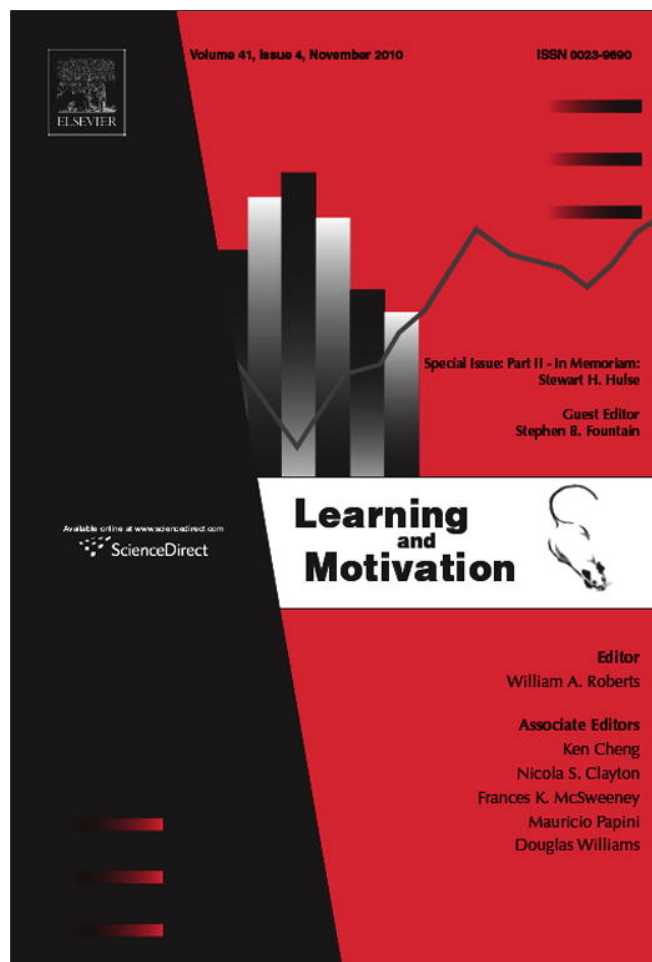


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Coding of stimuli by animals: Retrospection, prospection, episodic memory and future planning

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ABSTRACT

When animals code stimuli for later retrieval they can either code them in terms of the stimulus presented (as a retrospective memory) or in terms of the response or outcome anticipated (as a prospective memory). Although retrospective memory is typically assumed (as in the form of a memory trace), evidence of prospective coding has been found when response intentions and outcomes are particularly salient. At a more abstract level is the question of whether animals are able figuratively to travel back in time to recover memories of past events (episodic memory) and forward in time to predict future events (future planning). Although what would constitute adequate evidence of episodic memory and future planning is controversial, preliminary evidence suggests that animals may be capable of both forms of subjective time travel.

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When animals use past experiences to make current decisions, the memory is sometimes referred to as retrospective. If they use those past experiences to anticipate future responses, it is often called prospective memory. A distinction between retrospective and prospective memory can be made in principle by asking, when animals are required to delay a response, what do they remember during the retention interval. Do they remember the characteristics of the preceding event, retrospectively, or do they remember what response they will make at the end of the retention interval, prospectively? This question, first clearly articulated by Honig and Thompson (1982), has important implications for the nature of coding processes in animal memory. Specifically, if animals have the capacity to encode prospectively it suggests that they have the ability to represent future events.

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Retrospective versus prospective memory

Pavlovian conditioning

The simplest case of the anticipation of future events is Pavlovian conditioning. In Pavlovian conditioning, when a neutral stimulus (a conditioned stimulus, CS) is paired with a biologically important event (an unconditioned stimulus, US) that produces an unconditioned response (UR), one often sees evidence of the anticipation of the US in the form of a response (a conditioned response, CR) made to the CS. Although Pavlovian conditioning has often been thought of as a process involving simple reflexive responses, and thus having few cognitive implications, recent evidence suggests that the nature of what is learned can be quite complex (see e.g., Miller & Matzel, 1988). Nevertheless, the response measure used in Pavlovian conditioning is typically a reflexive response similar to that produced by the US. Better evidence for a prospective memory process would be obtained if a future event could serve as a cue for an instrumental choice response.

Simple versus conditional delayed discriminations

Honig and Wasserman (1981) tested pigeons for prospective memory using an instrumental go/no-go procedure. They trained one group of pigeons on a delayed conditional discrimination (or successive matching task) in which an initial stimulus (or sample) indicated which terminal stimulus (or comparison) would be followed by food. Thus, a red or green sample stimulus indicated whether pecking the single stimulus that followed (vertical or horizontal lines) would be reinforced. If the sample was red, then pecking the vertical lines but not the horizontal lines would be reinforced. If the sample was green, then pecking the horizontal lines but not the vertical lines would be reinforced.

A second group of pigeons was trained on a delayed simple discrimination involving the same stimuli but the contingencies of reinforcement were different. In the delayed simple discrimination, the same red or green sample stimulus was presented at the start of each trial but it indicated whether reinforcement would follow or not (independent of the stimulus that followed the color). Thus, for example a red sample indicated that pecking either line orientation would be reinforced, whereas a green sample indicated that pecking neither line orientation would be reinforced.

Honig and Wasserman (1981) argued that once the tasks had been well acquired and a delay was introduced between the hue sample and the line-orientation comparison stimulus, if the pigeons were remembering the samples during the delay (i.e., they were coding the samples retrospectively) the retention functions for pigeons performing the delayed conditional discrimination and those performing the delayed simple discrimination should look quite similar. That is, memory for the samples should decline similarly with increasing delay. On the other hand, if the pigeons were remembering a response intention—what they were going to do at the end of the retention interval (i.e., they were coding the comparisons prospectively) then the task for the pigeons performing the delayed simple discrimination should be easier (a decision to peck or not peck) than for pigeons performing the delayed conditional discrimination (e.g., a decision to peck if the comparison stimulus was vertical lines but to refrain from pecking if it was horizontal lines).

Honig and Wasserman (1981) found that the retention functions for the pigeons that had acquired the delayed simple discrimination were quite shallow, whereas those for the pigeons that had acquired the delayed conditional discrimination declined more rapidly with increasing delay (see Fig. 1), and they concluded that the pigeons were prospectively coding their response intentions.

However, Urcuioli and Zentall (1992) noted that the difference between the delayed conditional discrimination and the delayed simple discrimination involved more than a difference in response intentions. In the case of the delayed simple discrimination, the pigeons could not only develop an intention to peck or refrain from pecking, they could also develop an expectation of getting fed if the sample was red and of not getting fed if the sample was green. During acquisition, the pigeons may have learned that if they expected to get fed they should peck and if they expected not to get fed they should refrain from pecking. Thus, the fact that there were differential outcomes associated with the two samples may have mediated responding to the comparison stimuli.

