessions that tested delayed matching-to-sample on congruent and incongruent trials. Each pigeon was tested for 60 trials in each session, with an intertrial interval that varied randomly between 10 and 20 s. In delayed matching-to-sample sessions, pigeons were tested on six types of trials, each for 10 trials, which occurred in a random order. On all types of trials the PT of the sample stimulus

was 3 s. Two types of trials were congruent and incongruent trials tested at a 0-s retention interval. The other four types of trials occurred with a 3-s retention interval between the sample and comparison stimuli. On two sets of tests with congruent and incongruent sample and comparison stimuli, darkness filled the retention interval. On the other two sets of tests with congruent and incongruent stimuli, the house light was turned on for the 3-s retention interval. The house light was provided by a 0.1-A, 28-V lamp that was mounted within a metal shield that covered the top half of the lamp but left the bottom half exposed. The lamp and shield were attached to the panel containing the pecking keys, 5 cm above the upper rim of the center key, and projected 2.3 cm into the chamber.

Three additional control pigeons were tested. These birds had been trained on delayed matching-to-sample with red and green samples symbolically matched to vertical and horizontal striped comparison stimuli. They received no visual discrimination training with the vertical and horizontal striped stimuli and were tested only on delayed matching-to-sample. Three types of trials occurred within a 60-trial daily session, in random order. The pigeons were tested with a 0-s retention interval on 20 trials, and on two types of 3-s retention interval tests, each for 20 trials. On one type of trial, the retention interval was spent in darkness, and on the other type of trial, the retention interval was spent in house light. The control pigeons were tested to provide a baseline for the effects of house light on delayed matching-to-sample performance.

The control pigeons were tested on delayed matching-to-sample for five sessions. The birds tested on congruent and incongruent trials were also tested on delayed matching-to-sample for five sessions that alternated with five sessions of visual discrimination training, with the first session being visual discrimination training.

Results and Discussion

Pigeons continued to choose the correct visual stimulus over the five sessions of visual discrimination training. The mean percentage of correct choices was 97.66 ($SE = .69$).

The percentages of correct matches to sample are shown for experimental and control birds in Figure 3. The control pigeons showed the expected effects of retention interval and interpolated house light. At 0-s retention interval, they matched correctly on 88.33% ($SE = 4.41$) of the trials. Accuracy dropped for each of the three pigeons at the 3-s retention interval spent in darkness, with a mean of 80.33% ($SE = 2.33$) correct trials. Each of the control pigeons showed a further drop in accuracy on trials when the house light was turned on for 3 s, with a mean accuracy of 54.67% ($SE = 4.66$) correct trials. A one-way ANOVA comparing these three conditions was significant, $F(2, 4) = 187.71$, $p < .01$, $\eta_p^2 = .99$, 95% CI [.86, .99]. Most importantly, accuracy after the 3-s retention interval was significantly higher when the interval was filled with darkness than when it was filled with light, $F(1, 2) = 121.00$, $p < .01$, $\eta_p^2 = .98$, 95% CI [.00, .99]. Thus, house light acted as an interfering stimulus that reduced WM for the sample stimulus.

An examination of the percent correct on congruent and incongruent trials in Figure 3 suggests a replication of the effects found in Experiments 1 and 2. At the 0-s retention interval, there is little difference between congruent and incongruent tests, with incongruent trials showing slightly higher accuracy than congruent trials. After 3 s in darkness, however, there is a clear difference in

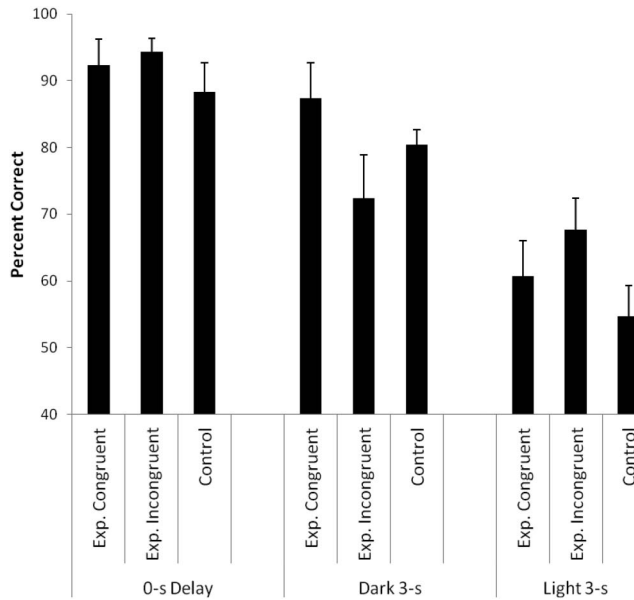


Figure 3. Percentage of correct matching responses at 0- and 3-s retention intervals for control and experimental pigeons in Experiment 3. Experimental pigeons were tested on congruent and incongruent trials. Error bars represent SEM.

matching accuracy that favors congruent over incongruent trials. This observation was supported by a Congruency \times Retention Interval ANOVA that showed significant effects of congruency, $F(1, 5) = 12.25, p < .05, \eta_p^2 = .71, 95\% \text{ CI} [.10, .83]$, retention interval, $F(1, 5) = 12.22, p < .05, \eta_p^2 = .71, 95\% \text{ CI} [.10, .83]$, and Congruency \times Retention Interval, $F(1, 5) = 16.00, p = .01, \eta_p^2 = .76, 95\% \text{ CI} [.16, .86]$.

