



The role of context in animal memory

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Abstract

Past research has shown that testing memory in the same context in which the memory was encoded leads to improved retention relative to testing memory in a new context. Context-dependent memory is directly related to the extent to which the encoding context can be reproduced. An experiment with pigeons is reported in which the context was a colored house-light that completely enveloped the learning and testing contexts. Under this condition, perfect retention of a visual discrimination that reversed at midsession was shown. Beyond reactivation of memory, new research with pigeons suggests that context provides access to different working and reference memory systems. Finally, experiments are reported that suggest context may selectively access information about features from the different dimensions of place, color, and time.

Keywords Context · Memory systems · Working memory · Reference memory · Place · Color · Time

Introduction

Context has long been recognized as an important retrieval cue for both human and animal memory. Definitions of context vary, however, but usually refer to the immediate environment in which a memory is encoded. In human studies, the context is often the room in which memory for a list of items or associations is formed, and changes in context from learning to test involve a change in rooms (e.g., Dalton, 1993; Fernandez & Glenberg, 1985; Smith, 1979). These experiments show *context-dependent memory*, in which retention of learned material is higher when subjects are tested in the same room where they studied than in a different room. Changes in context can reduce retroactive interference if target information is learned and tested in one context and the potentially interfering information is learned in a different context (Jensen, Dibble, & Anderson, 1971; Strand, 1970). There are some caveats to the effect of context on memory retrieval. In general, context-dependent memory effects are weaker in experiments where learned material may be more readily associated with cues other than the environment. In a meta-analysis of studies of environmental context-dependent memory, Smith and Vela (2001) found that retention was stronger

when subjects retrieved information using free recall than when association cues or recognition were used. Interestingly, the effect of changing the environment from study to test can be alleviated by instructing subjects to mentally reinstate the study environment (Smith, 1984).

Similar manipulations have shown context-dependent memory in animals. Context is manipulated by room cues and testing chamber cues that may involve visual, auditory, olfactory, and vestibular and kinesthetic senses. Additionally, internal context may be manipulated by different drug states. It has been argued that context reactivates memories formed earlier in the same context and may promote still later retention of the target memory (Spear, 1971, 1973, 1978, 1981). For example, Spear et al. (1980) trained rats in a two-compartment apparatus in which one compartment was white and the other was black. Rats initially ran from the white side to the black where they received a foot shock and rapidly learned to stay on the white side (passive avoidance). Next, they were trained on active avoidance in which they were shocked on the white side if they did not cross to the black side within 5 s, with the black compartment now the safe non-shock compartment. When tested 24 h later, rats normally show indifference between the compartments, suggesting both memories have been retrieved and are in conflict. When either different drug states or different room contexts were present during passive and active avoidance, however, rats stayed in the white compartment in the passive avoidance context and crossed to the black compartment in the active avoidance context. As another example, Thomas, McKelvie, and Mah (1985) trained pigeons to discriminate between S+ and S-

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wavelengths presented on keys in the presence of one house-light-noise context. The pigeons then learned the reversed discrimination in a different house-light-noise context. When tested 24 h later, pigeons responded appropriately when presented with each context.

In a review article, Bouton (1993) suggested that many of the phenomena found in Pavlovian conditioning can be understood as products of memory retrieval controlled by context cues. It was suggested that acquisition and extinction treatments may establish independent memories, with time serving as an important retrieval context. Thus, spontaneous recovery may arise from failure to retrieve memory of non-reinforced extinction trials. Latent inhibition may occur because the conditioning context retrieves memory of non-reinforced CS presentations. In particular, the renewal effect arises when different contexts are present during acquisition and extinction. Reappearance of the conditioned response occurs immediately after extinction when the acquisition context is presented.

The purpose of this paper was to present some findings from the author's laboratory that further indicate the importance of context for memory retrieval. These experiments emphasize two important points. First, an effective context should be based on an animal's dominant sensory system. It will be shown that perfect memory retrieval occurs in pigeons when the context used is a salient visual cue. The second point emphasized by the studies reported is that context may do more than provide access to memory in general. It may provide access to specific memory systems or types of information. Access to different forms of memory then will be shown by accurate responses based on the information they contain.

Perfect performance based on context in the pigeon

Since an initial paper by Cook and Rosen (2010), the *midsession reversal* procedure has been examined extensively in pigeons. Over an extended series of trials within a daily session, a pigeon chooses between two stimuli, S1 and S2, on each trial. For the first half of a session, choice of S1 is always reinforced and choice of S2 is always non-reinforced. At midsession, these contingencies reverse, with choice of S2 now reinforced and the choice of S1 non-reinforced. The obvious way to solve this problem from a human point of view is to use a win-stay, lose-shift strategy. That is, choose S1 as long as it pays off and immediately switch to S2 when it does not. Pigeons do not use such a strategy. In an experiment reported by MacDonald and Roberts (2018), pigeons chose between a red key and a green key on each trial of a 60-trial session. Choice of the red key was reinforced on trials 1–30, and choice of the green key was reinforced on trials 31–60. The Pre-Context curve found in the lower right panel of Fig. 1 shows pigeons' percentage of choice of S1 (red key) over blocks of five trials for the final ten sessions of training. The

curve is typical of many studies that have used midsession reversal, and shows that pigeons make *anticipatory errors* by choosing S2 (green key) before reversal (the vertical broken line) and make *perseverative errors* by choosing S1 after the reversal. Several manipulations of time before trials begin (McMillan & Roberts, 2015) or between trials (McMillan & Roberts, 2012) indicate that pigeons are using an internal clock to tell them when reversal occurs. Because an internal interval timer is inherently noisy and prone to error (Gibbon, 1977), pigeons sometimes choose S2 too early, leading to anticipatory errors, and sometimes choose S1 too late, leading to perseverative errors.

Hayden MacDonald and I (MacDonald & Roberts, 2018) asked if it might be possible to show more accurate midsession reversal in pigeons by presenting different context cues before and after reversal. We introduced context cues after the pre-context training shown in Fig. 1. As context cues, we presented different colored house-lights during trials 1–30 and trials 31–60. It is important to note that pigeons are very sensitive to color and that the house-lights completely bathed the operant chamber in their illumination. Thus, the pigeon's entire environment was immersed in the house-light color. A green house-light was presented during trials 1–30, and a red house-light was presented during trials 31–60. Thus, the house-light color was opposite the color of the correct key. Performance on blocks of five trials is shown session by session in Fig. 1. Performance was disrupted on Session 1 but began to recover on Session 2. As sessions proceeded, accuracy of reversal became more and more precise. On Session 7, pigeons showed perfect reversal, with no errors made by all six birds tested. Pigeons' performance was totally controlled by context. Pigeons had not learned to use a win-stay, lose-shift strategy, as they made no errors on trial 31, the first reversal trial. Rather, the shift in context led to immediate reversal. Further, context training did not lead to improved reversal performance without context. The Post-Context curve in Fig. 1 shows that pigeons immediately returned to their pre-context pattern of anticipatory and perseverative errors when the context cues were removed.

These findings are similar to the earlier context-dependent memory effects previously discussed. They differ, however, in the completeness with which context appeared to retrieve memory for "peck red" and "peck green" instructions. We attribute this total control by context to the use of house-light cues that provided ambient contexts. House-light cues were also used to instate different contexts in the further experiments discussed.

