Episodic-like memory: Pigeons can report location pecked when unexpectedly asked

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ABSTRACT

Pigeons were tested for their ability to report the location they recently pecked, without prior experience having to do so. They were first pretrained to report the location that they had just pecked. They were then trained on a conditional discrimination to associate yellow and blue samples with vertical and horizontal comparisons, respectively, independent of comparison location. On probe trials in testing, when after choosing a vertical or horizontal line following the yellow or blue sample, the pigeons were 'asked' which location they had just pecked, they showed a significant tendency to choose correctly in spite of the fact that location of the correct comparison was incidental to the task. Performing on probe trials is analogous to asking the pigeons an unexpected question about their recent behavior and it is similar to the episodic memory question asked of humans, "What did you have for breakfast this morning?".

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In a conditional discrimination (sometimes called matching-to-sample), a pigeon is presented with a sample stimulus that serves as a conditional stimulus to choose one of two comparison stimuli. For example, on some trials the pigeon is presented with a vertical-line sample, which indicates that choice of the red comparison will be reinforced. On other trials the pigeon is presented with a horizontal-line sample, which indicates that choice of the green comparison will be reinforced.

If differential responding is required to the two sample stimuli, for example, many responses are required to one sample and two responses spaced 3 s apart are required to the other sample, there is evidence that the two sample responses themselves can gain control over comparison choice (Urcuioli and Honig, 1980). Control of comparison choice by differential sample responding was demonstrated by training pigeons on a second conditional discrimination involving different samples and comparisons but the same differential sample responding and then on test trials, replacing the original samples with the new ones. Urcuioli and Honig found a high degree of transfer (about 85%) in spite of the fact that the differential sample response was the sole basis on which appropriate comparison choice could have been based.

In a typical conditional discrimination, one can view the presentation of the comparison stimuli as analogous to asking the pigeon, "What sample did you just see?" However, if differential sample responding controls comparison choice, presentation of the comparison stimuli can be viewed as analogous to asking the question, "What response did you just make?".

Zentall et al. (2001) trained pigeons to 'answer' this question by first training them to match vertical- and horizontal-line samples to red and green comparison stimuli with differential responding required to the two samples. Specifically, when the samples consisted of vertical lines, the first response after 4 s produced the comparison stimuli and the red comparison stimulus was correct. This requirement resulted in a high rate of pecking the vertical lines. When the samples consisted of horizontal lines, the pigeon was required to refrain from pecking for 4 s to produce the comparison stimuli and the green comparison stimulus was correct. This requirement quickly resulted in the absence of pecking the horizontal lines. Thus, if the pigeon had just pecked, it chose the red comparison stimulus and if it had just refrained from pecking, it chose the green comparison stimulus.

In the second phase of the experiment, Zentall et al. (2001) trained the pigeons on a differential autoshaping task in which on some trials a yellow stimulus was presented for 4 s and then the feeder was raised. On other trials, a blue stimulus was presented for 4 s but the feeder was not raised. Although food was presented non-contingently following presentation of the yellow stimulus, the pigeons typically pecked at it, whereas they generally refrained from pecking at the blue stimulus.

On test trials, the pigeons were presented with yellow and blue stimuli as samples followed by red and green comparison stimuli and positive transfer resulted. That is, when the sample was the

yellow stimulus that they had pecked because it had been followed by food, the pigeons tended to choose the comparison that in original training had been associated with sample pecking, whereas when the sample was the blue stimulus that they had refrained from pecking, they tended to peck the comparison that in original training had been associated with the absence of pecking (see also Urcuioli and DeMarse, 1994).

Zentall et al. (2001) argued that on test trials the pigeons were not anticipating being asked, "What did you just do?" and thus, unexpectedly, they had to refer back to their earlier behavior. Most important, they reasoned that to rule out the possibility that procedural or semantic memory is being used, evidence for episodic memory should demonstrate the ability to recover memory for an event that had not been expressly encoded. For example, if a human is asked, "What did you have for breakfast this morning?" it is unlikely that the answer was purposely encoded for later retrieval.