The data for congruent and incongruent tests after 3 s in house light provided a surprising outcome that did not support our theoretical prediction. As seen on the right side of Figure 3, performance was actually somewhat higher for incongruent trials than for congruent trials. A Congruency \times Retention Interval ANOVA using the delay spent in light data yielded a significant effect of retention interval, $F(1, 5) = 192.13, p < .01, \eta_p^2 = .98, 95\% \text{ CI} [.83, .98]$, but nonsignificant effects of congruency, $F(1, 5) = 1.26, p > .05$, and the Congruency \times Retention Interval interaction, $F(1, 5) = .20, p > .05$.

It was shown that house light acted as an interfering stimulus to produce forgetting of WM over 3 s in control birds, as had been shown in previous research (Grant & Roberts, 1976; Roberts & Grant, 1978). It was also clearly evident that weakened WM after 3 s in darkness led to a congruency effect caused by RM, as in Experiments 1 and 2. It was anticipated that the effect of congruency would be even stronger after 3 s of house light, but this prediction clearly was not borne out. As a tentative explanation for this failed prediction, we suggest that house light may in fact have a general disruptive effect on performance. If the house light caused a momentary loss of access to WM and RM, then the congruency effect would not be expected to appear. Of course, this suggestion needs to be tested in independent experiments that focus more specifically on the effects of chamber illumination on performance in memory tests.

Experiment 4

In Experiments 1–3, the interaction of WM and RM was shown by varying the strength of WM. Either lengthening the retention interval or decreasing the PT length led to weakened WM and increased control of delayed matching performance by RM. Similar effects have been reported in experiments with humans and monkeys (Hay & Jacoby, 1996; Tu & Hampton, 2013). However, these human and monkey experiments also manipulated the strength of RM through the use of probability learning. The strength of RM for responding with a particular item was increased by increasing the probability of that item. Memory tests carried out under congruent and incongruent conditions showed that RM competed more effectively with WM as the probability of the RM item, and hence its memory strength, increased. We carried out similar manipulations in Experiment 4 to see if variation in the strength of RM would influence the degree to which it interacted with WM.

Probability learning is an ideal way of manipulating RM in pigeons, because it has been shown that pigeons' response probability closely matches the probability of reinforcement in a simultaneous visual discrimination (Bullock & Bitterman, 1962; Graf, Bullock, & Bitterman, 1964). Pigeons in Experiment 4 were trained to discriminate between patterns containing vertical and horizontal stripes, with the probability of reinforcement for choice of each stimulus varied among phases of the experiment. In different phases of the experiment, the probability of reinforcement for choosing one stimulus versus the other was 50:50, 75:25, and 100:0. As pigeons performed probability matching at these different probabilities, they were tested for delayed matching-to-sample performance on alternate session trials in which the correct choice was either congruent or incongruent with the most frequently reinforced stimulus from the probability learning sessions. We predicted that the effect of RM on delayed matching accuracy would increase as the difference in probability of reinforcement increased, as shown by increased separation of congruent and incongruent curves.

Method

Subjects and apparatus. Six new pigeons were used in Experiment 4. They were maintained under the same conditions as the pigeons used in Experiments 1–3. The apparatus was the same as that used in the preceding experiments.

Procedure. The pigeons were trained for 37 daily sessions on symbolic delayed matching-to-sample with a 0-s retention interval on all trials. Over the 64 trials in a session, the sample was red on 32 trials and green on 32 trials, in random order, with choice of the vertical stripes comparison stimulus reinforced after a red sample and choice of the horizontal stripes comparison stimulus reinforced after a green sample. After completing initial training, the pigeons were tested for 10 sessions with retention intervals of 0, 3, 6, and 10 s interpolated between offset of the sample stimulus and presentation of the comparison stimuli.

After completing preliminary delayed matching-to-sample testing, the pigeons began probability learning. They were divided into three subgroups of two pigeons each. Each subgroup was trained on each of three different probability schedules but in different orders. One subgroup was trained in the order 50:50→75:25→100:0, another in the order 75:25→100:0→50:50, and the