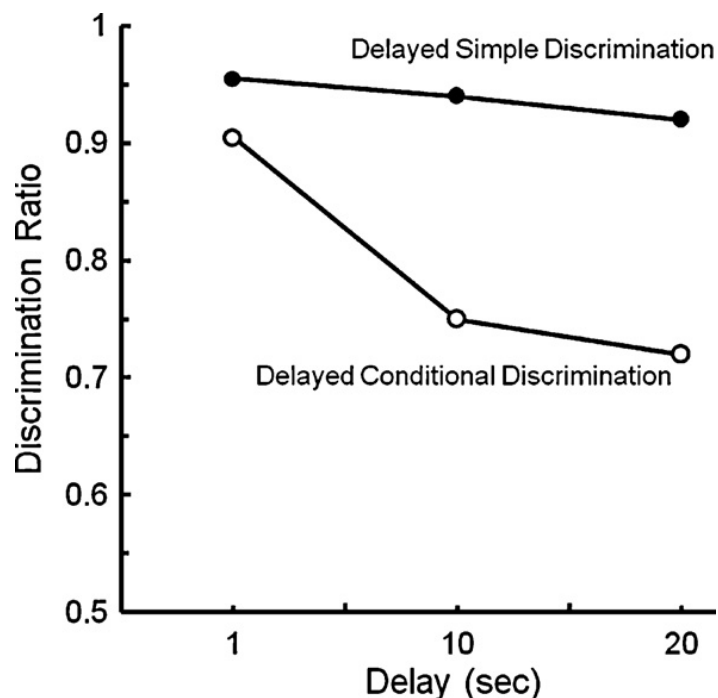


Fig. 1. Retention tests for pigeons trained on a successive delayed simple discrimination compared with retention tests for pigeons trained on a successive delayed conditional discrimination (see text). The discrimination ratio is the proportion of responses on reinforced trials to total responses (after Honig & Wasserman, 1981).

To test this hypothesis, as part of a larger study, Urcuioli and Zentall (1992) trained two groups, one trained with a delayed simple discrimination as did Honig and Wasserman (1981) and the other also trained with a delayed simple discrimination but the extinction schedule associated with two of the trial types was replaced with a differential reinforcement of other behavior schedule (i.e., on those trials, the absence of responding was reinforced). Thus, the outcomes following red and green samples were no longer differential, only the response required was differential.

Urcuioli and Zentall (1992) found that the pigeons trained with differential outcomes (food following one sample, no food following the other) produced high and flat retention functions similar to the retention functions reported by Honig and Wasserman (1981), whereas those trained with food outcomes following all correct responding (pecking following one sample, the absence of pecking following the other) produced retention functions that declined more rapidly with increasing delay similar to those reported by Honig and Wasserman following delayed conditional discrimination training (see Fig. 2). Thus, the prospectively coded differential response intentions were insufficient to account for the differences in retention functions reported by Honig and Wasserman. On the other hand, if differential outcomes result in flatter retention functions, it suggests a prospective memory process because the outcome, like the response intention, comes after the retention interval.

Delayed matching. In two-alternative matching-to-sample, presentation of a sample stimulus is followed by the presentation of two comparison stimuli. Choice of one comparison stimulus is correct following one sample and choice of the other comparison stimulus is correct following the other sample. In a typical identity matching task with, for example, red and green samples and comparison stimuli, it would be difficult to make a distinction between retrospective and prospective coding. For example, although there is evidence that identity matching with vertical and horizontal line stimuli takes more training to acquire and retention functions are steeper with increasing delays than identity matching with red and green hue stimuli (Farthing, Wagner, Gilmour, & Waxman, 1977), it is not clear whether a retrospective or prospective processes is involved because the representation of the sample and the correct comparison stimulus would likely be quite similar. However, if the relation between the sample and the correct comparison stimulus were symbolic (or arbitrary), the distinction between the two kinds of memory might be distinguishable. For example, if the samples were vertical and horizontal lines and the comparison stimuli were red and green hues, on a given trial, a pigeon could

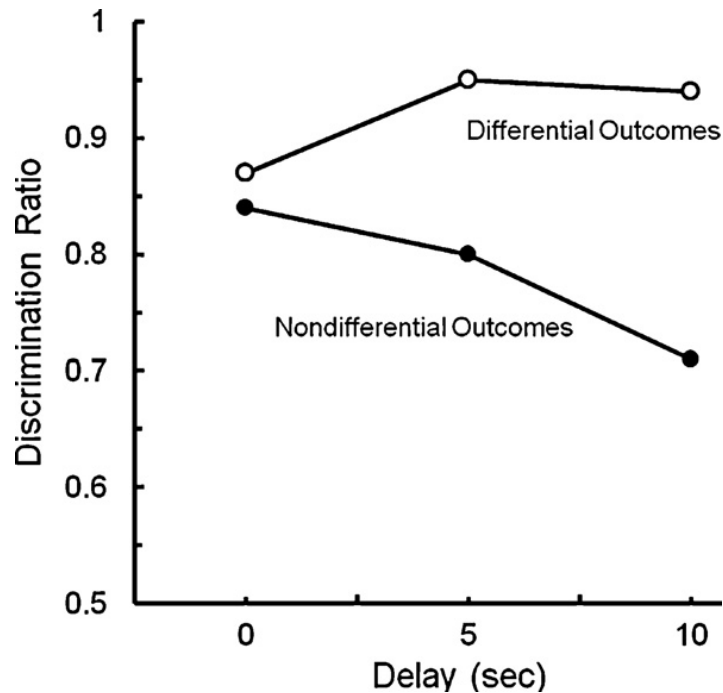


Fig. 2. Retention tests for pigeons trained on a successive delayed simple discrimination with differential outcomes or with nondifferential outcomes. The discrimination ratio is the proportion of responses on reinforced trials to total responses (after Urcuioli & Zentall, 1992).

encode the line sample (retrospectively) or it could translate the line sample into a response intention to choose the correct hue comparison (prospectively). If hues are remembered better than lines, the prospective coding of a response intention might lead to better matching accuracy with increasing delay.

Urcuioli and Zentall (1986) tested this hypothesis using a 2×2 design. For Group Hue–Hue both the samples and comparison stimuli were hues and for Group Line–Line both the samples and comparison stimuli were lines. For Group Hue–Line the samples were hues and the comparison stimuli were lines and for Group Line–Hue the samples were lines and the comparison stimuli were hues. All pigeons were trained to the same high level of matching accuracy with no delay between the offset of sample and the onset of the comparison stimuli, and then delays of variable duration were introduced. The results were quite straightforward. Both groups with hue samples showed relatively shallow retention functions, whereas both groups with line samples showed relatively steep retention functions (see Fig. 3). Furthermore, the dimension of the comparison stimuli had little effect on the slope of the retention functions. Urcuioli and Zentall concluded that under these conditions the pigeons appeared to code the samples retrospectively.