The assumption made by Zentall et al. (2001) was that on test trials, there were no residual motor aftereffects (proprioceptive cues) present at the time the comparison stimuli were presented to indicate which comparison stimulus should be chosen. However, when the behavior to be retrieved is responding versus refraining from responding, it is possible that the aftereffects of responding (e.g., a sensation in the beak or neck) may persist for a short time, long enough to serve as a cue for comparison choice.

Singer and Zentall (2007) attempted to correct for this by using a different kind of differential sample response, the location of the response. In Phase 1 of their experiment, they required pigeons to report the location (left or right) of a previous pecking experience to otherwise undifferentiated pecking keys by choosing a red or a green comparison stimulus. To avoid allowing the pigeon to use the position of its beak at the time of the appearance of the comparison stimuli, on every trial, following the left or right initial response, the pigeons were required to peck a triangle at a common location (on the center key). The common response also created a delay between the left or right pecking behavior and presentation of the comparison stimuli. The delay should have increased the necessity to retrieve the location pecked from memory. The pigeons were then trained on a symbolic matching task in which a vertical-line comparison stimulus was correct when the sample was a blue hue and a horizontal-line comparison stimulus was correct when the sample was a yellow hue, however, prior to the delivery of the food reinforcer, following all correct comparison responses, the pigeons were required to peck the triangle on the center key. Responses were reinforced to the vertical and horizontal lines, which appeared randomly on the left and right response keys. Thus, pecking at the different locations can be viewed as an incidental aspect of this task[1] (see Skinner, 1950). Finally, the pigeons were tested on probe trials on which, after the choice of line orientation, the pigeons received a triangle on the center key followed by a choice of red and green comparison stimuli. Thus, on these probe trials, the pigeons were unexpectedly asked which side key they had last pecked. Singer and Zentall found that the pigeons showed a significant tendency to select the comparison color that was appropriate for the comparison location recently pecked. It is possible, however, that
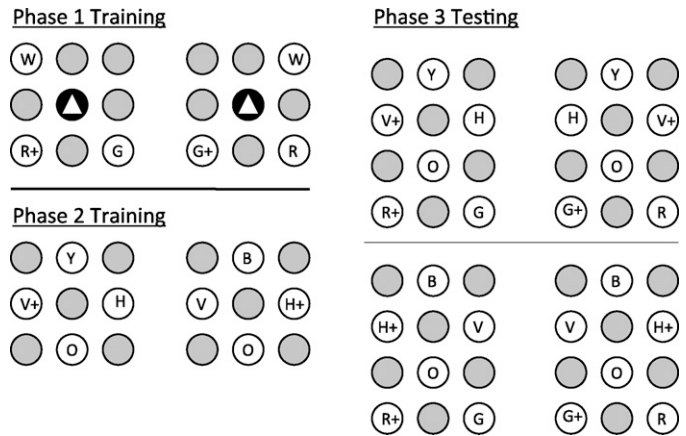
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[1] There is evidence that when sample stimuli appear in a fixed location during acquisition (e.g., on the center response key), moving them to one of the side keys results in very poor transfer (see Urcuioli, 2007). However, such a move represents a novel location for those stimuli. In the present case, there is nothing novel about the location of the comparison stimuli and it is assumed that the location of the correct comparison stimulus is an incidental aspect of this task. The implication of this assumption is there is no need for the pigeons to represent the comparison location pecked for the purpose of later retrieval. On the other hand, if, after its choice of the line-orientation comparison, one were to ask the pigeon what was the orientation of the line just pecked, one could not make the same assumption.

Fig. 1. Schematic of the design of the experiment. In Phase 1, pigeons were trained to peck a single side key and then to peck the center triangle. If the initial peck was to the left, the red comparison stimulus was correct. If the initial peck was to the right, the green comparison stimulus was correct. The position of the red and green comparison stimuli was counterbalanced. In Phase 2, yellow and blue samples were associated with vertical- and horizontal-line comparison stimuli, respectively. A peck to the orange stimulus on the center key was reinforced if the correct comparison had been selected. Test trials were similar to Phase 2 trials except a peck to the orange center stimulus was followed by choice red and green side keys with nondifferential reinforcement.

presentation of the triangle served as a cue to retrieve the memory of where they were pecking and since the triangle appeared immediately after pecking the side key and the pigeon could likely see the triangle as it was moving to peck the triangle, the direction of the pigeons movement rather than memory for the pecking location could have controlled choice following the offset of the triangle.