third in the order 100:0→50:50→75:25. On each session, a pigeon received 64 trials in which vertical stripes and horizontal stripes appeared simultaneously on left and right side keys, with the left-right positions of vertical and horizontal stripes balanced over trials. For one pigeon in each subgroup, vertical stripes were the most frequently reinforced stimulus; for the other pigeon, horizontal stripes were the most frequently reinforced stimulus. During 100:0 sessions, choice of the 100% stimulus was always reinforced with 2.5 s of access to grain, and choice of the 0% stimulus was never reinforced. During training on 75:25 sessions, choice of the 75% stimulus was reinforced on 48 trials and choice of the 25% stimulus was reinforced on 16 trials, with 25% trials randomly interspersed among 75% trials. During the 50:50 sessions, each stimulus was reinforced on 32 trials, with vertical stripes reinforced trials and horizontal stripes reinforced trials randomly intermixed with one another. To ensure probability matching, a guidance procedure was used (Bullock & Bitterman, 1962; Graf et al., 1964). On any trial in which a pigeon made an initial nonreinforced choice, the chamber darkened for a 6-s timeout. At the end of the timeout, just the correct stimulus appeared on its side key, and a peck to this stimulus produced reinforcement. Thus, each stimulus was reinforced according to its probability within a session. However, only initial responses were counted as stimulus choices.

After completing eight sessions of probability learning at a given probability schedule, pigeons were tested for three sessions on delayed matching-to-sample that alternated with sessions of probability learning. On delayed matching sessions, the sample stimulus was presented for 3 s on each of 64 trials, and pigeons were tested equally often at retention intervals of 0, 3, 6, and 10 s. Thus, each pigeon went through three phases of testing in each of which it first learned to match the probability of reinforcement used in that phase and then was tested for delayed matching accuracy with congruent and incongruent trials. Congruent trials were those in which the matching comparison stimulus was the most frequently reinforced stimulus in probability learning (100% or 75% stimulus), and incongruent trials were those in which the matching comparison stimulus was the least reinforced stimulus in probability learning (0% or 25%). When pigeons were tested with 50:50 probability learning, each pigeon's most and least reinforced stimuli in 75:25 and 100:0 training were used to determine performance on congruent and incongruent trials.

Results and Discussion

Pigeons showed steady improvement in delayed matching-to-sample over the 37 training sessions at a 0-s delay. On Sessions 1–5, the mean percentage of correct matches was 50.68 ($SE = 1.62$). Over Sessions 33–37, pigeons' mean accuracy was 87.40% ($SE = 3.05$). On the 10 sessions of testing with 0, 3, 6, and 10-s retention intervals, mean percentages of correct matches were 90.21, 71.67, 65.94, and 62.60, respectively ($SEs = 2.46, 5.76, 6.46, \text{ and } 6.09$).

Figure 4 shows the mean percentage of choices of the most frequently reinforced stimulus made by pigeons over the first 8 days of training under each probability learning schedule. These data show that pigeons fairly rapidly came to match the probability of reinforcement of the most frequently reinforced stimulus with their probability of choosing that stimulus. The mean percentages

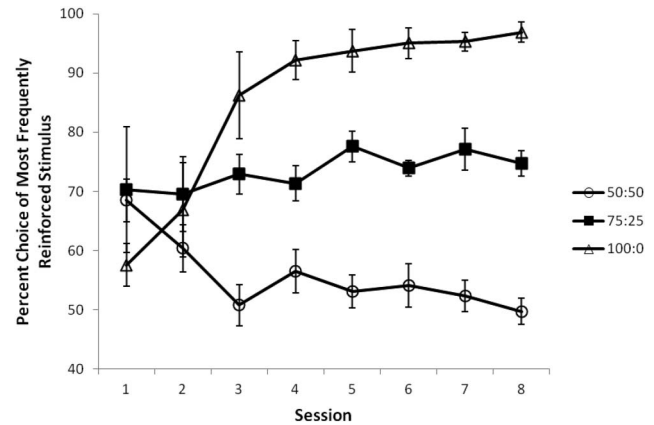


Figure 4. The acquisition of probability matching by pigeons when trained on 50:50, 75:25, and 100:0 probability schedules in Experiment 4. Error bars represent *SEM*.

of most reinforced stimulus choices over Sessions 4–8 on 50:50, 75:25, and 100:0 probability schedules were 53.18, 74.95, and 94.64 ($SEs = 2.10, 1.90, \text{ and } 2.34$), respectively.

A Probability Schedule \times Session ANOVA was performed on the percentages shown in Figure 4. It revealed significant effects of probability schedule, $F(2, 10) = 44.31, p < .01, \eta_p^2 = .90, 95\% \text{ CI } [.68, .93]$, session, $F(7, 35) = 4.24, p < .01, \eta_p^2 = .46, 95\% \text{ CI } [.14, .53]$, and the Probability Schedule \times Session interaction, $F(14, 70) = 7.36, p < .01, \eta_p^2 = .60, 95\% \text{ CI } [.38, .62]$.

Retention curves for congruent and incongruent tests are shown in Figure 5, with separate panels for each probability schedule. These curves show no effect of congruity at the 50:50 probability schedule but increasing separation of the curves as probability of the most reinforced stimulus rises to 75:25 and 100:0. In other words, RM had little differential effect on WM when both stimuli were equally reinforced, but RM came to exert greater control over delayed matching performance as the probability of reinforcement of the most reinforced stimulus increased.