Somewhat different results were reported by Zentall, Urcuioli, Jagielo, and Jackson-Smith (1989). They asked whether the number of samples that could be presented over trials and the number of pairs of comparison stimuli that had to be discriminated and potentially remembered over trials might encourage the pigeons to use one coding strategy or the other. They included four groups (see Table 1): Group 2-2 was a standard matching group (hues for one subgroup lines for the other). Group 4-4 was required to learn to match both hues and lines. Group 2-4 had only two possible samples (hues for one subgroup, lines for the other) and the comparisons were sometimes hues and sometimes lines. Group 4-2 had all four possible samples but only two comparisons (hues for one subgroup lines for the other). The results were somewhat unexpected. Overall, the two groups that had only one of two possible samples to remember showed shallower retention functions than the two groups that had one of four possible samples to remember. This result suggests that the pigeons were retrospectively coding the samples. However, the number of comparison stimuli also made a difference, but only when the samples were the harder to discriminate lines. That is, when the samples were the easier to discriminate hues, the pigeons appeared to retrospectively code the samples because the retention

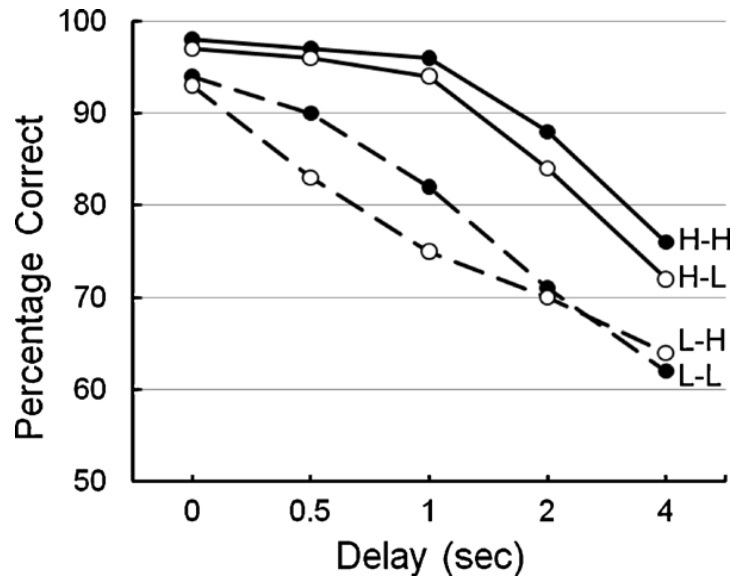


Fig. 3. Retention functions for pigeons trained on two-alternative matching with hue samples and hue comparisons (H–H), hue samples and line comparisons (H–L), line samples and hue comparisons (L–H), and line samples and line comparisons (L–L) (after Urcuioli & Zentall, 1986).

functions were flatter when there were two possible samples than when there were four possible samples, and the number of comparison stimuli did not make a difference. However, when the samples were the harder to discriminate lines, the pigeons appeared to prospectively code the comparisons (a response intention) because the slopes of the retention functions were shallower when only one pair of comparison stimuli could appear than if one of two pairs of comparison stimulus could appear. Thus, the pigeons appeared to develop a flexible coding strategy that was sensitive to the memory load.

Differential outcomes

Traditional theories of learning have emphasized the bond between a stimulus and a response or between two stimuli. According to Thorndike (1911), the function of a reinforcer is to strengthen the association between the stimulus and response and the reinforcer or outcome does not enter into the association. However, the demonstration of incentive contrast makes it clear that performance is affected by the nature of the outcome expected. That is, not only does the magnitude of reinforcement affect the rate of acquisition of the response and the performance of the response once it is acquired but the outcome obtained is also judged relative to the outcome that is expected. For example, Crespi (1942) found that rats that have been trained to run down an alley for five pellets of food but get only

Table 1
Trial types for the four groups.

2-2	2-4	4-2	4-4
R (R, G) G (G, R)	R (R, G) G (G, R) R (V, H) G (H, V)	R (R, G) G (G, R) V (R, G) H (G, R)	R (R, G) G (G, R) V (V, H) H (H, V)
	or		
V (V, H) H (H, V)	V (V, H) H (H, V) V (R, G) H (G, R)	V (V, H) H (H, V) R (V, H) G (H, V)	V (V, H) H (H, V) R (R, G) G (G, R)

Note: R = red, G = green, V = vertical lines, and H = horizontal lines. The first letter represents the sample stimulus. The two letters in parentheses represent the comparison stimuli. The first letter in parentheses is the correct comparison for that trial type.

one pellet run slower than rats that have been trained to run for one pellet of food all along. That is, the effect of the reinforcer depends not only on its absolute magnitude but also on its magnitude relative to what was expected.

As already noted, in a delayed simple discrimination, if responding following one stimulus is reinforced, whereas responding following the other stimulus is not, the retention functions are relatively flat (Urcuioli & Zentall, 1992). On the other hand, if responding following one stimulus is reinforced, whereas the absence of responding following the other stimulus is also reinforced, the retention functions are relatively steep. The only difference between these two tasks is whether the outcomes following the two behaviors are the same or different. Thus, if outcome expectations are different, they appear to facilitate memory.

There is also evidence that outcome expectation can serve as a cue for choice in two-alternative matching. In delayed matching-to-sample, the outcomes for comparison choice are generally the same for correct responses that follow each of the conditional stimuli or samples but when different outcomes follow correct responses to each of the comparison stimuli, matching acquisition may be faster (Trapold, 1970) and when a delay is inserted between sample offset and comparison onset, flatter retention functions are typically found. Furthermore, Peterson (1984) found that when the conditional stimuli in a matching task are replaced by stimuli associated with the same differential outcomes, comparison choices can be made solely on the basis of the differential anticipated outcome. In this case, outcome expectancies are able to serve as the sole basis for comparison choice because no direct association between the transfer stimuli and the choice stimuli has been trained (see Urcuioli, 2005, for a review).

Thus, it appears that following differential outcomes training, presentation of a sample evokes a representation of the expected outcome and that representation either facilitates sample memory or more likely it is at least as memorable as the sample itself because it can serve as the basis for correct comparison choice. Although differences in the value of the differential outcomes (e.g., large versus small magnitude of reinforcement) may contribute to the differential outcomes effect by creating the anticipation of a good versus a better outcome (i.e., a differential hedonic state), recent evidence suggests that the use of outcomes that differ only in the presentation of arguably neutral events such as a tone versus a light is sufficient to significantly facilitate delayed matching performance (Kelly & Grant, 2001; Miller, Friedrich, Narkavic, & Zentall, 2009; Williams, Butler, & Overmier, 1990; see also Friedrich & Zentall, *in press*).

Radial maze experiments

The radial maze task is quite different from the standard learning task. First developed by Olton and Samuelson (1976) for use with rats, it involves several (8–17) arms radiating out from a central platform (see Fig. 4). On each trial, the animal's task is to recover food placed at the end of each arm. Errors are scored for reentries into an already-visited arm.