The purpose of the present experiment was to rule out the possibility that the pigeons may have developed an expectation of being tested because presentation of the triangle was common to all three phases: Phase 1, during which the triangle signaled that the pigeon would be tested, Phase 2, during which the pigeon was not tested, and Phase 3 during which it was tested again. In the present experiment, the stimulus presented on the center key during Phase 1 (a triangle) was different from the stimulus presented on the center key during Phases 2 and 3 (an orange hue). Thus, because the stimuli that removed the pigeon from the side key just pecked in Phases 1 and 3 were different, the pigeon would have never experienced a test of location remembered following the orange center key, prior to the Phase 3 trials. A schematic of the design of the experiment is presented in Fig. 1.

1. Method

1.1. Subjects

The subjects were eight White Carneaux pigeons (*Columba livia*)—retired breeders, purchased from the Palmetto Pigeon Plant (Sumter, SC). One pigeon died prior to testing so the data from only seven pigeons were included in this study. They were maintained at 85% of their free-feeding body weight for the duration of the experiment, were caged individually with free access to grit and water in the home cage, and were cared for in accordance with University of Kentucky animal care guidelines. The colony room was maintained on a 12:12-h light:dark cycle. All pigeons had previous experience with simple simultaneous discriminations.

1.2. Apparatus

The experiment was conducted in a BRS/LVE (Laurel, MD) sound-attenuating pigeon test chamber. Three round response keys (2.5 cm diameter) were aligned horizontally on the response panel, 8 cm apart center-to-center and the bottom edge of the keys was 25 cm from the floor of the chamber. A 12-stimulus in-line projector (Industrial Electronics Engineering, Van Nuys, CA) with 28 V, 0.1 A lamps (GE 1820) was mounted behind each response key. The center response key projected blue, yellow, red, green, and orange hues (Kodak Wratten Filter Nos. 38, 9, 26, 60, and 22, respectively) and a small solid white equilateral triangle on a black background. The left and right response keys projected white (unfiltered), red and green hues, as well as three white vertical lines and three white horizontal lines on a black background. A houselight located at the center of the chamber ceiling provided general illumination during inter-trial intervals (ITI). A rear-mounted grain feeder provided mixed grain reinforcement (Purina Pro Grains) through an aperture centered horizontally on the response panel. Reinforcement consisted of 2.0 s access to mixed grain. An exhaust fan mounted on the outside of the chamber masked extraneous noise. The experiment was controlled and data collected by a microcomputer located in the adjacent room.

1.3. Procedure

1.3.1. Phase 1

Phase 1 consisted of conditional discrimination training. Each trial began with the onset of a white stimulus on the left or right side key. Five responses to the white key were followed by presentation of a small white triangle on the center key. The pigeons were required to peck the triangle once to turn it off and turn on red and green comparison stimuli on the two side keys. The location (left vs. right) of the comparison stimuli varied randomly from trial to trial. For four of the pigeons, choice of the red comparison stimulus was reinforced following the left white side key and choice of the green comparison stimulus was reinforced following the right white side key (see the top panel of Fig. 1). For the remaining pigeons, the contingencies were reversed. Pigeons were required to peck once at the comparison stimulus. Choice of the correct comparison was reinforced with 2 s access to mixed grain followed by a 10-s ITI that was lit by the houselight. Choice of the incorrect comparison was followed by a 10-s lit ITI only. Presentation of the red and green comparison stimuli could be viewed as analogous to asking the question "Where did you last peck a side key, on the left or on the right?".

All pigeons received 96 trials per session with equal numbers of trials initiated by the right and left side keys. The red and green comparison stimuli appeared equally often on the right and left side keys and their position varied randomly over trials. Sessions were conducted 6 days a week. Pigeons remained in Phase 1 until they reached a criterion of 90% correct on trial types initiated by each of the two side keys for two consecutive sessions.