Context and the retrieval of information from different memory systems

Two memory systems common to humans and animals are *working memory* and *reference memory* (Roberts & Santi,

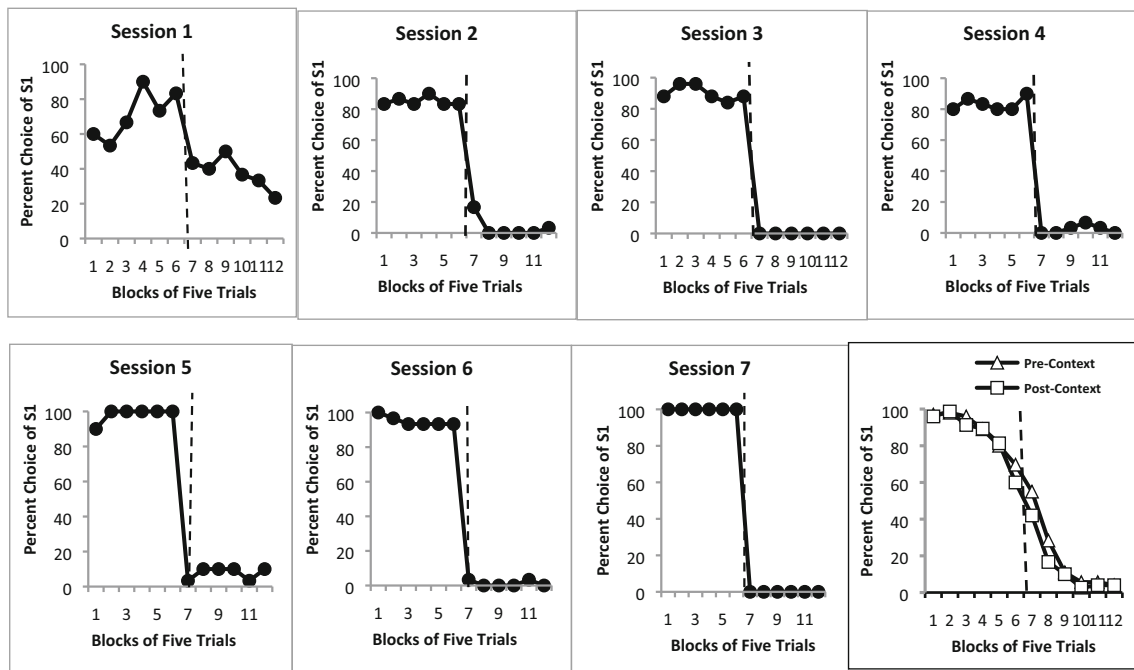


Fig. 1 Curves show the development of perfect midsession reversal over seven sessions. The bottom right panel shows midsession reversal performance without context control (from MacDonald & Roberts, 2018)

2017). Working memory refers to retention of information acquired in a single experience and retained for a relatively short period of time. Reference memory refers to information or behaviors acquired with repetition and maintained over extended periods of time. Working memory and reference memory may compete with one another. Having just been told the new password for my computer, I will retain it in working memory and use it immediately to gain access. However, the next day I may well fall back on the habit of my old password learned over repeated use during the past year. Thus, reference memory may over-ride working memory when working memory is weakened.

Working or short-term memory has long been studied in pigeons using the delayed matching-to-sample procedure. In a three-key apparatus, a pigeon is shown a sample stimulus on the center key. This stimulus then disappears and after a retention interval of a few seconds, different stimuli (comparison stimuli) appear on the two side keys. One comparison stimulus matches the sample and the other does not, and the pigeon can only obtain reinforcement by pecking the side key containing the comparison stimulus that matches the sample. When matching accuracy is plotted against the length of the retention interval using data collected over a large number of trials, performance drops progressively over 10 s, showing rapid forgetting of working memory for the sample stimulus.

Roberts, Strang, and Macpherson (2015) used the delayed matching procedure to examine the interaction between working and reference memory in pigeons. A variation of the delayed matching procedure was used called *symbolic delayed matching to sample*. In the symbolic procedure, the sample

and comparison stimuli come from different dimensions, and the pigeon is required to learn which comparison stimulus is matched to each sample stimulus. Roberts et al. used red and green sample stimuli and comparison stimuli that contained patterns of three horizontal or three vertical white stripes on a black background. After seeing a red sample stimulus, vertical stripes have to be chosen for reinforcement, but after seeing a green sample stimulus, horizontal stripes have to be chosen for reinforcement. When blackout retention intervals varying between 0 and 10 s are inserted between presentations of the sample and comparison stimuli, matching accuracy drops from about 90% to 60%.

In order to examine the relative influence of working and reference memory, Roberts et al. (2015) first trained pigeons to a high level of accuracy on symbolic delayed matching and then gave pigeons reference memory training using the comparison stimuli from the delayed matching task. Pigeons were given repeated trials in which only vertical and horizontal stripes appeared on the side keys, with the choice of only one stimulus always reinforced. Thus, a pigeon would have to always peck the key containing vertical stripes in order to obtain reinforcement. After pigeons had learned this reference memory discrimination to 90% accuracy or higher, we returned them to the symbolic delayed matching test using the *oppositional paradigm*. Note that depending on which sample stimulus is presented, working and reference memory may be in agreement (*congruent*) or in disagreement (*incongruent*). If the sample stimulus is red, then working and reference memory are congruent because both signal choice of the vertical stripes comparison stimulus. If the

sample stimulus is green, however, working and reference memory are incongruent because pigeons were trained to choose horizontal stripes after seeing a green sample stimulus (working memory) but were reinforced for choosing vertical stripes during discrimination training (reference memory). The results of this procedure are shown in Fig. 2. The strength of working memory was varied in two ways. By increasing the retention interval from 0 to 10 s, memory for the sample stimulus was progressively weakened. However, the initial strength of memory for the sample stimulus increases as the length of exposure to the sample stimulus (presentation time = PT) increases (Roberts & Grant, 1974). The relative effects of working and reference memory are best seen in the middle panel where PT = 3 s. At short retention intervals of 0 s and 3 s, the congruent and incongruent curves differ little, indicating that pigeons are using working memory for the sample stimulus to make their choice between comparison stimuli. At retention intervals of 6 s and 10 s, however, the curves separate, with the congruent curve staying much higher than the rapidly dropping incongruent curve. Thus, reference memory is taking over the control of performance as working memory weakens. The curves in the left panel show that when working memory for the sample is weak because the sample was only briefly exposed, performance is largely controlled by reference memory at all retention intervals. The opposite is seen in the curves shown in the right panel. When working memory is strong because the sample was shown for 6 s, it persists and dominates reference memory up to the 10-s retention interval.