Rats are extremely good at this task and within several trials they are able to complete a trial, often making no errors on a trial. In fact, if one is interested in identifying what the rats remember by analyzing the pattern of errors, it is necessary to interrupt the trial for several minutes before allowing the rat to complete the trial.

Cook, Brown, and Riley (1985), using a 12-arm maze, asked if the error rate would change as a function of where in a trial a delay (a trial interruption of 15 min) appeared. Their reasoning was, if the rat was remembering the places that it had already been (retrospectively) then the later in the trial the delay occurred, the more likely the rat would make an error because there would be more already-visited arms to remember. However, if the rat was remembering the places that it had yet to go (prospectively) then the earlier in the trial the delay occurred the more likely the rat would make an error because there would be more not-yet-visited arms to remember.

What they found was quite interesting. As the point of delay interpolation increased from two to four to six arms visited, the probability of making an error (corrected for opportunity) progressively increased, suggesting a retrospective memory process. However, as the point of delay interpolation increased from six to eight to ten arms visited, the probability of making an error progressively decreased, suggesting a prospective memory process (see Fig. 5). Taken together, the results suggested

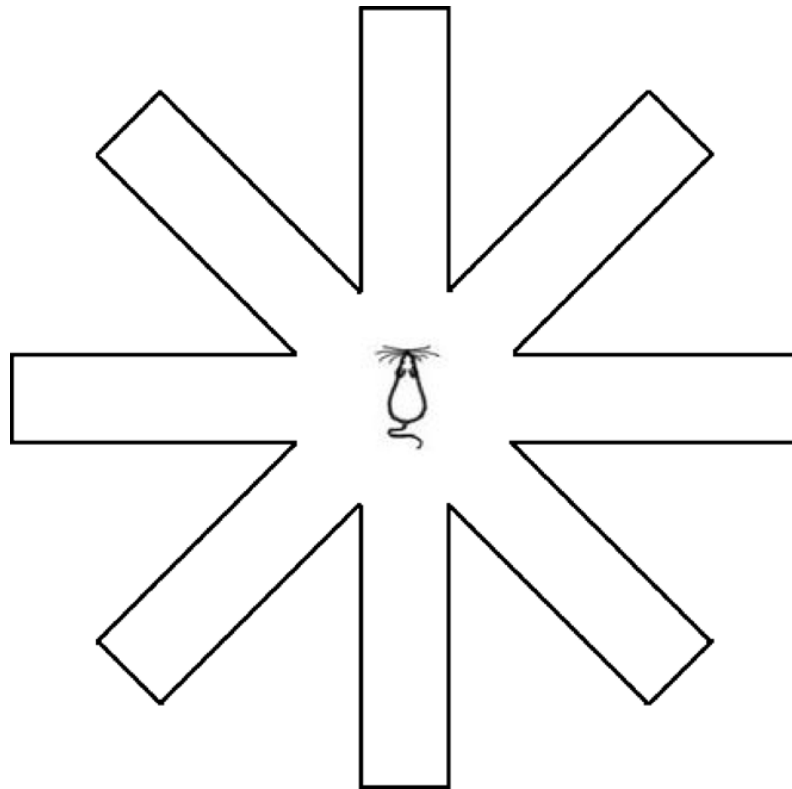


Fig. 4. A schematic of the 8-arm radial maze used by [Olton and Samuelson \(1976\)](#).

that during the delay the rats were remembering retrospectively early in the trial and prospectively later in the trial, depending on which was most efficient. When the number of arms already visited was fewer than the number of arms yet to be visited, they appeared to remember the arms already visited (retrospectively) but when the number of arms yet to be visited was fewer than the number of arms already visited, they remembered the arms yet to be visited (prospectively).

Rats have a natural tendency to shift to a different alternative following a reinforced choice (spontaneous alternation; [Dember & Fowler, 1958](#)). So for them the radial maze is an easy task to learn. Pigeons, on the other hand, have a natural tendency to stay following a reinforced choice (win stay; [Randall & Zentall, 1997](#)). For pigeons, a win-shift task should be more difficult to acquire but it would be of interest to know whether pigeons would show a similar combination of retrospective and prospective memory on such a task.

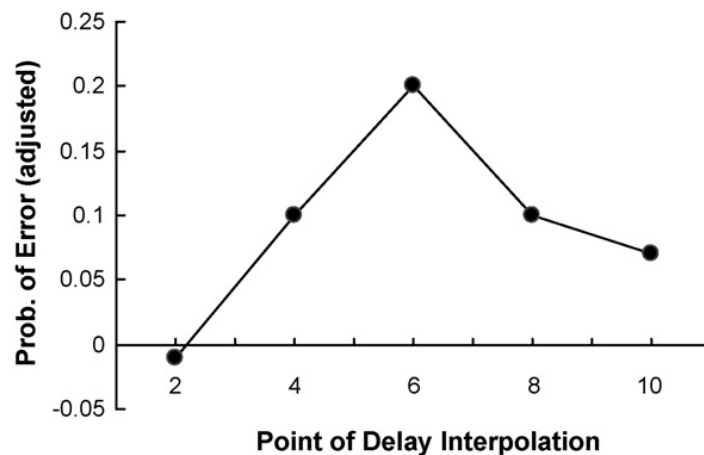


Fig. 5. The effect of a delay inserted during a trial with rats on the 12-arm radial maze as a function of the point in the trial at which the delay was inserted (the point of delay interpolation; after [Cook et al., 1985](#)).

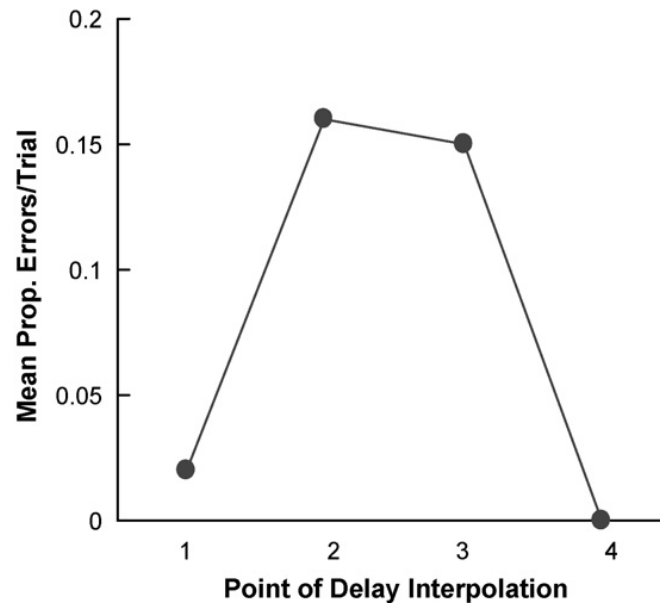


Fig. 6. The effect of a delay inserted during a trial with pigeons using the radial maze analog as a function of the point of delay interpolation (after Zentall et al., 1990).