1.3.2. Phase 2

Phase 2 consisted of symbolic matching-to-sample training in which hue samples (blue and yellow) were followed by line-orientation comparisons (vertical and horizontal). Each trial began with the presentation of a yellow or blue stimulus on the center response key. After the pigeon pecked the sample stimulus 10 times, the vertical and horizontal comparison stimuli were presented on the side keys. The location (left vs. right) of the comparison stimuli varied randomly from trial to trial. Five pecks were required to the line-orientation comparisons (the 5th peck to either key determined the pigeon's choice). For four of the pigeons, vertical lines were correct following a yellow sample and horizontal lines were

correct following a blue sample (see middle panel of Fig. 1). The contingencies were reversed for the remaining pigeons. Following choice of the vertical or horizontal-line comparison, the center key was illuminated with an orange hue and the pigeon was required to peck it once. If the comparison choice had been correct, the pigeon received 2-s access to mixed grain and the ITI. If the comparison choice had been incorrect, the pigeon received the ITI alone.

Each session consisted of 96 trials with an equal number of trials initiated by blue and yellow samples. The vertical- and horizontal-line comparison stimuli appeared equally often on the right and left response keys and their position varied randomly over trials. The first 72 trials were symbolic matching-to-sample trials. The last 24 trials served as refresher trials and were identical to Phase 1 trials. Pigeons were trained until they reached a criterion of 90% correct on all four trial types for two consecutive sessions. The pigeons then received training with the Phases 1 and 2 trials randomly mixed until they reached a criterion of 90% correct on all four trial types for two consecutive sessions.

1.3.3. Probe trials

During testing there were 104 trials per test session: 48 Phase 1 trials, 48 Phase 2 trials, and 8 probe trials. On probe trials, yellow and blue hues were presented on the center response key followed by vertical and horizontal-line comparisons and comparison choice was followed by presentation of the orange hue on the center key (as in Phase 2); however, a single peck to the center key was followed by the red and green comparison stimuli (rather than immediate reinforcement, see bottom panel of Fig. 1). Choice of either the red or green comparison stimulus was reinforced non-differentially (50% of the time). There were 12 test sessions.

2. Results

2.1. Training

It took the seven pigeons between 10 and 34 sessions to reach criterion in Phase 1 ($M = 23.00$, S.E.M. $= 3.39$) and between 16 and 89 sessions to reach the criterion in Phase 2 ($M = 54.29$, S.E.M. $= 33.79$). During Phase 1 training, each pigeon was observed while performing the spatial-sample matching task. All pigeons stood in front of the center key and reached to the left or right to peck the sample placing them in a good position to peck the center key again and then peck the side key that had the appropriate color. Thus, there was no evidence that any of the pigeons stood in front of the lit side key sample as an aid to remember where it had pecked after the sample was turned off.

By the end of Phase 1 training the pigeons were performing at a high level (94.7% correct, S.E.M. $= 0.97$, pooled over the last 5 training sessions). Similarly, by the end of Phase 2 training the pigeons were performing at a high level (97.1% correct, S.E.M. $= 0.59$, pooled over the last 5 training sessions).

2.2. Probe trials

On the first test session (involving the first 8 probe trials) the pigeons chose correctly on 62.5% of the trials. Over the first 6 test sessions (48 probe trials), the pigeons correctly reported the location that they had recently pecked 63.1% of the time, as indicated by a one sample, two-tailed t-test, $t(6) = 3.11$, $p = 0.02$. Over all 12 test sessions (96 probe trials) the pigeons correctly reported the location that they had recently pecked 60.6% of the time, a difference that was statistically significant, $t(6) = 3.57$, $p = 0.01$. Although the pigeons' percentage correct dropped from the first 6 test sessions (63.1%) to the last 6 test sessions (58.0%) the difference was not statistically significant, $t(6) = 1.22$, $p = 0.27$. Furthermore, the fact that
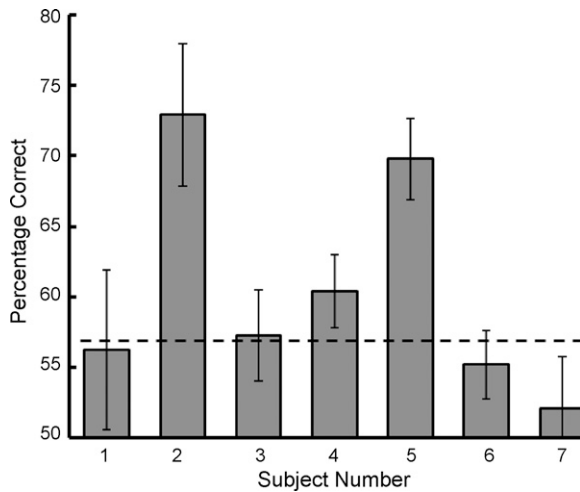
Fig. 2. Probe data pooled over the 12 test sessions for each of the pigeons. The dotted line represents the level of probe trial performance that is statistically different from 50% at the 0.05 level.

