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Radial Maze Analog for Pigeons: Evidence for Flexible Coding Strategies May Result from Faulty Assumptions

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Abstract

Previous research with the radial maze has found evidence that rats can remember both places that they have already been (retrospective coding) and places they have yet to visit (prospective coding; Cook, Brown, & Riley, 1985). Such *dual coding* also has been found in pigeons using a radial maze analog in which insertion of a delay at different points during a trial affects performance differentially depending on where in the trial it is inserted. When a delay is interpolated either early or late in a trial, there is minimal disruption of performance compared with when it is interpolated in the middle of the trial. However, the analysis required with this procedure requires the assumption that if errors made on control trials are subtracted from errors made in delay trials, the remaining errors can be directly attributed to the delay. But errors may also be attributed to the changing criterion for making a response as the trial proceeds. Furthermore, the animal's tendency to choose alternatives in a systematic order may also affect its need to remember the sequence of choices made (and yet to be made) on each trial. In the present research, we avoided having to make this assumption by giving the pigeons a two-alternative choice at the time of testing and by randomly determining for the pigeon the order of predelay choices on each trial. This change in procedure resulted in comparable performance as a function of where in the trial the test occurred on both control and delay trials. The effect of the delay was to produce a general decrement in performance independent of where it occurred in the trial.

Keywords

dual coding; prospective coding; retrospective coding; radial maze; pigeons

Delayed matching-to-sample is a procedure that is often used to assess working memory in pigeons. In this procedure, the presentation of an initial or sample stimulus is followed by test or comparison stimuli and the animal must choose the comparison that corresponds to the original sample stimulus. If a delay is inserted between the sample and comparison stimuli, one can ask what the animal remembers during the retention interval. One type of memory involves events that have already occurred, such as the sample (retrospective coding). Another type of memory involves the representation of a response intention such as the intention to choose the correct comparison (prospective coding; see Honig & Thompson, 1982).

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Evidence from matching-to-sample research suggests that during a retention interval, pigeons typically represent the sample rather than correct comparison because sample discriminability but not comparison discriminability has a systematic effect on delayed matching accuracy as the delay increases (Urcuioli, & Zentall, 1986; Urcuioli, Zentall, Jackson-Smith, & Steirn, 1989). However, there is also some evidence of a systematic effect of number of comparison stimuli as the retention interval increases (Zentall, Urcuioli, Jagielo, & Jackson-Smith, 1989; for further evidence of the development of flexible coding strategies by pigeons in delayed matching see Grant, 1993; Zentall, 1998).

Working memory in rats has often involved spatial learning using the radial maze (e.g., Olton & Samuelson, 1976; Cook, Brown, & Riley, 1985). The radial maze consists of a set of elevated arms (often 8 or 12) radiating out from a central platform. Typically, each arm is baited with food and entry into a previously entered arm is considered an error. Rats acquire this task quickly, often making less than one error per trial after minimal amounts of training. To assess the nature of the rats' working memory, Cook et al. (1985) inserted a delay into selected trials by removing the rat from the maze for several minutes and then allowing the rat to complete the trial. They reasoned that if the rats were remembering the arms that they had already entered retrospectively, the likelihood of making an error should increase as the delay was introduced later in the trial because the more arms the rats had to remember, the greater the chance that they would make an error. Conversely, if the rats were remembering the arms that they had yet to enter, the likelihood of making an error should decrease as the delay was introduced later in the trial because the fewer arms the rats had to remember, the less of a chance they would make an error.

Surprisingly, Cook et al. (1985) found that as the point of delay interpolation increased from 2 to 4 to 6 arms chosen the probability of making an error also increased, but, as the point of delay interpolation increased further to 8 and 10 arms chosen, the probability of making an error decreased. They concluded that the rats used a retrospective memory code early in the trial when there were only a small number of arms already entered but they used a prospective memory code later in the trial when there were only a small number of arms yet to be entered. This dual coding strategy required that at the time the rats were removed from the maze they chose to remember past choices retrospectively or future choices prospectively, depending on which memory load was smallest.