An ANOVA was performed on the data shown in Figure 5, with the factors being congruity, probability schedule, and retention interval. Significant effects were found for congruity, $F(1, 5) = 67.11, p < .01, \eta_p^2 = .93, 95\% \text{ CI } [.60, .96]$, retention interval, $F(3, 15) = 29.93, p < .01, \eta_p^2 = .86, 95\% \text{ CI } [.65, .89]$, and the Congruity \times Probability Schedule interaction, $F(2, 10) = 5.01, p < .05, \eta_p^2 = .50, 95\% \text{ CI } [.03, .66]$. No other effects were significant, $ps > .05$. Although the curves for 75:25 and 100:0 probability schedules appear to show the familiar pattern of increasing separation between congruent and incongruent trials as the length of the retention interval increases, separate Congruity \times Retention Interval ANOVAs performed on data from the 75:25 and 100:0 probability schedules failed to yield significant Congruency \times Retention Interval interactions, $ps > .05$.

General Discussion

These experiments report interaction between WM and RM in the pigeon. By requiring pigeons to symbolically match a sample stimulus (WM task) by choosing between comparison stimuli that had been trained as S+ and S- stimuli in visual discrimination

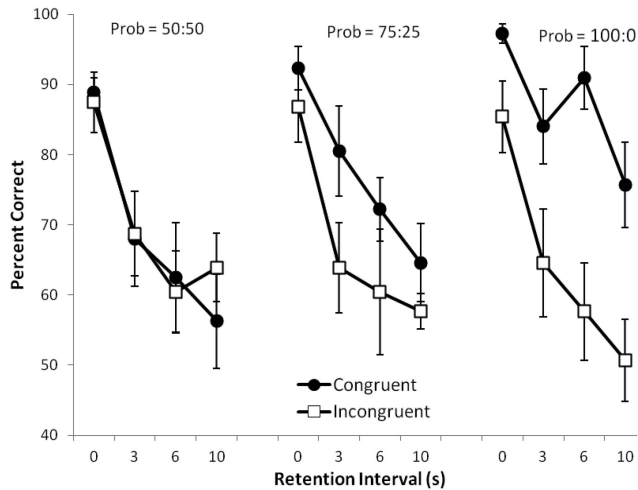


Figure 5. Retention curves for congruent and incongruent trials for pigeons tested after training on 50:50, 75:25, and 100:0 probability learning schedules in Experiment 4. Error bars represent SEM.

training (RM task), performance was examined when WM and RM choices were congruent and incongruent. The effect of congruency on delayed matching was clearly controlled by the relative strengths of WM and RM. In Experiments 1–3, RM was held constant and the strength of WM was varied. As WM was weakened by increasing the retention interval between sample and test, the effect of congruency became significantly more apparent. As the strength of WM grew by increasing the length of sample PT, congruency had progressively less effect on performance. In Experiment 4, the strength of RM was manipulated by training pigeons on probability reinforcement schedules that led them to match the probability of reinforcement of each visual stimulus with their probability of its choice. Delayed matching tests showed that the effect of congruency was strongly controlled by strength of preference for the most frequently reinforced stimulus in probability training. Thus, no congruency effect was seen after 50:50 training, but a strong separation between congruent and incongruent tests was seen after 75:25 and 100:0 training.

PDP Analysis

The findings reported here with pigeons strongly resemble those found in similar experiments with humans (Hay & Jacoby, 1996; Jacoby, 1991; Jacoby, Lindsay, & Toth, 1992) and with monkeys (Tu & Hampton, 2013; Tu et al., 2011). In those studies, the PDP analysis developed by Jacoby (1991) was used to derive measures of RM (habit) and WM (recollection of recently formed memories). More important, these measures suggested that the memory systems under study were independent of one another. That is, manipulations designed to affect strength of RM only affected RM scores and not WM scores, and manipulations designed to affect WM affected only WM scores and not RM scores.

The PDP analysis was applied to some of the pigeon data collected in the experiments reported here to test the independence of WM and RM. Based on Equations 1 and 2 shown in the introduction, the data from Experiment 4 were subjected to a PDP analysis. The results of this analysis are shown in Figure 6. The

upper panel shows WM PDP mean scores at the three levels of probability learning for each of the four delayed matching retention intervals. The PDP scores drop substantially as the retention interval is lengthened from 0 to 10 s. Within each retention interval, there is a slight increase in the PDP score as the probability of reinforcement of the most reinforced stimulus increases. A Probability \times Retention Interval ANOVA was performed on the PDP scores and showed a significant effect of retention interval, $F(3, 15) = 22.79, p < .01, \eta_p^2 = .82, 95\% \text{ CI } [.57, .87]$, but nonsignificant effects of probability, $F(2, 10) = 1.98, p > .05$, and the Probability \times Retention Interval interaction, $F(6, 30) = 1.99, p > .05$.