the pigeons' performance on the first test session was quite similar to their performance on all 12 of the test sessions suggests that the nondifferential reinforcement of choice on probe trials did not have a systematic effect on choice over the 12 test sessions.

Probe trial data for individual pigeons pooled over the 12 test sessions appear in Fig. 2. Although only four of the seven pigeons each chose the correct comparison stimulus at a level significantly above chance (57% correct or better, see dotted line in Fig. 2), every pigeon chose the correct comparison stimulus at a level above 50%, an effect which is statistically significant by a binomial test ($p = 0.008$).

During probe-trial testing matching accuracy on Phase 1 trials remained high (94.0% correct, S.E.M. = 3.76) as did matching accuracy on Phase 2 trials (92.3% correct, S.E.M. = 2.86). In neither case was there a significant difference in matching accuracy when compared to the last five sessions of Phases 1 and 2 training, $F < 1$ and $F(1, 12) = 2.70$, respectively.

Occasional observation of each pigeon while performing indicated that each pigeon stood in front of the center key similarly on all trials and reached to the left or the right to make its choice of sample stimulus in Phase 1 and comparison stimulus in Phase 2. That is, there was no indication that the pigeons positioned their body differently when the sample or correct comparison stimulus was on the right or the left.

3. Discussion

When pigeons were unexpectedly presented with the red and green comparisons (i.e., asked to report the location that they had most recently pecked) they responded correctly on almost 2/3 of the trials. One interpretation of this finding is that the pigeons were able to retrieve information about their past experiences. What makes this performance remarkable is the location of the comparison choice response in Phase 2 was incidental to the conditional discrimination. That is, in Phase 2 the pigeons were required to choose the correct comparison stimulus irrespective of its location. Furthermore, the common orange stimulus and its center key location that separated the conditional discrimination choice response from the unexpected probe-trial 'question' provided no indication of the possible location probe that was to follow. These results extend the findings of Zentall et al. (2001), which showed that pigeons could retrieve the action of pecking versus refraining from pecking when unexpectedly requested.

The distinction between episodic memory (memory for events) and semantic memory (memory for facts) is relatively easy to make at a subjective level. It is the difference between *knowing* something (I know how to get to work) and *remembering* something (I remember passing the intersection of Market and Main Street this morning on my way to work). Actually, in the case of animals it is difficult to distinguish between semantic memory and procedural or implicit memory because semantic memory is a form of declarative memory that in principle requires language. For the purpose of the present discussion we will use the term rule learning as an analog for semantic memory, a term that does not distinguish between implicit and explicit memory.

There has been some ambiguity over what constitutes human episodic memory. According to Tulving (1972), a person who has episodic memory must be able to identify a past personal experience in terms of what happened, where it happened, and when it happened. Although since then, Tulving (1985) has added additional cognitive features to his definition, such as self-awareness and autonoetic consciousness, those characteristics are difficult to assess in humans much less in nonverbal animals. As a result, Clayton and Dickinson (1999a,b) used what they described as Tulving's earlier *what*, *where*, and *when* criterion to establish a behavioral test of episodic-like memory in animals. Clayton and Dickinson allowed scrub jays to cache two types of food, wax worms and peanuts (what), in distinctive locations (where). The scrub jays discovered that their preferred food, wax worms, went bad over time, but the less preferred peanuts did not (when). The jays learned to recover the wax worm if relatively little time had passed but to retrieve the peanuts if more time had passed since caching. Thus, it appears that the scrub jays learned about the what, when, and where of a previous food-caching experience.