Supporting evidence for this dual-coding strategy was found when the errors attributable to the delay were plotted as a function of the serial position of the choice prior to the delay. If the rats were retrospectively representing choices already made, one might expect later predelay choices to interfere with the memory of earlier predelay choices producing a serial position effect. However, if the rats were prospectively representing choices yet to be made one would not expect to find a serial position effect based on the order of predelay choices. In fact, Cook et al. (1985) found a serial position effect (recency) when the delay was interpolated after 2, 4, and 6 predelay choices but no serial position effect when the delay was interpolated after 8 and 10 predelay choices.

Rats have a natural tendency to use a *shift* response strategy (e.g., they have a natural tendency to spontaneously alternate in a T maze; Dember & Fowler, 1958). In fact, rats tend to explore each of the arms on a radial maze even when the arms are not baited (Timberlake & White, 1990). This may account for the rapid learning of the radial maze by rats. Pigeons on the other hand, more typically have a natural tendency to *stay* following reinforcement (Randall & Zentall, 1997). It is easier to train pigeons to return to a location they have recently pecked than to shift to a new location. For this reason, Zentall, Steirn, and Jackson-Smith, (1990) asked whether pigeons would develop a similar coding strategy when trained on an analog of a radial maze. With this procedure, on each trial a pigeon could receive reinforcement for pecking each

of 5 response locations on a response panel. Choice of an already chosen location on that trial was not reinforced.

Zentall et al. (1990) found that consistent with pigeons' natural stay response strategy, they had a difficult time learning this task. In fact, pigeons' initial performance was poorer than chance (random responding); however, they did acquire the task to a reasonable criterion. Furthermore, when delays were introduced at various points during the trial and the pigeons were allowed to complete the trial after the delay, errors attributable to the delay as a function of the point of delay interpolation showed an inverted U shaped function that was similar to that of the rats (see also Steirn, Zentall, & Sherburne, 1992). Thus, it appears that pigeons too can develop a flexible coding strategy based on reducing the number of alternatives that need to be remembered by selectively remembering retrospectively or prospectively depending on where in the trial the delay occurs. Zentall et al.'s result may be surprising because pigeons do not naturally use a shift strategy when foraging. On the other hand, the task for the pigeons should have been somewhat easier because there were only 5 possible choices to be made whereas the rats had 12 choices.

It should be noted that with the typical radial-maze procedure in which the animals are allowed to complete the trial following the interpolated delay, comparison of an animal's memory over various points of delay interpolation requires that one correct the error rate for the changing probability of making an error by chance. Thus, in the case of the procedure used with pigeons, following the first correct response, the probability of making an error by chance is only .20, whereas following the fourth correct response, the probability of making an error by chance increases to .80. To correct for this changing probability of making an error, the number of errors made should be compared to the total number of errors possible at each point of delay interpolation.

In addition to this correction for opportunity to make an error, a further correction is needed to obtain an estimate of the errors attributable to the delay. This second correction is needed because animals appear to choose more carefully towards the end of a trial than at the beginning of a trial, whether a delay is encountered or not, such that on control trials (without a delay) the proportion of errors made to total errors possible actually tends to decrease with increasing point of delay interpolation (see Zentall et al., 1990). More direct evidence for such a criterion shift was reported by Brown, Wheeler, and Riley (1989) using a signal detection analysis. Cook et al. (1985) corrected for this criterion shift by subtracting relative control-trial errors from delay-trial errors for each animal.

The potential problem with correcting for a criterion shift by subtracting the proportion of control trial errors from the proportion of delay trial errors is one must assume that the only difference in performance between control and delay trials is the delay itself. Thus, one must assume that the criterion shift on control trials is the same as the criterion shift on delay trials. Although this assumption is not unreasonable, it is also possible that the criterion shift is greater on delay trials because the animal has learned that it is more likely to make an error on a delay trial and it is thus even more careful on those trials. In fact Brown et al. (1989) argued that a combination of retrospective coding of places already visited and an artifact produced by differential criterion shift on control and delay trials could have resulted in the quadratic relation between choice accuracy and increasing point of delay interpolation. Importantly, however, this hypothesis cannot account for the serial position data reported by Cook et al. (1985).