The bottom panel of Figure 6 shows mean RM PDP scores for each probability level at retention intervals 0 to 10 s. The PDP scores at each retention interval rise as the probability of reinforcement of the most reinforced stimulus increases but show little systematic change across retention intervals. A Probability \times Retention Interval ANOVA performed on these PDP scores revealed a significant effect of probability, $F(2, 10) = 7.90, p < .01, \eta_p^2 = .61, 95\% \text{ CI } [.14, .73]$, but nonsignificant effects of retention interval, $F(3, 15) = .22, p > .05$, and the Probability \times Retention Interval interaction, $F(6, 30) = 1.23, p > .05$.

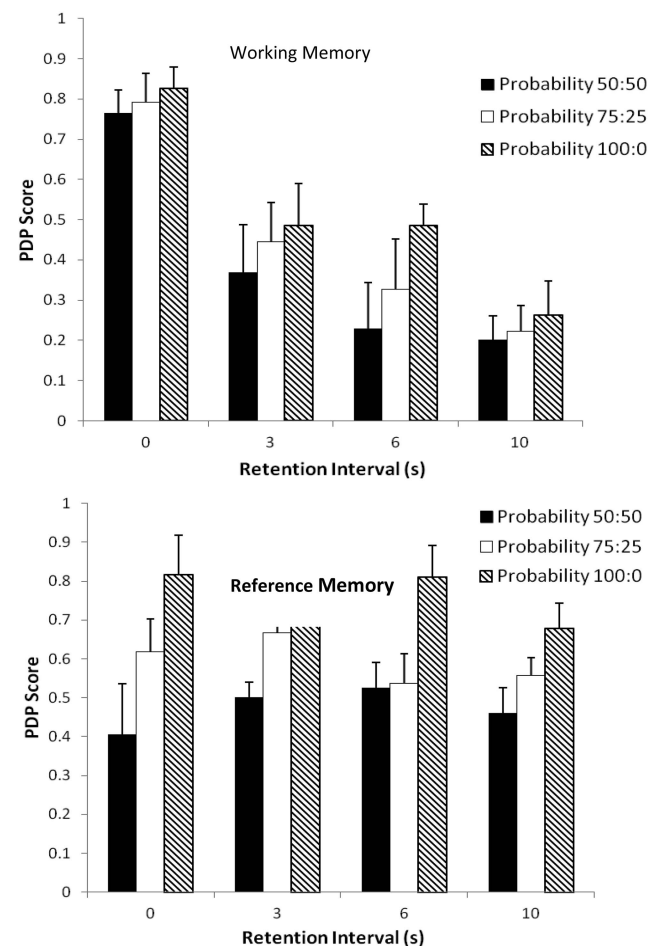


Figure 6. Process dissociation procedure (PDP) scores for working and reference memory based on data taken from Experiment 4. Error bars represent SEM.

These analyses indicate a double dissociation between variables and type of memory score. That is, lengthening the retention interval significantly lowered the WM PDP score but had little effect on the RM PDP score. By contrast, raising the probability of reinforcement of the most frequently reinforced stimulus in probability learning significantly raised the RM PDP score but had no significant effect on the WM PDP score. In agreement with studies of human and monkey memory (Hay & Jacoby, 1996; Jacoby, 1991; Jacoby et al., 1992; Tu & Hampton, 2013; Tu et al., 2011), these analyses suggest that independent memory systems are being examined.

A major difference between the pigeon studies reported here and the human and monkey studies showing independence of memory systems is that the primate studies used many different items (words for humans and images for monkeys) but the pigeon experiments used only two sample stimuli and two comparison stimuli. Thus, a major confound between species could be strong proactive interference effects in the pigeon experiments but not in the primate experiments. That is, a reinforced comparison choice on Trial $n - 1$ might establish a memory that carried over to Trial n and increased the probability of an error or correct choice. Although proactive interference among trials does occur in pigeon delayed matching to sample, it is minimal when a longer intertrial interval is used (Grant, 1975; Roberts, 1980; Roberts & Kraemer, 1982). Because the intertrial interval used in the present experiments varied between 10 and 20 s, proactive interference should not have had a strong effect on the findings reported here. In fact, it is remarkable that the PDP analysis of pigeon data closely mirrors those reported for humans and monkeys. The comparative implication is that interacting WM and RM systems may be found in both mammals and birds.

A Model of Memory Interaction

Although the PDP analysis suggests that WM and RM are independent memory systems in the pigeon, the findings reported here clearly indicate that these memory systems interact and compete with one another for control of performance in the delayed matching-to-sample task. The curves shown in Figure 7 suggest a model for the underlying processes causing memory interaction in these experiments. The curves plot memory strength over a 10-s retention interval for WM and RM. The WM curve showing memory decay was generated by Equation 3,

$$WM = 1/\exp(RI)^d \quad (3)$$

in which RI = retention interval and the decay parameter (d) is set at .3. The flat parallel lines represent different strengths of RM that would be established for the most reinforced (strong) and least reinforced (weak) stimuli in probability learning. The total memory strength for choosing a comparison stimulus that matches the sample would be WM + RM, but the total memory strength for choosing a nonmatching comparison stimulus would be only its RM. To show the combined influences of WM and RM on performance, the probability of choosing the correct matching stimulus on congruent and incongruent trials was calculated as a discrimination ratio (DR) based on the total memory strengths for matching and nonmatching stimuli. On congruent trials, $DR = [WM + RM(\text{strong})]/[WM + RM(\text{strong}) + RM(\text{weak})]$. On