Babb and Crystal (2006) used a similar approach to study episodic-like memory in rats. They first allowed rats to enter several baited arms of a radial maze, one of which contained a unique chocolate reward. The baited arms, including the chocolate arm, changed location on each trial. Either later that day or 24 h later, with all arms open, they allowed the rats to complete the trial (enter the remaining arms which were baited) and depending on the time between the initial entries and the later test, the arm that had previously been baited with chocolate was again baited with chocolate or not. Babb and Crystal found that the rats were more likely to enter the arm that had contained the chocolate at the appropriate time (either later that day or 24 h later, depending on when they had learned that the chocolate would be replenished) than at the inappropriate time, indicating that they too had learned about the what, when, and where of a previous experience.

An important question is whether the what–where–when criterion for episodic-like memory sufficiently distinguishes it from rule learning. Most memory research with animals is thought to be rule-based. A delayed conditional discrimination involves the acquisition of a set of rules (e.g., choose the comparison color that is the same as the sample color). In principle, one could develop a task that would satisfy the what–where–when criterion for pigeons. For example, pigeons might be able to learn to match the color of the sample (red or green) when it appeared on the right response key but to mismatch the color of the sample when it appeared on the left response key (see, Edwards et al., 1985; Urcuioli, 2007). But those rules would apply only if the sample had been presented recently (e.g., within the past 2 s). If the sample had appeared 5 s before, the pigeons would be rewarded for matching the color of the sample when it appeared on the left and for mismatching the color of the sample when it appeared on the right (see White and Cooney, 1996, for a simpler version of a conditional discrimination based on the duration of the delay). Although this task would

likely be quite difficult for pigeons to acquire, we do not believe that it corresponds to what is considered episodic memory. Instead, it may consist of eight acquired rules that would be better characterized as a form of knowing (semantic memory or rule learning). This is essentially what the what–where–when task is for animals (e.g., Babb and Crystal, 2006; Clayton and Dickinson, 1999a), which suggests that successful acquisition of the task may not qualify as episodic memory.

To better characterize the distinction between episodic and rule-based memory, consider the example of episodic memory given earlier: the answer to the question "What did you have for breakfast this morning?" That memory is assumed to be episodic because there was no expectation at the time the meal was consumed (or even shortly after the meal) that the question would be asked. But now consider that the question is asked every day. It is quite possible that after several days, the responder would begin to use a language-based rule contingent on what was present on the table at breakfast. A rule such as, "remember to say, 'toast and coffee'". At the time memory is requested, one may not need to go back to the earlier episode to retrieve the memory. Instead, one need only retrieve the semantic information "toast and coffee." The difference between these two kinds of memory is when asked initially, the responder presumably had to mentally 'travel back in time' to retrieve the *remembered* episode, whereas after s/he was asked on many occasions the responder could encode the stimuli at the time of their presentation and use a *know* rule, today the answer to the question is "toast and coffee".

The critical aspect of the question is that at the time of encoding, there should be no expectation that one would be asked to retrieve the information (see White, 2002). Imagine that the question about what was eaten was asked one day and the next day the target of the question, upon seeing the questioner again, wonders if the same question will be asked. One might then consider the question to be expected (at least shortly before it is asked) but it would still likely require episodic memory because the earlier event would have to be retrieved by traveling back in time. On the other hand, if I am unexpectedly asked for my phone number, it would not require episodic memory because the requested information was encoded earlier with the expectation that a request for it would be made at a later time.

Thus, the key to this distinction is whether the question has been asked repeatedly or can be expected at the time of encoding (see Zentall, 2006). In the animal research cited (Clayton and Dickinson, 1999a,b; Babb and Crystal, 2006) subjects are trained to acquire specific rules. This is analogous to answering an *expected* question. In the case of the scrub jays, the acquired rule might have been "if the memory (trace) of having cached worms is strong, look where you cached the worms but if the memory of having cached worms is weak, look where you cached the peanuts."