Zentall, Steirn, and Jackson-Smith (1990) trained pigeons on a simple version of an analog of the radial maze. In an operant chamber, pigeons were presented with five response keys and choice of each was reinforced once per trial. Each trial ended when the pigeon had selected each key at least once. Pigeons received 10 trials a day separated by a 1 min intertrial interval. Once the pigeons had acquired this task, a delay was inserted at a point in the trial that varied from trial to trial. When their performance was plotted as a function of the point in the trial at which the delay was inserted, the pigeons showed a function similar to that of the rats (see Fig. 6). That is, when the delay was inserted after the first correct choice or the fourth correct choice, errors were few, but they increased when the delay was inserted after the second or third correct choice (see also Steirn, Zentall, & Sherburne, 1992).

However, conclusions about the nature of the coding process used in the radial maze task require making certain assumptions that, although reasonable, may not be correct. The most critical assumption is related to the fact that the probability of making an error by chance increases as the trial progresses. Thus, for the five alternative version of the task, on the first choice there is no chance of making an error but after one correct choice the probability of making an error by chance increases to 20% and after four correct choices the probability of making an error by chance is 80%. To correct for this difference in the number of ways in which one can make an error, the number of errors made should be divided by the number of opportunities to make an error. But this correction assumes that the care with which the pigeon chooses is constant throughout the trial and there is evidence that as the trial progresses and errors are more likely, the pigeons become more careful. If one examines performance on control trials on which there is no delay, one finds that although the absolute number of errors increases as the trial progresses, the relative number of errors (corrected for opportunity) actually decreases (Zentall et al., 1990). That is, the pigeons become more careful in making their choices as the trial progresses. One way to deal with this changing criterion for making a choice is to use errors on control trials as a measure of this change in criterion. Thus, if a delay is inserted after the second correct choice, one can subtract the number of errors made on the control trial after the second correct choice from the number of errors made on the delay trial after the second correct choice to estimate the number of errors attributable to the delay. But this calculation assumes that the pigeons will not be more careful after a delay than they were at the same point in a control trial without a delay.

One way to get around this problem is to change the procedure. Instead of allowing the pigeon to complete the trial following the delay, one can give the pigeon a choice between two response keys,

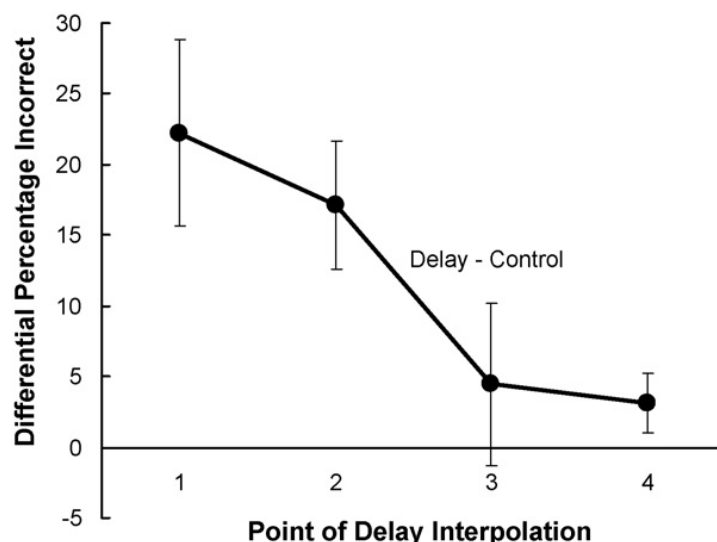


Fig. 7. The effect of a delay inserted during a trial with pigeons using the radial maze analog as a function of the point of delay interpolation and controlling for the opportunity to make an error by providing only two-alternative choices (after DiGian & Zentall, 2007).

one key that the pigeon has already chosen and the other that the pigeon has not yet chosen (see Cook et al., 1985). By giving the pigeon a two-alternative choice following each delay, regardless of the point in the trial at which the delay occurs, one does not have to correct for opportunity because the opportunities are equal and the probability of making an error by chance does not increase as the trial progresses. When we conducted such an experiment, we found that the probability of making an error decreased as the trial progressed (DiGian & Zentall, 2007), suggesting that the pigeons were using a prospective memory code throughout the trial (see Fig. 7).

However, another assumption that is made is that the order in which the response alternatives are selected by the pigeon does not affect the probability of making an error. But what if a pigeon has a strong preference for one response key? Not only will it tend to select that key first but if the delay follows that choice, it will get to choose between that key (incorrect) and one of the remaining keys (correct). However, later in the trial, say after the fourth correct choice, the pigeon will be presented with one of the already chosen keys and the remaining unchosen key. So the chance that the pigeon will be presented with the preferred, first chosen and now incorrect response key is only 25%. This would make errors following a delay more likely early in a trial and result in the appearance of a prospective coding strategy.

To avoid this problem, we repeated the experiment but prior to the delay we forced the pigeons to peck the keys in a random order on each trial. Following the delay, we tested the pigeons' memory with a two-alternative choice, an already chosen key and a not yet chosen key (Gipson, DiGian, Miller, & Zentall, 2008). Under these conditions, the pigeons produced flat retention functions. That is, the effect of the delay was to increase the probability of making an error but that effect was independent of the point in the trial at which it was inserted (see Fig. 8). Thus, it appears that under these conditions, the pigeons remembered both the choices they had already made and the choices they had not yet made, and the effect of the delay did not depend on where in the trial the delay had appeared.

The results of these experiments can be interpreted in one of two ways. First, it is quite possible that the assumptions made to calculate errors attributable to the delay were wrong. It may not be appropriate to simply subtract errors on control trials from errors on delay trials. Also, allowing the pigeons to choose alternatives prior to the delay may differentially bias the probability of making an error as a function of the point of delay interpolation.