In a different experiment, Roberts et al. (2015) manipulated the strength of reference memory. This was accomplished by training pigeons on reference memory discriminations that

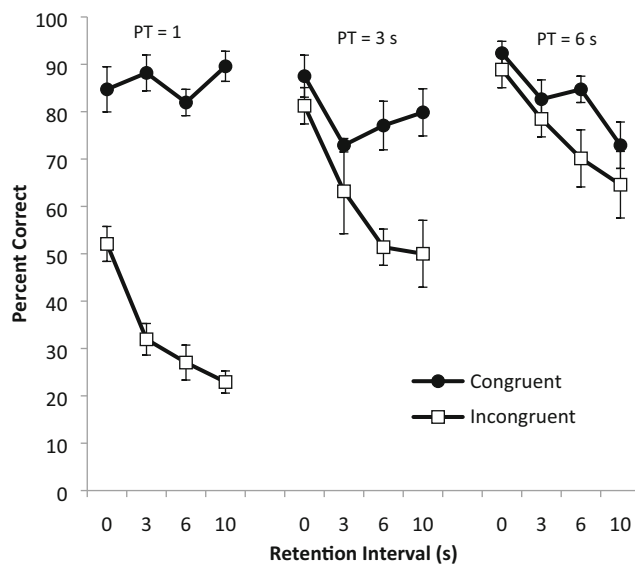


Fig. 2 Working memory retention curves for trials when working memory and reference memory correct choices are congruent and incongruent. Strength of working memory was controlled by presentation time (PT) of the sample stimulus. Error bars are standard error of the mean (from Roberts et al., 2015)

varied the probability with which one stimulus versus the other was reinforced. In the current experiment, pigeons were tested on delayed matching to sample after discrimination training at probabilities of 100:0, 75:25, and 50:50. At probabilities of 100:0, the procedure used was the same as described in the preceding experiment, with the choice of vertical stripes always reinforced and choice of horizontal stripes always non-reinforced. In the 75:25 problem, however, choice of vertical stripes was reinforced on 75% of the trials, and choice of horizontal stripes was reinforced on 25% of the trials. In the 50:50 problem, choice of each stimulus was equally often reinforced. During discrimination training, pigeons' probability of choosing each stimulus matched its probability of reinforcement. Performance on delayed matching at different retention intervals is shown for each reference memory discrimination in Fig. 3. Here we see that reference memory had the greatest effect on choice after 100:0 training and its influence weakened at 75:25 training, and had no effect at 50:50 training.

The importance of these experiments is that they clearly show the interactive effects of two different memory systems in pigeons. Further analyses of these data using Jacoby's process dissociation procedure (PDP; Jacoby, 1991) showed manipulations of retention interval and sample presentation time only affected the working memory PDP scores, and that manipulation of reinforcement probability in discrimination training only affected the reference memory PDP scores.

Could the working memory and reference memory systems be independently accessed by context cues? Roberts, Macpherson, and Strang (2016) addressed this question using the oppositional paradigm with pigeons. Pigeons were initially trained to perform delayed symbolic matching to sample

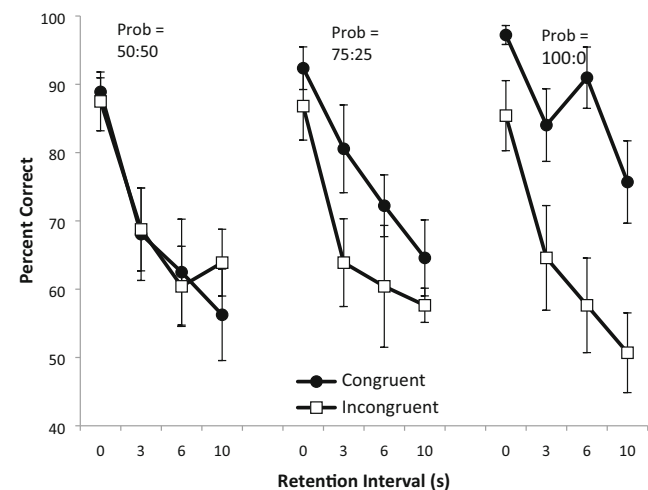


Fig. 3 Working memory retention curves for trials when working memory and reference memory correct choices are congruent and incongruent. The sample stimulus was presented for 3 s. Panels show performance when the probability of choosing the correct choice in reference memory discrimination training was 50:50, 75:25, and 100:0. Error bars are standard error of the mean (from Roberts et al., 2015)

(working memory), with blue and white center keys as the sample stimuli and vertical and horizontal stripes presented on the side keys as comparison stimuli. Choice of vertical stripes was reinforced after presentation of the blue sample stimulus, and choice of horizontal stripes was reinforced after presentation of the white sample stimulus. The new factor introduced in this experiment was the presentation of a house-light context cue 1 s before presentation of the comparison stimuli that remained on until a choice was made. The context cue was either a red or green ambient house-light, as used in the previously discussed MacDonald and Roberts (2018) experiments. In separate training sessions, pigeons were given discrimination training between vertical and horizontal stripes (reference memory), with choice of one line orientation always reinforced. The same house-light context cue presented during matching-to-sample training was presented 1 s before presentation of the line orientation stimuli and remained illuminated until a choice was made. Once pigeons were discriminating at a high level of accuracy, they were returned to delayed matching and tested at retention intervals of 1, 3, 6, and 10 s, with the context cue presented on each trial. Retention curves for congruent and incongruent trials are shown in Fig. 4. The results are similar to those reported by Roberts et al. (2015). Little difference in working memory is seen at the short 1-s retention interval. The curves then progressively separate at longer retention intervals, with little drop in accuracy on the congruent trials and a drop to below chance accuracy on the incongruent trials.

Thus, when the same context cues working and reference memory, we once again see that reference memory comes to

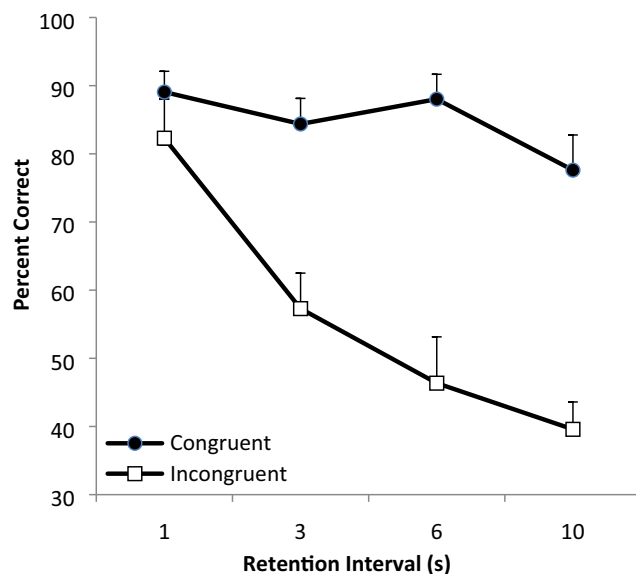


Fig. 4 Working memory retention curves for trials when working memory and reference memory correct choices are congruent and incongruent and the same context is present during both types of memory training and testing. Error bars are standard error of the mean (from Roberts, Macpherson, & Strang, 2016)

dominate choice as working memory weakens. It may be argued that the same context of a darkened chamber also gave simultaneous access to working and reference memory in the Roberts et al. (2015) experiments. In Experiment 2, Roberts, Macpherson et al. (2016) asked what would happen if different contexts cued working and reference memory. The same sample and comparison stimuli used in Experiment 1 were used in Experiment 2, but the context cue changed between working and reference memory training. Thus, in one condition, a red house-light illuminated the chamber during presentation of the comparison stimuli in delayed matching-to-sample training (working memory), and a green house-light illuminated the chamber during discrimination training (reference memory). On subsequent test sessions, pigeons were tested on congruent and incongruent trials at different retention intervals with either the working memory context or the reference memory context presented during choice between the comparison stimuli. Figure 5 shows the results of this manipulation. The results are strikingly different from those seen in Fig. 4. When the working memory (WM) context was presented, almost identical retention curves are seen for congruent and incongruent trials. There is no hint that reference memory interfered with retention on incongruent trials. When the reference memory (RM) context was presented, however, we see two parallel curves, one at 90% for congruent trials and the other at 10% for incongruent trials. These curves show that choice was completely controlled by reference memory when the reference memory context was present.