Cook et al. (1985, Experiment 4) tested the hypothesis that the evidence for prospective coding was an artifact resulting from the incorrect assumption of comparable criterion shift by modifying their procedure such that following a delay, the rats were not permitted to complete the trial. Instead, following the delay they were given a two-alternative choice between one

arm that had already been entered before the delay and one arm that had not yet been entered. This meant that the probability of making an error by chance was .50, independent of the point of delay interpolation, and error rate could be compared over the various points of delay interpolation without having to make assumptions about the similarity between control and delay trials in the changing criterion due to changing probability of making an error by chance. In this experiment, Cook et al. (1985, Experiment 4) still found evidence of dual coding in the form of an inverted V-shaped point-of-delay-interpolation function.

Recently, DiGian and Zentall (2007) asked whether pigeons too would show evidence of dual coding if they were given a two-alternative choice following a delay with the radial-maze analog task. Thus, following each delay the pigeons were offered a choice between a response key that they already had chosen on that trial and a response key that they had not yet chosen on that trial. Surprisingly, they found evidence for prospective coding but no evidence for retrospective coding. That is, the probability of making an error decreased systematically with increasing point of delay interpolation. Furthermore, consistent with a prospective coding interpretation of these findings, DiGian and Zentall found no evidence of a serial position effect for choices made prior to the delay.

DiGian and Zentall (2007) suggested that when pigeons are given adequate experience with the radial-maze analog task, they may come to expect to make a series of choices prospectively, especially if the probability of making an error by chance is never greater than .50. If the pigeons did represent the choices yet to be made prospectively, it is possible that their performance was affected by the fact that their predelay choices were self selected. That is, it is possible that their predelay choices were not random but followed a repeating pattern from trial to trial.

When patterning of predelay choices was examined by Zentall et al. (1990), the results were inconclusive. On the one hand, when the number of different patterns pooled over trials was examined they accounted for over 80% of the 120 possible patterns and the most frequently occurring pattern of choices for each bird accounted for only 16.4% of its errorless trials. This suggests that there was not much patterning found.

On the other hand, within blocks of trials there was some evidence of patterning, for example, for each pigeon there was a high correlation between the first key pecked on trial n and the first key pecked on trial $n + 1$. Thus, it is possible that prospective coding by the pigeons resulted from their ability to choose the response keys in a similar order from trial to trial. It should be noted, however, that if the pigeons had relied solely on a preset pattern of choices from trial to trial it would have allowed the pigeons to limit their memory load to a single item (either the last response key pecked prior to the delay or the next response key to be pecked when the delay is over) regardless of the point of delay interpolation. Had this been the case, the resulting error functions would have been flat. The fact that the pigeons exposed to the two-alternative choice following the delay showed improved choice accuracy as a function of the increasing point of delay interpolation (DiGian & Zentall, 2007) suggests that a fixed memory load strategy was not adopted.

Experiment 1

If the pigeons are allowed to choose among the five response keys prior to the test, some degree of patterning is likely to result and it is possible that such patterning could affect the pigeons' memory strategy. Thus, the purpose of Experiment 1 was to examine the pigeons' coding strategies (1) in the absence of an obviously changing criterion for making a choice produced by requiring the pigeons to complete the trial following a delay and (2) when the pigeons could not develop a pattern of responding by forcing them to choose the response keys in a set random order prior to the delay. To accomplish this, the two-alternative post-delay test procedure used by DiGian and Zentall (2007) was modified to prevent patterning. At the start of each trial, a

single randomly chosen (by the computer) response key was presented to the pigeon. Five pecks to the lit response key produced reinforcement. Then the response key that had just been pecked and another randomly selected response key were presented to the pigeon. Five pecks to the new response key were reinforced and pecks to the already pecked response key were not. Following reinforcement, the two response keys that had already been pecked and another randomly selected response key were presented to the pigeon and so on. Depending on whether the trial was a control trial (0-s delay) or a delay trial and which point of delay interpolation was assigned to the trial, the pigeon received a choice between a single response key that it had already pecked and one that it had not yet pecked to determine how choice accuracy changed as a function of the delay and of the point of delay interpolation.