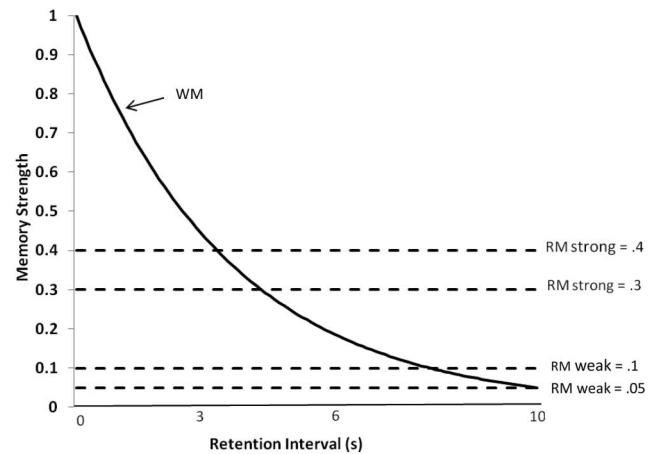


Figure 7. A model for the interaction of working memory (WM) and reference memory (RM). The curves show decay of WM and weak and strong constant levels of RM.

incongruent trials, $DR = [WM + RM(\text{weak})]/[WM + RM(\text{strong}) + RM(\text{weak})]$.

Figure 8 shows discrimination ratios plotted over retention intervals for congruent and incongruent tests based on values taken from the curves shown in Figure 7. The top panel shows retention curves when the difference in memory strength between matching and nonmatching RM strengths is relatively small (.3 vs. .1), and the bottom panel shows retention curves when the difference is relatively large (.4 vs. .05). Both sets of curves show increasing separation as the retention interval becomes longer. The separation grows wider for the larger difference between RM than for the smaller difference between RM. Thus, the model predicts both the effect of retention interval and the effect of probability learning on performance seen in Figure 5.

The other parameter that can be manipulated in this model is the decay rate of WM. Although the decay parameter was set at .3 to obtain the WM curve shown in Figure 7, lowering the decay rate parameter leads to congruent and incongruent forgetting curves that show little loss of memory and only slight separation over the duration of the retention interval, much like the curves seen in the right-hand panel of Figure 2. Raising the decay parameter leads to an increased rate of forgetting that is more marked for the incongruent condition than for the congruent condition, as found in the left-hand panel of Figure 2.

Conclusions

Interaction between WM and RM may be a pervasive phenomenon. People often experience it, as in the forgotten phone number example described in the introduction. Formal demonstrations of the interaction between habit and recently formed memory are found in primate experiments with humans (Hay & Jacoby, 1996; Jacoby, 1991; Jacoby et al., 1992) and monkeys (Tu & Hampton, 2013; Tu et al., 2011). Guitar and Roberts (2014) have reported evidence of similar WM and RM interaction in rat spatial memory. The experiments reported here now extend the interaction between WM and RM to birds.

The model shown in Figure 7 and the effects derived from it in Figure 8 suggest competition between a dynamic, rapidly forgotten

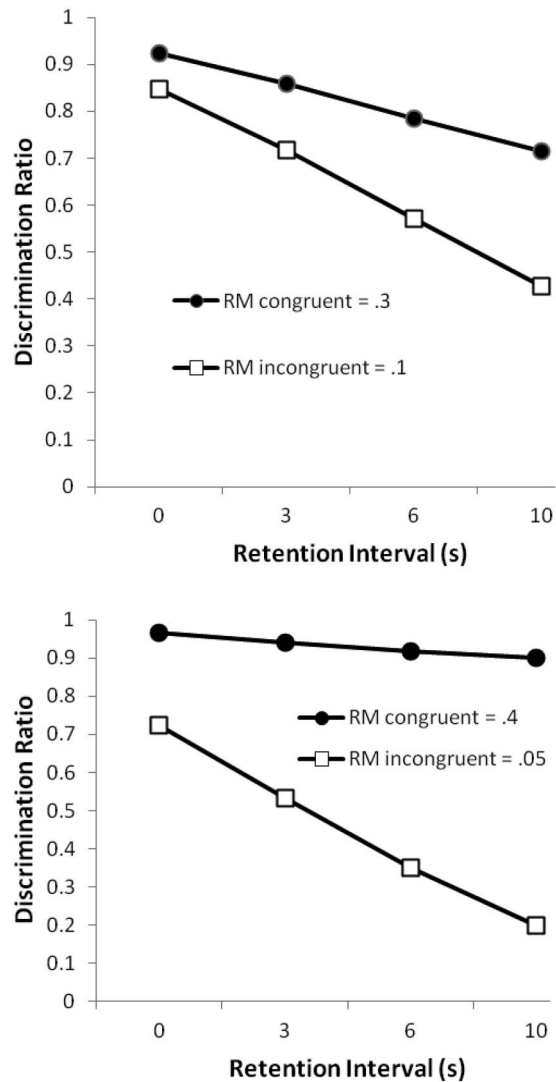


Figure 8. Discrimination ratios for congruent and incongruent trials based on the model shown in Figure 7. The upper panel shows scores when a relatively small difference in reference memory (RM) is assumed, and the lower panel shows scores when a relatively large difference in RM is assumed.