These findings suggest that context cues accessed different memory systems, which then yielded different information

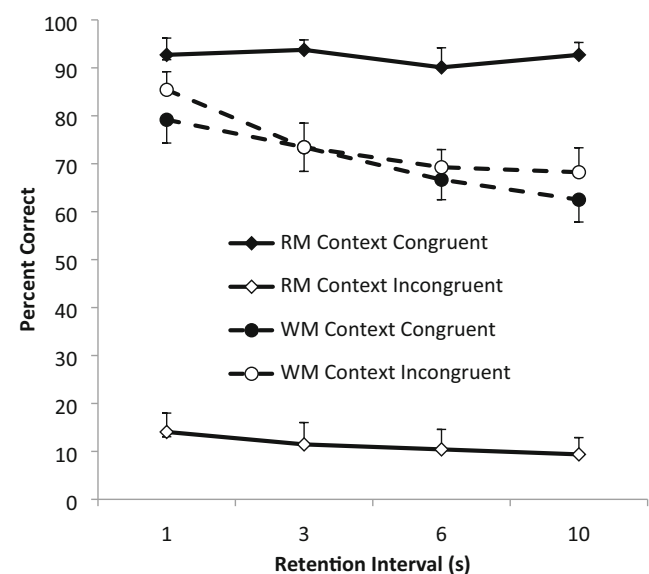


Fig. 5 Working memory retention curves for trials when working memory (WM) and reference memory (RM) were congruent and incongruent and when different contexts were presented in WM and RM training and testing. Error bars are standard error of the mean (from Roberts, Macpherson, & Strang, 2016)

about which stimulus to choose. They cannot be readily explained by context simply cueing a response. Importantly, the sample stimulus was presented initially in the absence of the context cue, and the context cue was only presented after the sample and 1 s before presentation of the comparison stimuli. Thus, the context cue yielded access to working memory and its contents up to 10 s after presentation of the sample. In the case of the reference memory context, working memory had no effect on performance. Even at the 1-s retention interval, when working memory is strongest, pigeon choice was totally controlled by reference memory.

Contextual control of access to working memory from different stimulus dimensions

Another question that can be addressed experimentally is whether context can be used to access different dimensions of a working memory. The fact that memories are often multidimensional has become particularly important with respect to the question of whether animals have episodic memory. Episodic memory refers to a human's ability to remember the details of particular events experienced in the past. Tulving (1972) suggested that these details should include what happened, where it happened, and when it happened. Although Tulving argued that episodic memory would only be found in humans (Tulving, 1983), experiments have now found evidence of what-where-when (WWW) memory or *episodic-like memory* in birds (Clayton & Dickinson, 1998; Feeney, Roberts, & Sherry, 2009, 2011; Meyers-Manor, Overmier, Hatfield, & Crosswell, 2014; Zinkivskay, Nazir, & Smulders, 2009), rodents (Babb & Crystal, 2006; Naqshbandi, Feeney, McKenzie, & Roberts, 2007), and primates (Martin-Ordas, Haun, Colmenares, & Call, 2010; Schwartz, Hoffman, & Evans, 2005).

Given that animals can encode memories that contain WWW features, a related question has been how these memories are stored. Are WWW features bound together into a single memory, or is each feature stored as an independent code? Although evidence of feature binding has been reported in studies of human WM (Allen, Baddeley, & Hitch, 2006; Baddeley, Allen, & Hitch, 2011; Wheeler & Treisman, 2002), findings from animal studies have been mixed. Crystal and Smith (2014) found evidence to suggest that rats bind together what, where, source, and context features of memories formed on a radial maze. In delayed matching-to-sample experiments, animals have been trained to symbolically match samples that vary in appearance (what: color or pattern), location (where), and duration (when). Test trials were performed in which samples varying along all three dimensions were presented, and matching tests for each dimension were given in sequence. Memory binding of WWW features would be supported if retention or forgetting of features was correlated within trials. Skov-Rackette, Miller, and Shettleworth (2006) found no evidence that pigeons bound WWW features in

a delayed matching task, and suggested that memories for sample appearance, location, and duration may be stored independently of one another. Using a similar procedure, Hoffman, Beran, and Washburn (2009) reported that some rhesus monkeys in some experiments showed evidence of binding.

Three new experiments are reported here that address the question of whether the features of a multidimensional memory can be selectively dissected for retrieval. If an animal stores such a memory by binding the features, can these features be unbound to access one dimension of the memory? Alternatively, if the features are stored independently, can the file for any one dimension be selectively accessed? To answer this question, pigeons were trained to symbolically match comparison stimuli containing vertical and horizontal lines to sample stimuli from different dimensions. A critical aspect of this procedure is that the same comparison stimuli were used with each dimension, but different contextual stimuli were presented during training with sample cues from different dimensions. On probe test trials, ambiguous samples were presented that contained cues from two dimensions, each of which required choice of a different matching comparison stimulus. Different contexts were presented on probe trials to see whether pigeons would choose the comparison stimulus that matched the sample dimension cued by the context.

Experiment 1: Color and location

In an initial training phase, pigeons learned to symbolically match vertical and horizontal line comparison stimuli projected on the side keys to the right or left location of a white sample key. During a subsequent training phase, pigeons learned to symbolically match vertical and horizontal lines to red and green sample stimuli presented on the center key. Throughout location training, a green house-light contextual cue appeared for 1 s after the sample terminated and before the comparison stimuli appeared. The contextual cue remained on until a pigeon chose one of the comparison stimuli. Throughout training to match the color cue, a red house-light appeared before and during the presentation of the line comparison stimuli.

When pigeons had achieved a high level of accuracy on both delayed matching problems, they were tested for 10 sessions. Within each session, location- and color-matching trials identical to those used in training occurred in random order. Ambiguous probe trials were randomly inserted among these training trials (see Fig. 6). On half the probe trials, the sample stimulus was a red field presented on the left key; on the other half of the probe trials, the sample stimulus was a green field presented on the right key. Thus, a peck on one comparison stimulus was a correct match to color, and a peck on the other comparison stimulus was a correct match to location. A peck on either comparison stimulus was reinforced. To