Recently, Clayton et al. (2003a,b) have suggested two additional behavioral criteria that define episodic memory. In addition to the content of episodic memory (what, where, and when), they proposed that episodic memory also have structure and flexibility. The term structure suggests that the three components of episodic memory, what, where, and when, form an integrated unit. That does seem reasonable for an episodic memory because it implies that the information is retrieved as a whole rather in separate parts, however, how one would assess such a unit is not clear.

The second criterion, flexibility, suggests that if one is given new information, about the status of an outcome, one should be able to modify one's behavior accordingly (see Babb and Crystal, 2006). Although flexibility can be considered an important cognitive ability, it is not clear how it is either a necessary or sufficient condition for episodic memory. In a typical devaluation experiment (see, e.g., Colwill and Rescorla, 1985) rats trained to make response (A) for one kind of pellet (X) and a different response (B) for a different kind of pellet (Y) will show flexibility in responding depending on whether they recently been fed large amounts of A or B.

What distinguishes the current experiment (see also Singer and Zentall, 2007; Zentall et al., 2001) from the others is the use of an unexpected question at the time of encoding. On occasional probe trials, after choosing a line-orientation following the yellow or blue sample, the pigeon is unexpectedly presented with the red and green comparison stimuli. This is analogous to unexpectedly asking the pigeon if it can remember which side key it had recently pecked, much like asking a person, "What did you have for breakfast this morning?" It is important that the question be unexpected not because expected questions cannot be answered using episodic memory but because if the question is expected, one cannot exclude the use of semantic or rule-based memory to answer the question. Furthermore, unlike the training procedures used in the what–where–when research, the present research involved infrequently presented and nondifferentially reinforced probe trials.

Is it reasonable to argue that the probe trials were unexpected over the 96 probe trials that occurred in Phase 3? Unfortunately, there is no means of obtaining an adequate sample of the pigeon's choice behavior while at the same time ensuring that the probe trials are completely unexpected. The fact that there were only 8 probe trials scattered among 96 training trials suggests that they were unpredictable within a session, however, better evidence comes from the pigeons' performance on the first test session. Pigeons chose correctly on 62.5% of the probe trials on Session 1 of Phase 3, a level that was very similar to the level of accuracy over the 12 test sessions (60.6%).

One might argue that episodic memory is typically associated with memory for an event that has taken place sometime before. The question about breakfast this morning would usually be asked minutes or even hours after the event and some episodes can be retrieved years after the event. But it is not clear in what sense a long delay between the event and the retrieval is necessary to conclude that the memory is episodic. Imagine the following scenario: I am about to leave the house and I notice that I do not have my glasses. In my mind's eye (episodically) I can retrace my steps and recall that just before I got ready to leave, I had answered the phone in the kitchen so I return there to look for my glasses. Thus, to qualify as episodic, it should not be necessary to be able retrieve a distant memory. In fact, Baddeley and Wilson (2002) have proposed that an important component of working memory is an episodic buffer. Thus episodic memory can be thought of as an integral component of both working and reference memory.

One further point should be made about the present experiment as well as Singer and Zentall (2007). Our earlier research (Zentall et al., 2001) involved what was nominally a 0-s delay between the pecking and not-pecking behavior that was retrieved. In the present experiment, almost 2 s elapsed on average between the to-be-retrieved response and the unexpected request to retrieve it, lending added credibility to the proposition that memory was involved.

The results of the present experiment and those of Zentall et al. (2001) and Singer and Zentall (2007) may not qualify as a rigorous demonstration of episodic memory in nonhuman animals in the same way that it occurs in humans because language ability allows one to probe beyond the simple question to better distinguish between the semantic memory ("I had toast and coffee for breakfast. I must have because that's what I always have.") and episodic memory ("I had toast and coffee for breakfast. I remember because I burned the toast."). However, as we refine the conditions under which we can demonstrate memories that likely cannot be accounted for using semantic or rule-based processes, we can

approach the kind of evidence that will allow us to conclude that the ability to recover memories episodically does not inevitably distinguish humans from other animals.

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