Alternatively, it may be that the change in procedure, not allowing the pigeon to choose among all of the response keys prior to the delay and following the delay, may alter the pigeons' coding strategy. That is, the task used by Gipson et al. (2008) is more like a serial-probe-recognition task in which a series of stimuli is presented and the pigeon is given a choice between a stimulus that appeared in the

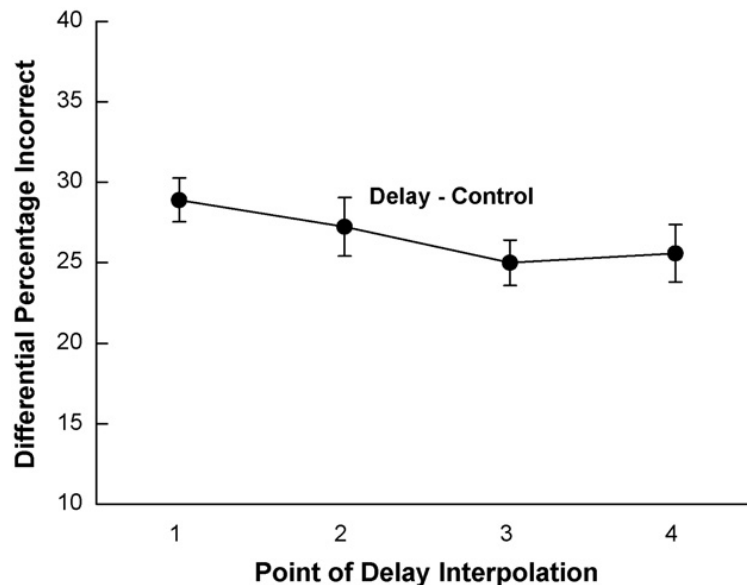


Fig. 8. The effect of a delay inserted during a trial with pigeons using the radial maze analog as a function of the point of delay interpolation with randomized pre-delay experiences and controlling for the opportunity to make an error by providing only two-alternative choices (after Gipson et al., 2008).

series and one that did not. Whether a similar argument can be made for the results of the experiments with rats is not clear. Cook et al. (1985) suggest that it cannot (but see Brown, 1992).

The importance of the finding by Gipson et al. (2008) is that one must be careful in interpreting the results of experiments that require making untested assumptions. Furthermore, if at all possible, it is best to use data that require the least amount of transformation.

Episodic memory and future planning

Episodic memory

Episodic memory is the subjective experience that humans often have when they are asked about a personally experienced past event. They may figuratively (in their mind's eye) travel back in time and imagine reexperiencing the event. Tulving (1985) has referred to episodic memory as *autonoetic* (self-knowledge) because it requires consciousness (or imagery). Episodic memory in humans can be distinguished from semantic memory which can be described as knowing facts or having rule-based memories.

It is difficult enough to study episodic memory in humans because the imagery that one experiences can only be described to others in words. In fact, the best evidence for a distinctive memory system for personal experiences in humans comes from research with brain injured individuals who have lost the ability to remember those experiences but have normal semantic memory (Vargha-Khadem et al., 1997). With humans it is assumed that consciousness is necessary for one to have episodic memory so it may not be possible to demonstrate such a capacity in animals because, in the absence of a well-developed language system, it is not clear what would constitute evidence of consciousness. For this reason, the term *episodic-like memory* has been used when referring to analogous memory processes in animals (Clayton & Dickinson, 1999).

Tulving (1972) proposed a more tractable approach to the study of episodic memory in animals. He noted that a person who has access to an episodic memory should be able to identify a past event in terms of what happened, where it happened, and when it happened. Clayton and Dickinson (1999) used this definition to test for episodic memory in scrub jays. They trained scrub jays to cache, in distinctive locations (where) for later retrieval, more preferred wax worms or less preferred peanuts (what). Because the more preferred wax worms spoiled within a couple of days, time since caching (when) was manipulated as well. As evidence of episodic memory (according to the what–where–when criterion),

the jays learned to choose the location where they cached the wax worms if the time to recovery was relatively short and to choose the location where they cached the peanuts if the time to recovery was relatively long (see also Babb & Crystal, 2006).

However, the procedures used to get animals to report what, where, and when involve training, and such training makes it possible for the memories to become semantic (or in the case of animals, rule based). To see more clearly how such training may lead to a reliance on semantic or rule-based memory, rather than episodic memory, imagine the following scenario: One sees a friend in the morning and asks him (unexpectedly) what he had for dinner last night. After a few seconds of reflection (presumably to search for the episode) he says, “Spaghetti.” Imagine now that one asks him the same question every morning. Now, at dinner one evening, while eating chicken, he may say to himself, “When I am asked tomorrow what I had for dinner I will say chicken.” The next day when asked the question, he may not have to think back about what he had for dinner because he *knows* to say chicken. That would be an example of semantic or rule-based memory rather than episodic memory and it could be the basis for performance of any task that involves training. It is for this reason that accurate performance by pigeons on a delayed conditional discrimination cannot be taken as evidence for episodic memory. Any task in which training involves what could be described as the acquisition of a set of rules cannot preclude knowing, for example, “If the sample was a vertical line then the red comparison is correct, if it was a horizontal line then the green comparison is correct.” This is true even if, in a more complex version of this task, the sample requires memory for not only *what* was the sample, but also *where* did it appear, and *when* was it presented.

Of course, one could contend that the ability to anticipate the question (e.g., “What did you have for dinner last night?”) represents a case of considerable future planning (to be discussed later). But I would argue that repeated trials involving the same question may lead to the development of an *association* that is retrieved by asking the question (rather than requiring the retrieval of an episode).

We have argued that to qualify as a clear case of episodic memory, it must not be expected that the experienced event will have to be retrieved (Zentall, Singer, & Stagner, 2008), as was the case the first time the friend was asked what he had for dinner last night. If retrieval is expected, rule-based memory cannot be eliminated as an account.

To determine if pigeons can answer an unexpected question, we first had to pretrain the pigeons to “answer a question.” To accomplish this we trained the pigeons to peck when we presented them with vertical-line samples and to refrain from pecking when we presented them with horizontal-line samples (Zentall, Clement, Bhatt, & Allen, 2001). We then trained them to choose a red comparison stimulus after having pecked the sample and to choose a green comparison stimulus after having refrained from pecking the sample. This became the source of the question “What did you just do, peck or refrain from peck?” We then gave the pigeons experience with a yellow stimulus that was always followed by food (and to which they pecked) and a blue stimulus that was never followed by food (and to which they refrained from pecking). On selected probe trials, following presentation of the yellow or blue stimulus, we presented the pigeons with a choice between the red and green comparison stimuli, effectively asking them “What did you just do, peck or not peck?” (see Fig. 9 for a schematic of the design). We found that on these arguably unexpected tests, the pigeons reliably chose the comparison stimulus according to their recent behavior. In follow-up experiments we found that pigeons could report the location that they had pecked when unexpectedly asked (Singer & Zentall, 2007; Zentall et al., 2008; see also Maki, 1979, who found that pigeons could report whether they had been fed or not when unexpectedly asked). Taken together, these experiments suggest that pigeons can retrieve the memory of recent experiences that they had not been explicitly trained to report (see also Mercado, Murray, Uyeyama, Pack, & Herman, 1998, for related research with dolphins).

Future planning

An important characteristic of human behavior is the ability to plan for a future event. When going on a trip, we can pack items that we know we will need at a later date. We can even plan for the distant future by saving money for retirement.