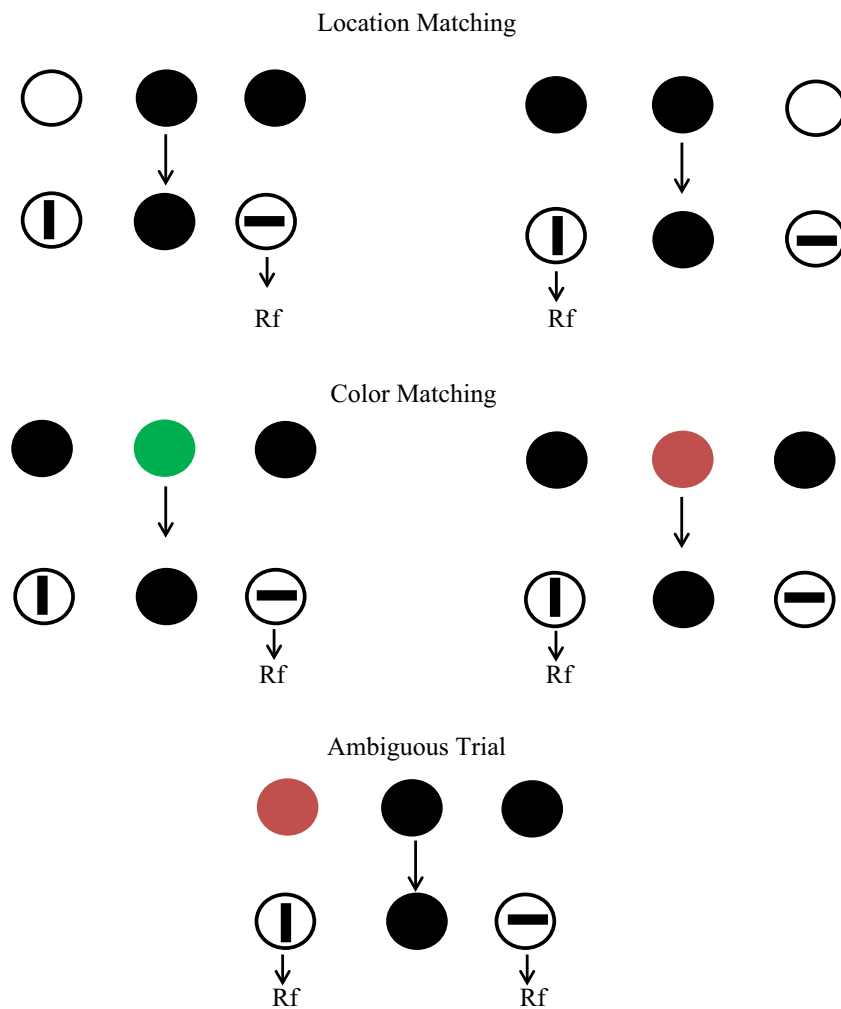


Fig. 6 Examples of location and color sample stimulus matching to common comparison stimuli and an ambiguous trial in which each comparison matches one dimension of the sample Rf = Reinforcement

disambiguate probe trials, the green contextual cue was presented on half the probe trials, and the red contextual cue was presented on the other half of the probe trials. Correct responses on probe trials then were scored as choice of the comparison stimulus correct for the dimension cued by the contextual cue. Significantly higher than chance performance would support the hypothesis that context acts to selectively access information from one dimension or the other.

Method

Subjects Six adult White King pigeons were tested. These birds had been used previously in studies of timing and mid-session reversal. 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 °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. Care and testing of these pigeons

was approved by the Western University Animal Care Committee and followed the guidelines of the Canadian Council on Animal Care.

Apparatus Two enclosed, sound-attenuating operant chambers measuring 31 × 35.5 (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. Mixed grain reinforcement 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. A rectangular box measuring 10.5 × 5 × 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 the 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 illumination of either the left or right side key with white light and the comparison stimuli were vertical and horizontal striped patterns presented on the side keys. Each trial began with the presentation of either the left or right sample key. A pigeon had to complete a fixed ratio (FR) of ten pecks on the sample stimulus. The sample was then turned off and a green ambient context cue appeared for 1 s. 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 counter-balanced across trials. The reinforcement contingencies were programmed so that a peck on vertical stripes was required for reinforcement after pecking the right sample stimulus and a peck on horizontal stripes was required for reinforcement after pecking the left 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 non-matching 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 s and 30 s. There were 64 trials in each session, and there were 12 training sessions, at the end of which the pigeons' mean accuracy at choosing the matching comparison stimuli was over 85%.

The pigeons then were trained to symbolically match horizontal and vertical line comparison stimuli to red and green sample stimuli presented on the center key. Each trial began with presentation of red or green, and a pigeon had to complete ten pecks on the key to terminate the sample stimulus and progress to the matching test. As soon as the sample went off, a red house-light contextual cue came on for 1 s, followed by the appearance of the stripes comparison stimuli on the side keys. A peck on the vertical stripes key was reinforced when the sample had been red, and a peck on the horizontal stripes key was reinforced when the sample had been green. The red house-light remained on until a choice was made. The events following a correct or incorrect choice were the same as in the sample location training, and there were 64 trials in each session. Pigeons were trained for 18 sessions and were performing above 85% accuracy at the end of training.

All six pigeons then were tested over ten sessions in which there were 72 trials in each session. Among these trials, 24 were location-matching trials identical to those given in location training, and 24 were color-matching trials identical to

those given in color training. The remaining 24 trials were probe test trials on which ambiguous sample stimuli were presented (see Fig. 6). Each of three blocks of 24 trials contained eight location training trials, eight color training trials, and eight ambiguous probe trials, in random order. On half of the ambiguous trials in each block, the left key was illuminated with red light; on the other half of the ambiguous trials, the right key was illuminated with green light. After the pigeon pecked the sample ten times, either the red or the green context cue appeared, followed 1 s later by the line comparison stimuli. The green and red context cues appeared equally often following each ambiguous sample. A peck on either comparison stimulus yielded 2.5 s of reinforcement, but the computer only recorded a correct choice if the comparison stimulus chosen matched the sample dimension indicated by the context cue. Thus, after presentation of the red-left sample, choice of vertical stripes was correct if the context was red, but choice of horizontal stripes was correct if the context was green. Similarly, after presentation of the green-right sample, choice of horizontal stripes was correct if the context was red, but choice of vertical stripes was correct if the context was green.

Results and discussion

Pigeons learned to match location sample stimuli rapidly. Mean matching accuracy was 52.08% ($SE = 2.12$) on the first session of training and reached 94.53% ($SE = 1.60$) on session 12. The color-matching task was learned at a somewhat slower rate, with mean matching accuracy improving from 48.96% ($SE = 2.96$) on session 1 to 90.63% ($SE = 3.13$) on session 18.

Over the ten sessions of testing, pigeons received 72 trials in each session, which included 24 color training trials, 24 location training trials, and 24 novel ambiguous trials that combined color and location sample cues. On the 24 ambiguous trials, 12 presented the green location context during presentation of the comparison stimuli, and 12 presented the red color context during presentation of the comparison stimuli. Because choice of either comparison stimulus was reinforced on ambiguous trials, a concern is that pigeons might have learned to choose non-differentially on ambiguous trials as sessions proceeded. Separate analyses of variance (ANOVA) were performed on the data from training trials and from ambiguous trials that contained the factors of dimension (location vs. color) and session. The analysis of training trials yielded no significant effect of session, $F(9, 45) = .54, p > .05$, but did reveal a significant session \times dimension interaction, $F(9, 45) = 2.52, p < .05, \eta_p^2 = .34$. This interaction appeared to result from a slight improvement over sessions in location matching and a slight decline over sessions in color matching. However, one-way ANOVAs showed no significant effect of session on location sample tests, $F(9, 45) = 1.16, p > .05$, or on color

sample tests, $F(9, 45) = 1.12, p > .05$. The analysis of performance on ambiguous trials showed no significant effects of session, $F(9, 45) = .18, p > .05$, or the session \times dimension interaction, $F(9, 45) = .14, p > .05$. Performance was averaged over the ten sessions for presentation of mean accuracy in Fig. 7.