Method

Subjects—Six unsexed White Carneaux pigeons (retired breeders) purchased from the Palmetto Pigeon Plant (Sumter, NC) served as subjects. All of the pigeons had previous acquired delayed matching-to-sample unrelated to the procedures used in the current experiment. The pigeons were free fed until their weights stabilized and then were put on a restricted diet to reduce them to 85% of their free-feeding weights. The pigeons were housed in a colony room kept at a constant temperature, were placed on a 12:12 light-dark cycle, and were cared for in accordance with University of Kentucky animal care guidelines. Grit and water were provided ad lib in their home cages.

Apparatus—A standard operant chamber (BRS/LVE, Beltsville, MD) was used. The interior dimensions of the chamber were 35 cm high, 30 cm deep, and 35 cm wide. A houselight was located in the center of the ceiling 13 cm from the response panel and 16 cm from the door of the chamber. The response panel contained 25 response keys that were arranged in a 5 × 5 matrix. Five keys were used during the experiment, the four corner keys and the key in the center of the matrix. Each key was 1.6 cm in diameter with 3.1 cm separating the centers of adjacent keys. Each key was illuminated with a hue (blue on the top left, red on the top right, green on the bottom left, yellow on the bottom right, and white in the center). The hues remained in those locations for all of the pigeons throughout the experiment. Thus, hue and spatial location provided redundant cues (see Zentall et al., 1990). A feeder provided mixed grain through a central opening located 6 cm above the floor of the chamber. The feeder was 5.7 cm high and 5.1 cm wide.

Procedure

Pretraining: During the first phase of pretraining, one key was illuminated at a time. A single peck to the illuminated key turned it off and resulted in 1.5 s access to mixed grain followed immediately by the illumination of a different key. After each key had been pecked once, there was a 10 s intertrial interval (ITI) during which the houselight was illuminated. The first session consisted of two trials. They were then given two sessions each with 12 trials, and the ITI was increased to 60 s. The peck requirement was then increased to three pecks for two sessions and to five pecks for two more sessions.

Training: During the first phase of training, at the start of each trial a single randomly selected key was lit and five pecks to the lit key resulted in reinforcement. Following reinforcement, the first lit key and another randomly selected key were lit and the pigeon was required to peck the newly lit key. Choice of the originally lit key resulted in a 1.5 s time out and repeat of the choice. Reinforcement followed choice of the newly lit key, and, following reinforcement, the first two keys were lit together with another randomly selected key. At a randomly selected point in the trial immediately following reinforcement, the pigeon was tested by giving it a choice between one of the keys it had already pecked and a randomly selected key not yet presented on that trial. Reinforcement was provide for choosing the key not yet presented on

that trial. Choice of the previously chosen key was not reinforced and was considered an error. A 60 s ITI, during which the houselight was illuminated, followed the test. Each session consisted of 12 trials, three of which involved each of the four points in the trial at which the test could occur (i.e., with the test after 1, 2, 3, or 4 keys had been chosen). The pigeons were each trained to a criterion of 80% correct or above on each trial type. These trials, without a delay inserted prior to test, defined the control trials.

During the second phase of training, delay trials were introduced. On a delay trial, a 15 s delay was inserted prior to the two-alternative choice test. Pigeons remained on this procedure for 10 sessions.

The third phase of training was similar to the second phase except the delays were increased to 30 s. Pigeons remained on this procedure until they reached a criterion level of 80% correct or above on all trial types.

The fourth phase of training included an alternating schedule of sessions with control trials (0s delay) and delay trials (30 s delay) every day. The pigeons received training with these alternating sessions for a total of 110 sessions, 55 control (0 s delay) sessions and 55 delay (30 s delay) sessions.