One can argue that planning for the future involves more than the ability to act appropriately in the present to obtain a future goal because that could be explained in terms learning with a long delay

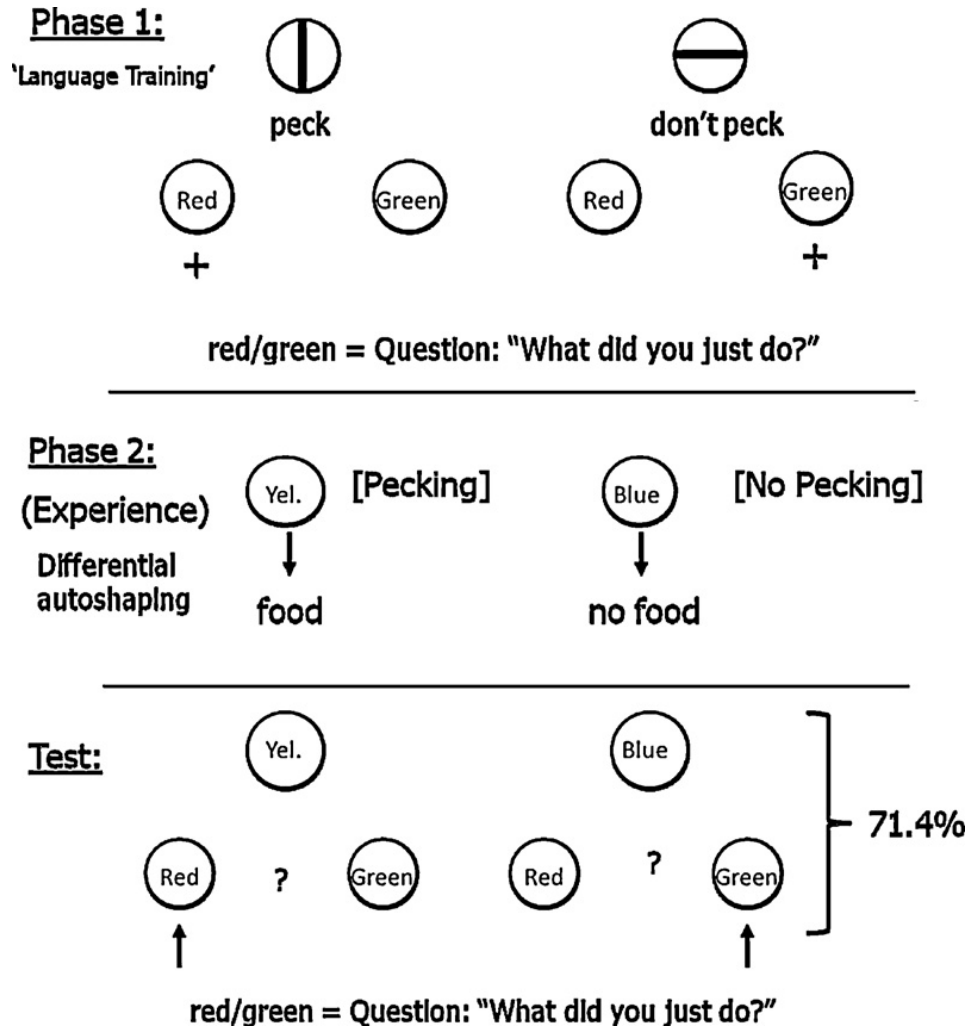


Fig. 9. Schematic of the design of Zentall et al. (2001).

of reinforcement. For a behavior to qualify as future planning, it should involve planning for a future need in the absence of that current specific need. The Bischof–Kohler hypothesis suggests that animals other than humans are not capable of anticipating their future needs (Bischof, 1978).

Roberts (2002) refers to the inability to anticipate a future need as *temporal myopia*. He gives as an example of this failure of future planning the case of cebus monkeys which are given their daily portion of food in the morning and once they have eaten all they care to eat, they often throw the remaining food outside their cage. Later in the afternoon, when they are again hungry, the remainder of their daily allocation of food is not available. Had they not thrown out the remaining food, they would have had more to eat.

Further support for the Bischof–Kohler hypothesis comes from an experimental study which showed that although macaque monkeys and a chimpanzee preferred alternatives that satisfied their current motivational state over those that did not (e.g., they preferred two bananas over one banana), they showed indifference when both alternatives satisfied their current motivational state (e.g., they did not prefer 10 bananas over 5 bananas, Silberberg, Widholm, Bresler, Fujita, & Anderson, 1998).

The problem with research of this kind is it assumes that saving food for later is generally an appropriate strategy. In natural environments, animals that live in social groups may not be able to maintain supplies of food greater than they can consume immediately. Similarly, given that primates typically live in mobile troops, it is unlikely that they would be able carry with them food that they were not able to consume at one sitting.

Of course, many animals do hoard food for future consumption (e.g., Clark's nutcrackers, scrub jays, and even rodents) but for these animals hoarding is a genetically predisposed adaptive strategy

that in the case of rodents, at least, requires little memory because the food is cached in the home burrow.

Similar evidence for the absence of future planning comes from the relative deficiency of self-control behavior in rats and pigeons (Mazur & Logue, 1978; Tobin, Chelonis, & Logue, 1993). Animals often choose small immediate rewards over larger delayed rewards, whereas humans are better able to maximize rewards (King & Logue, 1987). However, humans may have acquired those strategies through social learning (a form of rule learning rather than actual planning). Furthermore, the poor self-control often found in animal experiments may result from the conflict between predisposed impulsive behavior and planning for the future (but see Tobin, Logue, Chelonis, Ackerman, & May, 1996, for evidence that monkeys may also show self-control). That is, in nature, delayed rewards typically mean uncertain rewards (environments generally do not remain stable over time) and thus, in some species self-control may be selected against. If humans are expected to behave “rationally” it would be difficult to explain why they are often willing to incur the sometimes high cost of finance charges for the immediacy of possessing houses, cars, appliances, and even clothes. It may be that the evidence against planning in animals comes largely from the underestimation of the costs associated with delayed rewards. Thus, if one wants to argue that choice of a smaller immediate reward represents the failure to plan ahead, then humans, who clearly are able to plan ahead, often appear to be unable or unwilling to do so as well (see Green, Fry, & Myerson, 1994). Perhaps if animals (including humans) are given sufficient experience with the outcomes associated with their choices, they might make more “rational” choices (see, e.g., Eisenberger & Adornetto, 1986 for self-control training with children). Some evidence that this might be the case for animals as well comes from recent research by McKenzie, Cherman, Bird, Naqshbandi, and Roberts (2004) who found that monkeys can be trained to choose a smaller amount of food over a larger amount if (1) more food is provided later after selecting the smaller amount but not the larger amount or (2) if choosing the larger amount results in the pilfering of much of what was selected.

Tulving (2004) proposed that cognitive time travel, in the form of planning ahead, involves the ability to foresee a future need at a time when that need is not present. He called this ability the *spoon test* based on the folk story of the little girl who showed up at a party without her spoon. The spoon was needed to eat ice cream so she had to go without. The next time she is invited to a party she anticipates that she will need her spoon and remembers to take it with her.