The Location Train and Color Train bars in Fig. 7 show that pigeons were somewhat more accurate when location was the sample stimulus ($M = 81.67\%$, $SE = 3.25$) than when color was the sample stimulus ($M = 73.44\%$, $SE = 2.40$). However, this difference did not reach significance, $F(1, 5) = 3.55, p > .05$. On ambiguous tests, a correct choice was scored when the comparison stimulus was chosen that agreed with the dimension signaled by the context (location or color). The bars for ambiguous trials show a more marked superiority of location tests ($M = 81.67\%$, $SE = 3.87$) over color tests ($M = 48.33\%$, $SE = 7.71$), and this difference was significant, $F(1, 5) = 16.19, p = .01, \eta_p^2 = .76$. Most importantly, mean accuracy on ambiguous trials was 65% ($SE = 4.48$), and this mean was significantly higher than the chance level of 50%, $t(5) = 3.35, p < .01$.

The important finding here is that pigeons used context to resolve an ambiguous sample memory. When the location component of the sample memory indicated choice of one comparison stimulus, and the color component indicated choice of the other comparison stimulus, pigeons significantly preferred to respond on the basis of the component signaled by the contextual cue.

Experiment 2: Location and time

In order to study pigeons' memory for location/time compounds, birds were trained to match time-duration sample stimuli. Samples consisted of the presentation of a white center key for 2 s or 8 s. The comparison stimuli presented after

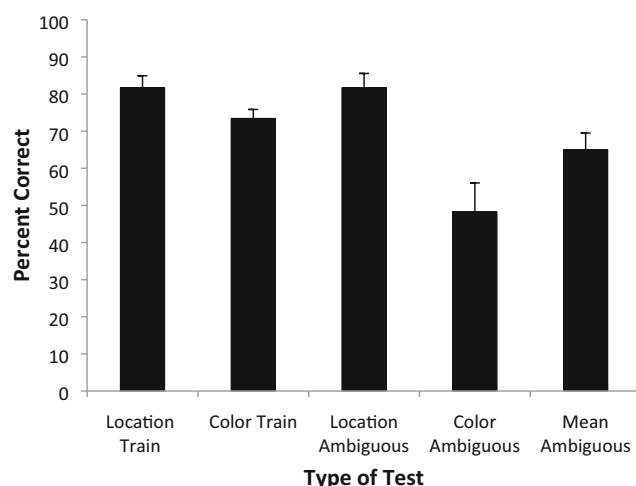


Fig. 7 Mean percentage of correct choices for each type of test trial in Experiment 1: Location and color. Accuracy on ambiguous trials indicates correct responses to the context cue. Error bars are standard error of the mean (data presented are previously unpublished)

the sample were again horizontal and vertical striped patterns presented on the side keys, with vertical stripes as the reinforced choice after the 8-s sample and horizontal stripes as the reinforced choice after the 2-s sample. The contextual cue present for 1 s after the sample and during presentation of the comparison stimuli was a darkened chamber. After pigeons learned to match temporal samples at a high level of accuracy, test sessions were run that contained location-training trials, time-training trials, and ambiguous test trials. On ambiguous trials, a white side key was presented for 2 s or 8 s, such that during presentation of the comparison stimuli, choice of one comparison stimulus was the correct response to location, and choice of the other comparison stimulus was the correct response to time. On half of the ambiguous trials, the green context used during location training was presented, and on the other half of the ambiguous trials, the dark context used during time training was presented. The question of interest was whether pigeons would choose the comparison stimulus, which was the correct response to the sample dimension (location or time) signaled by the context.

Method

The same pigeons and apparatus used in Experiment 1 were used in Experiment 2. Pigeons were trained on temporal delayed matching to sample. Within 64 daily trials, the sample stimulus was a 2-s presentation of the white center key on half the trials and an 8-s presentation of the white center key on the other half of the trials, with the order of samples randomized. When the sample ended, the chamber remained dark for 1 s, followed by presentation of vertical and horizontal stripes patterns on the side keys in the still darkened chamber. If the sample had lasted for 2 s, choice of horizontal stripes was reinforced, and choice of vertical stripes ended the trial without reinforcement. After an 8-s sample, choice of vertical stripes was reinforced, and choice of horizontal stripes ended the trial without reinforcement. The intertrial interval was spent in darkness and lasted for 10–30 s. Training on temporal matching lasted for 39 sessions, at the end of which all pigeons were performing above 85% accuracy. The pigeons then were given three sessions of retraining on location matching.

Ten sessions of testing followed that each contained 24 time training trials, 24 location training trials, and 24 time/location ambiguous test trials. On half of the ambiguous test trials, a white sample was presented for 2 s on the right key. Notice that the right key location signaled choice of the vertical stripes comparison key and 2 s signaled choice of the horizontal stripes comparison key. On the other half of the ambiguous test trials, a white sample was presented for 8 s on the left key. The left key location signaled choice of the horizontal stripes comparison key, but 8 s signaled choice of the vertical stripes comparison key. On half of each type of

ambiguous trials, the context was green before and during presentation of the comparison stimuli, and choice of the comparison stimulus that matched location was scored as a correct choice. On the other half of each type of ambiguous trials, the context was darkness, and choice of the comparison stimulus that matched time was scored as a correct choice. Choice of either comparison stimulus on ambiguous trials was reinforced.

Results and discussion

Analysis of performance on training trials over the ten test sessions showed no significant effects of session, $F(9, 45) = 2.05, p > .05$, or of the session \times dimension interaction, $F(9, 45) = .93, p > .05$. The same analysis done on ambiguous trials found no significant effects of session, $F(9, 45) = .38, p > .05$, or the session \times dimension interaction, $F(9, 45) = .99, p > .05$.

Mean choice accuracy on training and ambiguous trials for each dimension (location and time) are shown in Fig. 8. The bars for performance on location- and time-training trials show matching accuracy was nearly equal on location trials ($M = 87.92\%$, $SE = 4.17$) and on time trials ($M = 85.69\%$, $SE = 4.44$), and no significant effect of dimension was found, $F(1, 5) = .30$. The bars for performance on ambiguous trials were also nearly identical when cued by location context ($M = 60.42\%$, $SE = 4.33$) and by time context ($M = 59.72\%$, $SE = 4.85$), and showed no significant difference, $F(1, 5) = .02, p > .05$. Most importantly, the mean performance on ambiguous trials ($M = 60.07\%$, $SE = 3.73$) was significantly higher than the chance value of 50%, $t(5) = 2.70, p = .02$. As in Experiment 1, using location and color dimensions, pigeons were able to respond to ambiguous samples by selecting the comparison

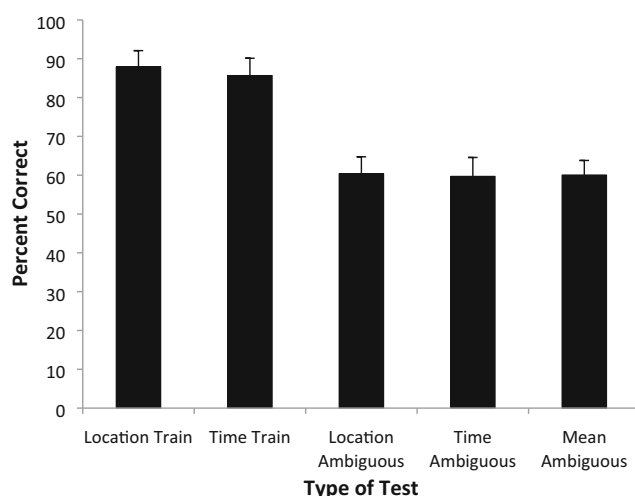


Fig. 8 Mean percentage of correct choices for each type of test trial in Experiment 2: Location and time. Accuracy on ambiguous trials indicates correct responses to the context cue. Error bars are standard error of the mean (data presented are previously unpublished)

stimulus appropriate for the location or time dimension signaled by the context cue.