WM and a relatively static RM. Interference with choice based on WM from RM becomes stronger as WM wanes. The behavioral data shown in these experiments support this model, but it may still be asked whether the underlying basis of WM and RM is the same or different neural systems. Tu et al. (2011) reported that monkeys with perirhinal cortex lesions showed lower WM scores than normal monkeys, but no difference between lesioned and normal monkeys was found for RM scores. The rodent research reviewed in the introduction further suggested different neural systems for WM and RM. Lesions in the hippocampus led rats to perform poorly on spatial WM tests but not RM tests. Conversely, lesions to the caudate nucleus impaired spatial RM but not WM (Packard et al., 1989). In pigeons, it has been found that lesions of the 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). Further, in a visual delayed go-no-go task, Diekamp, Kalt, and Gunturkun (2002) found that firing of single cells in the NCL was correlated with accuracy of response on go trials. Rose and Colombo (2005) have shown that activity in pigeon NCL cells is controlled by remember and forget cues: The spike rate was higher after seeing a visual sample and hearing a remember tone than after seeing a sample and hearing a forget tone. Researchers might then begin to examine the question of independent neural systems for WM and RM in pigeons by testing birds with NCL lesions on delayed matching under congruent and incongruent test conditions. Would a PDP analysis show reduced WM but not RM in pigeons with NCL lesions relative to control pigeons without NCL lesions?

These experiments showed interaction between WM for colors and RM for striped patterns using an oppositional procedure. The types of memory studied in people and animals have expanded substantially in recent years, and it would be of interest to examine interaction between different types of memory or memory for different dimensions. Examples of memory for different dimensions are spatial memory based on the encoding of geometric and landmark information (Kelly & Spetch, 2012), temporal memory (Spetch & Wilkie, 1983), and numerical memory (Roberts, Macuda, & Brodbeck, 1995). In addition to memory for habits and single recent events, as studied here, other types of memory recently studied in animals are episodic-like memory (Babb & Crystal, 2006; Clayton & Dickinson, 1998; Roberts, 2006) and source memory (Crystal, Alford, Zhou, & Hohmann, 2013). Would all of these kinds of memory interact competitively, or would some memory systems be immune to competition with one another?

The study of memory interaction in animals may have practical applications. Memory confusion is common in human dementia and Alzheimer's disease. The development of animal models of memory systems competition might provide models of memory confusion to which various treatments could be applied to alleviate confusion. Drugs and other physiological interventions come to mind, but behavioral treatments might also alleviate memory confusion. In the pigeon experiments reported here, birds were trained and tested on WM and RM in the same context, a darkened operant chamber. Suppose WM and RM were established in different contexts. Might this reduce memory competition? Could subjects be trained to overcome memory competition? Some years ago, Grant (1976) showed that through intensive training, pigeons could learn to remember sample stimuli and match them correctly over a retention interval as long as 60 s. Would pigeons that had achieved that level of WM show increased resistance to the effects of RM at longer retention intervals? We suggest that memory experiments with animals may be of considerable value in the study of memory interaction and in the possible discovery of techniques for the alleviation of memory confusion.

References

- Babb, S. J., & Crystal, J. D. (2006). Episodic-like memory in the rat. *Current Biology*, 16, 1317–1321. <http://dx.doi.org/10.1016/j.cub.2006.05.025>
- Bullock, D. H., & Bitterman, M. E. (1962). Probability-matching in the pigeon. *The American Journal of Psychology*, 75, 634–639. <http://dx.doi.org/10.2307/1420288>