Results

Acquisition—The pigeons took an average of 28.8 sessions ($SEM \pm 2.73$) to acquire the original training task (without delays).

Delay Testing—The percentage of errors was calculated for each bird at each point of delay interpolation on data from the last 10 control (0s delay) sessions and the last 10 delay (30s delay) sessions. As can be seen in Figure 1, errors on control trials were lower than they were on delay trials and there was a small effect of point of delay interpolation.

A two-way repeated measures analysis of variance (ANOVA) was performed on the test data with point of delay interpolation (PDI, 1, 2, 3, or 4) and Condition (control vs. delay) as factors. The analysis indicated that there was a significant main effect of condition, $F(1, 4) = 437.5$, $p < .001$, and a significant main effect of PDI, $F(3, 12) = 4.45$, $p = .02$, however, the PDI X Condition interaction was not statistically significant, $F < 1$.

A separate repeated measures ANOVA was performed on the data from delay trials relative to chance. The analysis indicated that delay performance was significantly better than chance, $F(3, 15) = 10.32$, $p = .02$, and that the difference from chance did not vary significantly as a function of the point of delay interpolation, $F(3, 15) = 1.33$, $p < .05$.

Serial Position Data—For the last 20 sessions of delay testing (10 delay and 10 control sessions) errors were divided according to their serial position prior to test. The proportion of errors at each serial position was calculated by dividing the number of errors by the number of correct choices plus the number of errors at each serial position for each point of delay interpolation and the results were plotted in Figure 2.

For delay trials, the serial position of errors was analyzed using one-way repeated measures ANOVAs for each point of delay interpolation beyond the first. At PDI 2 and PDI 3, the effect of serial position was not significant, $F(1, 5) = 1.29$ and $F < 1$, respectively. There was a significant effect of serial position, $F(3, 15) = 5.11$, $p < .05$, at PDI 4, however, neither the linear component of the serial position effect, $F(1, 15) = 3.46$, $p > .05$, nor the quadratic component, $F < 1$, was statistically significant. Thus, there was no consistent (interpretable) change in error rate as a function of serial position.

To get an estimate of the serial position effect attributable to the delay, the proportion of control trial errors was subtracted from the proportion of delay trial errors at each serial position and the difference scores were analyzed using one-way repeated measures ANOVAs. The analyses indicated that there were no significant effects of serial position at PDI 2, 3, or 4, $F < 1$, $F < 1$, $F(3, 15) = 2.51$, $p > .05$, respectively. The absence of systematic serial position effects is consistent with the absence of a retrospective coding strategy.

Discussion

The purpose of Experiment 1 was to examine the performance of pigeons on an analog of the radial maze. Earlier research by Zentall et al. (1990) had suggested that pigeons, much like rats, are capable of dual coding. That is, they can remember locations to which they have already been (retrospectively) or locations that they have yet to visit (prospectively), depending on which represents the smaller memory load (see also DiGian & Zentall, 2007; Steirn et al., 1992). More recently, DiGian and Zentall (2007) found that when a more direct measure of performance at the different points of delay interpolation is used, one that equates the probability of being correct by chance, over the different points of delay interpolation, pigeons show evidence of prospective coding but not retrospective coding.

In the present experiment we prevented the pigeons from developing a pattern of pre-delay choices by randomly selecting the order of pre-delay responses for them. The resulting error rate showed a small but reliable decrease as a function of PDI but more important the difference between control and delay performance did not vary significantly as a function of the point of delay interpolation. Thus, it appears that when it is not necessary to make assumptions about the similarity of criterion shift as a function of increasing point of delay interpolation on delay and control trials and when the pigeons cannot choose the order in which they peck the response keys, they do not differentially remember the keys already pecked and the keys not yet pecked. That is, in the present experiment there was no evidence of either retrospective or prospective coding.