Experiment 3: Color and time

The remaining combination of color and time sample stimuli was examined in Experiment 3. Because pigeons had learned to match the vertical and horizontal stripe comparison stimuli to color and time duration sample stimuli in the preceding experiments, they were given reminder training sessions to make sure they were matching samples at high levels of accuracy on both dimensions. Testing then involved ten sessions that contained color training, time training, and ambiguous trials. On half of the ambiguous trials, the sample was a red center key presented for 2 s, and on the other half of the ambiguous trials, the sample was a green center key presented for 8 s. For the 2-s red sample, choice of the vertical stripes comparison stimulus matched its color and choice of the horizontal stripes comparison stimulus matched its time duration. For the 8-s green sample, choice of the horizontal stripes comparison stimulus matched its color and choice of the vertical stripes comparison stimulus matched its time duration. The context cues of red and dark chambers were each presented on half of the probe trials with each ambiguous sample stimulus. The purpose of this experiment was to find out if context could selectively access memory for time or color.

Method

The pigeons used in Experiments 1 and 2 were also tested in Experiment 3. Pigeons were given one reminder training session with color (red and green) sample stimuli presented on the center key and the red house-light context presented for 1 s before and during presentation of the vertical and horizontal stripes comparison stimuli. They were also given one reminder training session with time sample stimuli (a white center key presented for 2 s or 8 s) and the darkened chamber context presented for 1 s before and during the comparison stimuli.

Ten sessions of testing followed, each of which contained 24 color-training trials, 24 time-training trials, and 24 ambiguous trials. Eight of each type of trial occurred in successive blocks of 24 trials, in random order. Over the session, there were 12 ambiguous trials that presented a red sample for 2 s on the center key and 12 ambiguous trials that presented a green sample for 8 s on the center key. On six of the ambiguous trials of each type, the red context cue appeared after the sample; the darkened chamber context cue appeared after the sample on the other six ambiguous trials of each type. Although a choice of either comparison stimulus was reinforced on ambiguous trials, a correct response was recorded only if the comparison stimulus chosen was the correct match to the dimension (color or time) signaled by the context cue.

Results and discussion

On the reminder session with color sample stimuli, mean accuracy was 88.20% ($SE = 1.58$) correct choices. On the reminder session with time sample stimuli, mean accuracy was 88.54% ($SE = 2.78$) correct choices.

A dimension \times session ANOVA was performed on the training trials data from the ten test sessions. Although it revealed no effect of session, $F(9, 45) = .60$, $p > .05$, the interaction of session \times dimension was significant, $F(9, 45) = 2.26$, $p < .05$, $\eta_p^2 = .31$. The interaction arose from higher accuracy on color sample trials than on time sample trials over the first two sessions, followed by superior accuracy on time sample trials over sessions 3–9 and equal performance on session 10. Overall, however, accuracy on color-training trials ($M = 81.10\%$, $SE = 4.10$) was close to accuracy on time-training trials ($M = 83.06\%$, $SE = 4.12$), and the means did not differ significantly, $F(1, 5) = .76$, $p > .05$.

A session \times dimension ANOVA performed on percentage of correct choices made on ambiguous test trials yielded non-significant effects of session, $F(9, 45) = 2.02$, $p > .05$, and the session \times dimension interaction, $F(9, 45) = 1.35$, $p > .05$. Mean accuracy across all sessions is shown in Fig. 9 for training trials, ambiguous test trials, and for the mean of ambiguous trials. Accuracy on training trials differed little between color-matching trials ($M = 81.10\%$, $SE = 4.10$) and time-matching trials ($M = 83.06\%$, $SE = 4.12$) and did not differ significantly, $F(1, 5) = .10$, $p > .05$. Although the mean of ambiguous trials that presented the color contextual cue ($M = 72.92\%$, $SE = 5.61$) was higher than the mean of ambiguous trials that presented the time contextual cue ($M = 63.89\%$, $SE = 5.85$), the means did not differ significantly, $F(1, 5) = .91$, $p > .05$. Of most importance, the mean accuracy on all ambiguous trials was 67.71% ($SE = 1.88$), and this mean significantly exceeded chance, $t(5) = 9.43$, $p < .01$. Thus, as in the preceding two experiments with color/location and time/location dimensions, pigeons were able to access from memory the correct dimension signaled by a context cue when ambiguous color/time sample stimuli were tested.

General discussion

In three successive studies, six pigeons were tested for their ability to selectively retrieve information from the memory of compounds that contained location and color, location and time, and color and time information. Each study involved delayed symbolic matching-to-sample training in which the comparison stimuli were vertical and horizontal lines. Critical tests with ambiguous sample stimuli were given in which one component of the sample directed pigeons to choose one comparison stimulus and the other component of the sample directed pigeons to choose the other comparison

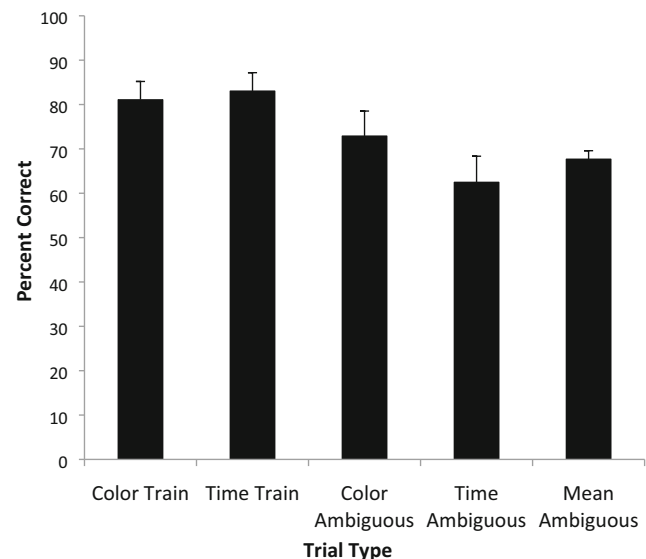


Fig. 9 Mean percentage of correct choices for each type of test trial in Experiment 3: Color and time. Accuracy on ambiguous trials indicates correct responses to the context cue. Error bars are standard error of the mean (data presented are previously unpublished)

stimulus. Based on prior training, ambient context cues could disambiguate these sample stimuli by indicating response to one dimension or the other. The results indicated that pigeons used the context cue to direct their choice to the comparison stimulus correct for the dimension cued by context.