- Clayton, N. S., & Dickinson, A. (1998). Episodic-like memory during cache recovery by scrub jays. *Nature*, *395*, 272–274. <http://dx.doi.org/10.1038/26216>
- Crystal, J. D., Alford, W. T., Zhou, W., & Hohmann, A. G. (2013). Source memory in the rat. *Current Biology*, *23*, 387–391. <http://dx.doi.org/10.1016/j.cub.2013.01.023>
- Diekamp, B., Gagliardo, A., & Güntürkün, O. (2002). Nonspatial and subdivision-specific working memory deficits after selective lesions of 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.
- Graf, V., Bullock, D. H., & Bitterman, M. E. (1964). Further experiments on probability-matching in the pigeon. *Journal of the Experimental Analysis of Behavior*, *7*, 151–157. <http://dx.doi.org/10.1901/jeab.1964.7-151>
- Grant, D. S. (1975). Proactive interference in pigeon short-term memory. *Journal of Experimental Psychology: Animal Behavior Processes*, *1*, 207–220. <http://dx.doi.org/10.1037/0097-7403.1.3.207>
- Grant, D. S. (1976). Effect of sample presentation time on long-delay matching in the pigeon. *Learning and Motivation*, *7*, 580–590. [http://dx.doi.org/10.1016/0023-9690\(76\)90008-4](http://dx.doi.org/10.1016/0023-9690(76)90008-4)
- Grant, D. S., & Roberts, W. A. (1976). Sources of retroactive inhibition in pigeon short-term memory. *Journal of Experimental Psychology: Animal Behavior Processes*, *2*, 1–16. <http://dx.doi.org/10.1037/0097-7403.2.1.1>
- Guitar, N. A., & Roberts, W. A. (2014). The interaction between working and reference spatial memories in rats on a radial maze. *Behavioural Processes*. Advance online publication. <http://dx.doi.org/10.1016/j.beproc.2014.10.007>
- 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. <http://dx.doi.org/10.1037/0278-7393.22.6.1323>
- 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. [http://dx.doi.org/10.1016/0749-596X\(91\)90025-F](http://dx.doi.org/10.1016/0749-596X(91)90025-F)
- Jacoby, L. L., Lindsay, D. S., & Toth, J. P. (1992). Unconscious influences revealed. Attention, awareness, and control. *American Psychologist*, *47*, 802–809. <http://dx.doi.org/10.1037/0003-066X.47.6.802>
- Kelly, D. M., & Spetch, M. L. (2012). Comparative spatial cognition: Encoding of geometric information from surfaces and landmark arrays. In T. R. Zentall & E. A. Wasserman (Eds.), *The Oxford handbook of comparative cognition* (pp. 366–389). New York, NY: Oxford University Press.
- Levin, E. D., Kim, P., & Meray, R. (1996). Chronic nicotine working and reference memory effects in the 16-arm radial maze: Interactions with D₁ agonist and antagonist drugs. *Psychopharmacology*, *127*, 25–30. <http://dx.doi.org/10.1007/BF02805971>
- Olton, D. S., & Paras, B. C. (1979). Spatial memory and hippocampal function. *Neuropsychologia*, *17*, 669–682. [http://dx.doi.org/10.1016/0028-3932\(79\)90042-3](http://dx.doi.org/10.1016/0028-3932(79)90042-3)
- 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. *The 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. <http://dx.doi.org/10.1037/h0032796>
- Roberts, W. A. (1980). Distribution of trials and intertrial retention in delayed matching to sample with pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, *6*, 217–237. <http://dx.doi.org/10.1037/0097-7403.6.3.217>
- Roberts, W. A. (2006). Animal memory: Episodic-like memory in rats. *Current Biology*, *16*, R601–R603. <http://dx.doi.org/10.1016/j.cub.2006.07.001>
- Roberts, W. A., & Grant, D. S. (1974). Short-term memory in the pigeon with presentation time precisely controlled. *Learning and Motivation*, *5*, 393–408. [http://dx.doi.org/10.1016/0023-9690\(74\)90020-4](http://dx.doi.org/10.1016/0023-9690(74)90020-4)
- 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., & Grant, D. S. (1978). An analysis of light-induced retroactive inhibition in pigeon short-term memory. *Journal of Experimental Psychology: Animal Behavior Processes*, *4*, 219–236. <http://dx.doi.org/10.1037/0097-7403.4.3.219>
- Roberts, W. A., & Kraemer, P. J. (1982). Some observations of the effects of intertrial interval and delay on delayed matching to sample in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, *8*, 342–353. <http://dx.doi.org/10.1037/0097-7403.8.4.342>
- Roberts, W. A., Macuda, T., & Brodbeck, D. R. (1995). Memory for number of light flashes in pigeons. *Animal Learning & Behavior*, *23*, 182–188. <http://dx.doi.org/10.3758/BF03199933>
- Rose, J., & Colombo, M. (2005). Neural correlates of executive control in the avian brain. *PLoS Biology*, *3*, e190. <http://dx.doi.org/10.1371/journal.pbio.0030190>
- Shen, J., Barnes, C. A., Wenk, G. L., & McNaughton, B. L. (1996). Differential effects of selective immunotoxic lesions of medial septal cholinergic cells on spatial working and reference memory. *Behavioral Neuroscience*, *110*, 1181–1186. <http://dx.doi.org/10.1037/0735-7044.110.5.1181>
- Spetch, M. L., & Wilkie, D. M. (1983). Subjective shortening: A model of pigeons' memory for event duration. *Journal of Experimental Psychology: Animal Behavior Processes*, *9*, 14–30. <http://dx.doi.org/10.1037/0097-7403.9.1.14>
- Squire, L. R. (2004). Memory systems of the brain: A brief history and current perspective. *Neurobiology of Learning and Memory*, *82*, 171–177. <http://dx.doi.org/10.1016/j.nlm.2004.06.005>
- 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. <http://dx.doi.org/10.1037/a0030496>
- 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. <http://dx.doi.org/10.1523/JNEUROSCI.2338-11.2011>

Received September 2, 2014

Revision received November 24, 2014

Accepted December 16, 2014 ■