According to this definition, the monkeys which threw their remaining food out of their cage (Roberts, 2002) were not able to plan for the future because when they were not hungry, they did not anticipate being hungry in the future and they did not save their remaining food for later. But is the spoon test a sufficient criterion for future planning?

Imagine the following variation on the spoon test. Every morning, as I get dressed, I take my car keys from the dresser and put them in my pocket. I will not need my keys until later in the morning when I go to start my car, so this should qualify as the anticipation of a future need. But, in fact, I may not have planned ahead for my future need for the keys. Instead, I may habitually grab my keys in the morning without regard for my future need. The habit may have been acquired by trial and error (occasionally arriving at my car without my keys and having to go back to retrieve my keys from the dresser), in much the same way that pigeons have acquired matching-to-sample. Learning by trial and error may also account for the McKenzie et al. (2004) finding that monkeys which learned to select the smaller amount rather than the larger amount because after a delay the initially smaller amount would be augmented or because the initially larger amount would be pilfered. Although this behavior would be considered learning with a long delay of reinforcement, it does not necessarily require future planning.

I suggest that if one wants to be sure that correct anticipation does not involve rule learning, one must test for the anticipation using a transfer of training test as was done to study episodic memory. In other words, one must ask the subject a question that was unexpected at the time the event was experienced.

Such a test has been conducted recently with scrub jays which lived in a three-compartment chamber (Raby, Alexis, Dickinson, & Clayton, 2007). Every evening they were made to spend the night in one of the end compartments. If it was the left compartment, they were fed peanuts in the morning. If it was the right compartment, they were fed dog kibble in the morning. On the test day they were

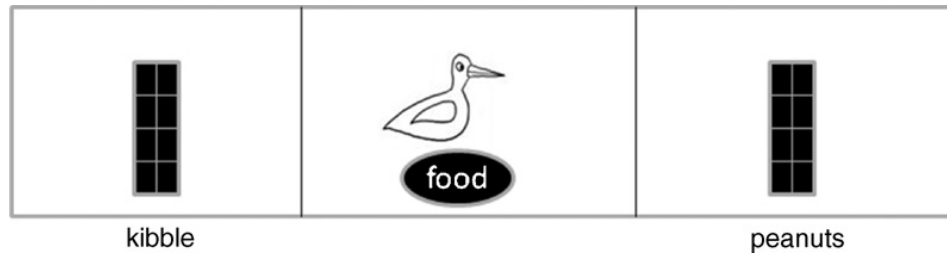


Fig. 10. Schematic of the apparatus used by Raby et al. (2007).

given peanuts and dog kibble in the evening and were given the opportunity to cache either food in either end compartment (see Fig. 10). The authors assumed that the jays would prefer to have a varied diet in the morning and asked if the jays would cache peanuts in the compartment in which they had come to expect kibble and kibble in the compartment in which they had come to expect peanuts. They found that the jays showed a significant tendency to do so. Thus, at a time when both foods were plentiful, the jays were able to anticipate that in the morning they would be fed one food if they were housed in one compartment and the other food if they were housed in the other compartment, and they prepared for either eventuality accordingly. Although Roberts and Feeney (2009) have argued that scrub jays may have a predisposition to cache food in locations where they have not encountered that food before and such a predisposition could account for their behavior, there is no evidence that these birds do have such a predisposition.

Correia, Dickinson, and Clayton (2007) provided further evidence that scrub jays can anticipate future specific hunger in the absence of current immediate needs. Scrub jays that are pre-fed one kind of food (A) will preferentially cache a different kind of food (B). However, between caching and recovery, one group of scrub jays was pre-fed food B that they preferentially cached. The next day, after they were pre-fed food A, instead of caching food B, they preferentially cached food A that they were pre-fed in anticipation of being pre-fed food B after caching and prior to recovery. Thus, in the absence of a specific hunger for food A, they preferentially cached food A, in anticipation of being pre-fed food B prior to recovery.

To date, the findings reported by Raby et al. (2007) and by Correia et al. (2007) are the best evidence for the ability of animals to plan for the future. It is interesting that it was found in a species that has evolved an excellent ability to remember where it cached food. These results have implications for research with other species. In principle, if an animal is to demonstrate that it has a particular ability, one must ensure that it “understands” that it would be useful to use that ability in the context of the procedure used. Often we design procedures from our own perspective rather than from that of the animal. If we do so, we risk negative findings. Granted, it may be difficult to take the perspective of an animal but one can attempt to design tasks that try to take advantage of the natural behavior of the species studied. The success that Clayton and her colleagues have had with the study of “time travel” in scrub jays likely resulted from the fact that they started with the natural food caching behavior of these birds and took advantage of the fact that these birds are omnivores and are thus, opportunistic feeders. Ultimately, the question is an empirical one, the answer to which depends on the results one obtains. Evidence in support of a particular ability generally indicates that one has been successful, however, the absence of evidence does not distinguish between the absence of the ability and the failure to find the right way to engage the ability.

Conclusions

With regard to the question of retrospective versus prospective memory, it appears that animals are capable of both. Under many conditions animals represent stimuli already experienced. However, it appears that they can also anticipate the occurrence not only of biologically important events but also of neutral stimuli like lights and tones. The best evidence for prospective memory comes from the use of differential outcomes as cues for comparison choice in conditional discriminations. It is particularly impressive when those differential outcomes do not have differential hedonic value because it suggests

that animals can represent those stimuli and are not just responding to the differential hedonic states that those outcomes elicit. It should be noted, however, that the evidence for flexible retrospective and prospective representation of alternatives already selected and those not yet selected in the radial maze task may rely on unconfirmed assumptions that may be problematic.

The question of episodic memory and future planning is a bit more complicated because the concepts are more abstract. The fact that we do not have an adequate definition of episodic memory makes it difficult to show evidence for it in animals. Clearly, the what, where, and when criterion is inadequate. The idea of unexpectedly asking a question about a past event has greater potential but it relies on the assumption that there is no expectation that a question would be asked about the past event. Furthermore, the evidence for episodic memory in animals obtained in this way (primarily with pigeons) involves events that occurred in the very recent past (no more than a few seconds before). Whether such effects can be found with longer delays remains to be seen.

Suddendorf and Corballis (2007) have questioned the adaptive value of episodic memory and have concluded that it provides the information needed for future planning. The ability to plan or simulate the future would have adaptive value because in many cases it would avoid trial and error learning. Although evidence for future planning in animals is quite modest, especially if it is required that the animals not be reinforced specifically for that behavior (as in a delay of reinforcement procedure), fortunately, recent evidence with scrub jays (Correia et al., 2007; Raby et al., 2007) suggests that they have some ability to plan for the future in the absence of current need.

Episodic memory and future planning in animals are exciting areas of research that challenge the comparative psychologist to discover effective procedures to assess the ability of animals to use them. What once seemed to be insurmountably difficult problems to study may be limited only by our inability to discover clever ways to take the perspective of the animals we are studying.

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