Alternative ways in which pigeons might have processed ambiguous samples seem to be problematic. When encoding an ambiguous compound sample stimulus, a bird might encode it as a completely new stimulus. In this case, it should have no basis for choosing one comparison stimulus over the other, and performance should be no better than chance. An alternative possibility is that a pigeon would attend to only one dimension of the sample. Thus, when presented with red on the left side key, a pigeon might encode only the spatial feature of leftness, or it might encode only the color feature of redness. In both of these cases, the pigeon could respond correctly to the comparison stimuli at no better than chance (50%) accuracy. For example, if a pigeon always attended to the spatial dimension and encoded the sample as left, it would always be correct on the half of the trials when the green location context was presented and it chose horizontal stripes, but it would always be incorrect on the half of the trials when the red color context was presented and it chose horizontal stripes. If a pigeon's attention varied randomly among trials between location and color, it again should perform no better than chance at matching the feature from the dimension cued by context. The fact that pigeons did match ambiguous samples significantly above chance accuracy suggests that both dimensions of the samples were encoded. Thus, in the above example, pigeons formed a memory that contained both color and location features.

One concern that may be raised about these experiments is that performance on test trials with ambiguous sample stimuli was not high. Mean choice of the correct comparison stimulus cued by the colored house-light or darkness ranged from 60% in the location and time study to 65% in the location and color study to 67.7% in the color and time study. Why was choice of the correct stimulus not higher? One answer is that performance suffered from generalization decrement. The ambiguous stimulus presented on test sessions was a novel stimulus. That is, a compound of the training sample stimuli was used that had not been seen by the pigeon previously. In the location and color study, a red sample appeared on the left side key and a green sample appeared on the right side key for the first time. In the location and time study, a white sample lasting 2 s appeared for the first time on the right key and a white sample lasting 8 s appeared for the first time on the left key. Experiments by Lionello-DeNolf and Urcuioli (2000) and Urcuioli (2007) have shown that location of a sample stimulus is an important cue for delayed matching-to-sample in pigeons. After training pigeons with samples presented on the center key and comparison stimuli presented on the side keys, pigeons' matching accuracy fell to near chance when they were tested with samples presented on a side key and comparison stimuli then presented on the remaining keys. The lower performance on ambiguous trials particularly seen in the location/color and location/time studies could have arisen from the presentation of a cue on the side keys that had only been seen on the center key in training. Nonetheless, pigeons chose the comparison key that matched the sample dimension cued by the context cue significantly above chance. Thus, performance decrement caused by shifting the position of the sample did not completely over-ride the context cue's retrieval of relevant dimensional information from the sample memory.

Interestingly, these findings have implications for the theory that pigeons code the sample stimulus into a prospective instructional code (Honig & Thompson, 1982). A prospective code would take the form of an instruction to “peck vertical stripes” or “peck horizontal stripes.” When presented with an ambiguous compound, however, the feature from one dimension would be coded as “peck vertical stripes,” and the feature from the other dimension would be coded as “peck horizontal stripes.” The pigeon would then be faced with conflicting instructions when presented with the comparison stimuli, and should perform no better than chance accuracy. The fact that pigeons were better than chance accuracy on ambiguous test trials suggests that they were not using a prospective code. Rather, a retrospective code was held in memory until the context cue signaled one dimension. The feature from that dimension was then retrieved and used as the code for making a choice response between the comparison stimuli.

This analysis then suggests that pigeons encoded a memory of the ambiguous sample stimulus that included information

about both dimensions presented. The features from each dimension might have been bound together into a single memory or might have been stored independently. Although some evidence for binding has been found with rats (Crystal & Smith, 2014) and monkeys (Hoffman et al., 2009), Skov-Rackette et al. (2006) found no evidence of binding in pigeons. Based on the Skov-Rackette et al. paper, it may be best to assume that the features of ambiguous sample compounds were encoded separately. In this case, the contextual cue acted to direct retrieval of the “correct” feature. It should be emphasized that the context did not specify this feature. Rather, the contextual cue specified the dimension along which memory of the sample compound contained the feature. Thus, the green context indicated retrieval of the location memory, but the memory retrieved could be of the sample on either the left or right.

General conclusions

The studies reviewed here suggest a progression of understanding about the role of context in memory retrieval. Earlier research with both humans and animals showed that memory encoded in one context could be reactivated by testing for retention in the encoding context. Reinstatement of room or chamber cues provided to several sensory modalities led to retrieval of language or visual associations in people and to recovery of otherwise forgotten or extinguished conditioned responses in animals. The influence of contextual cues on memory retrieval was particularly shown in the experiment by MacDonald and Roberts (2018): In a midsession reversal task, pigeons showed perfect reversal of stimulus choice after seven sessions of training. We attributed this complete control by context first to the use of colored house-light cues that first took advantage of pigeons' sensitivity to color (Waldvogel, 1990) and second to the presentation of these house-light cues in an operant chamber that guaranteed the context cue was ambient and the only context cue.

The role of context cues was then extended in our studies of the interaction between working and reference memory. It appears that context controls access to working memory and reference memory systems. When the same chamber contextual cue is present during working memory and reference memory training, either a darkened chamber (Roberts et al., 2015) or a red- or green-colored chamber (Roberts, Macpherson et al., 2016, Experiment 1), the congruency of working memory and reference memory interacts strongly with retention interval. When working memory and reference memory direct the pigeon to choose the same comparison stimulus (congruent trials), retention remains high over retention intervals extending to 10 s. When working memory and reference memory direct the pigeon to choose different comparison stimuli (incongruent trials), equivalent matching

accuracy is found at short retention intervals, but the retention curve then shows a steep decline at longer retention intervals. Thus, both working memory and reference memory systems are accessed, with working memory dominating choice immediately after sample presentation but then weakening and giving way to reference memory dominance at longer retention intervals. When different color cues serve as contexts for working memory and reference memory (Roberts, Macpherson et al., 2016, Experiment 2), this pattern completely disappears. In the working memory context, retention curves are completely uninfluenced by reference memory, and in the reference memory context, retention curves are flat and completely controlled by reference memory.

The final experiments presented here suggest that context may also be used by pigeons to access different dimensions along which features of a memory are stored. These dimensions include location, color, and time. When different context cues were presented on trials that required pigeons to match comparison stimuli to place, color, or time sample stimuli, these context cues selectively directed birds to choose the correct match when ambiguous sample stimuli from two dimensions were presented. Thus, it appears that a context cue present only during the test or matching phase of training trials became sufficiently associated with a dimension of memory (location, color, or time) that it could selectively access that memory system or dimension. Once the memory system or dimension was accessed, the relevant sample memory or dimensional feature was retrieved.

These strong effects of context on access to memory systems and dimensions of encoded memories may be further examined with other species and types of memory. Recent evidence indicates that context partially controls access to working memory and reference memory in rats on a radial maze (Roberts, Guitar, Marsh, & MacDonald, 2016). Recent findings reported by Panoz-Brown et al. (2016) indicate that rats show episodic memory for odors experienced in different visual contexts. The time sample stimulus used in the location/time and color/time studies was clearly a time-duration or how-long-ago cue (Roberts et al., 2008). Could context act to access memory for “when” in past time an event occurred (Feeney et al., 2011; Meyers-Manor et al., 2014; Zhou & Crystal, 2009)? The role of context in access to memories from other dimensions of experience might be explored, such as number, sensory modalities, or social encounters.

Finally, the neural processes involved in these context effects should be considered. If context acts as a gateway to different memory systems and dimensions of experience, what parts of the brain and neural pathways are involved? Procedures such as those used by Diekamp, Kalt, and Gunturkun (2002) to examine neural firing in pigeons during delayed matching may ultimately shed light on how an ambient environmental context can direct the avian brain to particular memory systems or dimensions.

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