The fact that the pigeons appeared to be more accurate on earlier PDIs than on later PDIs on both control and delay trials suggests that there may be general interference as a function of the retrospective memory load; however, the fact that it occurs equally on control trials and on delay trials suggests that it is not a memory effect. Furthermore, the serial position data from the present experiment are consistent with the absence of retrospective coding. If retrospective memory load were responsible for the decline in accuracy with increasing PDI, one might expect a serial position effect (i.e., either a primacy effect or a recency effect) but none was found. Although the absence of a serial position effect could reflect the prospective coding of choices not yet made (see Cook et al., 1985), there is no evidence of prospective coding in the analysis of errors at the different points of delay interpolation. That is, there is no evidence of a decrease in errors with increasing point of delay interpolation.

Experiment 2

A potential problem in interpreting the results of Experiment 1 is the high error rate found on delay trials. Although accuracy on delay trials was significantly better than chance and there was no effect of PDI on delay trials, the error rate on delay trials averaged over 40% when pooled over PDIs and it reached 47% at PDI4. Thus, it is possible that an interaction between delay and PDI was obscured by a ceiling effect. To investigate this possibility, in Experiment 2 we repeated the training procedure used in Experiment 1 but we tested the pigeons with a shorter delay (10 sec) that would still produce a decrease in choice accuracy but would result in a level of choice accuracy sufficiently below 50% to allow for the unobstructed appearance of a Delay X PDI interaction were one to be present.

Method

Subjects and Apparatus—Six subjects similar to those used in Experiment 1 took part in Experiment 2 and they were cared for similarly as well. The apparatus was the same as that used in Experiment 1.

Procedure—The procedure was similar to that used in Experiment 1 with the following exceptions. When delay sessions were introduced, the delay was 10 sec throughout testing. In Experiment 2, the pigeons received 60 sessions of training with alternating control and delay sessions (30 control and 30 delay sessions).

Results

Acquisition—The pigeons took an average of 35.3 sessions ($SEM \pm 4.74$) to acquire the original training task (without delays).

Delay Testing—The percentage of errors was calculated for each bird at each point of delay interpolation on data from the last 40 sessions (the last 20, 0 sec delay control sessions and 20, 10 sec delay sessions). As can be seen in Figure 3, there were fewer errors on control trials than there were on delay trials and there was a small effect of point of delay interpolation. A two-way repeated measures ANOVA was performed on the test data with point of delay interpolation (PDI, 1, 2, 3, or 4) and Condition (control vs. delay) as factors. The analysis indicated that there was a significant main effect of condition, $F(1, 5) = 2034.0$, $p < .001$. However, the effect of PDI was not statistically significant, $F(3, 15) = 3.05$, $p = .06$, nor was the PDI X Condition interaction, $F < 1$.

Serial Position Data—For the last 40 sessions of testing (20 delay sessions and 20 control sessions) errors were divided according to their serial position prior to test. The proportion of errors at each serial position was calculated by dividing the number of errors by the number of correct choices plus the number of errors at each serial position for each point of delay interpolation and the results were plotted in Figure 4.

For delay trials, the serial position of errors was analyzed using one-way repeated measures ANOVAs for each point of delay interpolation beyond the first. The effect of serial position was not significant at PDI 2, PDI 3, or PDI 4, all $F_s < 1$. Thus, there was no evidence for a retrospective memory process in the error rate as a function of serial position.

To get an estimate of the serial position effect attributable to the delay, the proportion of control trial errors was subtracted from the proportion of delay trial errors at each serial position and the difference scores were analyzed using one-way repeated measures ANOVAs. The analyses indicated that there were no significant effects of serial position at PDI 2, 3, or 4, $F(1, 5) = 1.62$, $F(2, 10) = 3.41$, $F < 1$, respectively. Again, the absence of systematic serial position effects is consistent with the absence of a retrospective coding strategy.

Discussion

The results of Experiment 2 are consistent with those of Experiment 1. The significant effect of delay indicates that a 10 sec delay was sufficient to produce a large drop in accuracy with this task. Although the effect of PDI was not quite significant, it was in the same direction as it was in Experiment 1. More important, once again there was not a significant interaction suggesting that the introduction of delays did not result in the use of either dual coding as suggested by the results of Zentall et al. (1990) or prospective coding as suggested by the results of DiGian and Zentall (2007).

General Discussion

The results of the present study with pigeons differ somewhat from results reported by Cook et al. (1985) with rats. In Experiment 4 of Cook et al., a procedure was used that was similar to that used in the present study. As in the present experiment, the rats were forced to enter the arms of the maze in a randomly predetermined order prior to the delay (or prior to the test on control trials) and all trials involved a two-alternative test involving a choice of one arm already entered and one arm not yet entered. Under these conditions Cook et al. found evidence for dual coding. Relative to control trials, the error rate on delay trials increased from PDI 2 to PDI 4 and again from PDI 4 to PDI 6 but it then began to decrease from PDI 6 to PDI 8 and it decreased still further from PDI 8 to PDI 10.

Although the reason for the difference between the performance of rats and pigeons is not clear, there are at least two possibilities. The most interesting may be differences in the way rats and pigeons approach this *shift* task. Rats have a natural tendency to shift (see Timberlake & White, 1990), whereas pigeons have a natural tendency to stay (Randall & Zentall, 1997). Thus, rats acquire the radial maze task (without delays) very rapidly, whereas pigeons do so with considerably difficulty; in spite of the fact that the number of alternative responses that have been used for pigeons (5) has been fewer than those used for rats (12, Cook et al., 1985).

Brown et al. (1989) argued that rats actually code the choices that they have made retrospectively and the evidence for prospective coding may be an artifact associated with a response bias. Nevertheless, under the present conditions, the error functions with increasing point of delay interpolation that have been found for rats appear to be quite different from those that have been found for pigeons.

A second difference between the rat and pigeon studies concerns differences in the apparatus and procedure. Although conceptually the rat and pigeon tasks are quite similar, two important differences can be noted. First, rats are placed on the central platform of an elevated maze with abundant extra-maze cues and their response alternatives involve travelling 80 cm along each arm, whereas pigeons are placed in an operant chamber in front of a panel with the response alternatives located relatively close together. Thus, the stimulus and proprioceptive feedback from having made a response on the elevated radial maze is likely to be quite different for the rats than pecking at different locations on a response panel is for the pigeons.

Second, the rats encounter reinforcement at distinctive locations (at the end of each arm on an elevated maze), whereas the pigeons encounter reinforcement at a central feeder (common for all correct responses). There is evidence that when different locations of reinforcement are correlated with different correct responses (a differential outcomes procedure), the outcomes can serve as an effective cue for choice (Freidrich, 2007; Williams, Butler, & Overmier, 1990).

It may be that the different results that were found in the present study and those reported by Cook et al. (1985) can be attributed either to inherent differences in response strategy by rats and pigeons or to procedural or apparatus differences. However, in either case, the previous findings of dual-coding by pigeons reported by Zentall et al. (1990), Steirn et al. (1992), and DiGian and Zentall (2007) as well as the findings of prospective coding alone reported by DiGian and Zentall (2007) may be attributed to the particular procedure used in those studies rather than to a general coding strategy used by pigeons when acquiring this analog of the radial-maze task.

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Figure 1.

Experiment 1: Mean adjusted errors for delay and control trials as a function of point of delay interpolation (PDI).

Figure 2.

Experiment 1: Proportion of errors attributable to the delay as a function of the pre-delay serial position at each point of delay interpolation (filled triangle, PDI 1; open triangles, dotted line, PDI 2; filled circles, dashed line, PDI 3; open circles, solid line, PDI 4).

Figure 3.

Experiment 2: Mean adjusted errors for delay and control trials as a function of point of delay interpolation (PDI).

Figure 4.

Experiment 2: Proportion of errors attributable to the delay as a function of the pre-delay serial position at each point of delay interpolation (filled triangle, PDI 1; open triangles, dotted line, PDI 2; filled circles, dashed line, PDI 3; open circles, solid line, PDI 4).