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FLEXIBLE CODING STRATEGIES IN PIGEONS: RETROSPECTIVE AND PROSPECTIVE CODING USING A RADIAL MAZE ANALOG TASK

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ABSTRACT OF DISSERTATION

Kelly Ann DiGian

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2005

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RETROSPECTIVE AND PROSPECTIVE CODING
USING A RADIAL MAZE ANALOG TASK

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ABSTRACT OF DISSERTATION
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A dissertation submitted in partial fulfillment of the
requirements for the degree of Doctor of Philosophy in the
College of Arts and Sciences
at the University of Kentucky

By
Kelly Ann DiGian

Lexington, Kentucky

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Lexington, Kentucky

2005

ABSTRACT OF DISSERTATION

FLEXIBLE CODING STRATEGIES IN PIGEONS:
RETROSPECTIVE AND PROSPECTIVE CODING
USING A RADIAL MAZE ANALOG TASK

Zentall, Steirn, and Jackson-Smith (1990) found evidence for dual coding in

pigeons in a radial maze analog task. Specifically, they found that pigeons used

retrospective coding in which previously chosen keys were remembered when a delay

was interpolated early in a trial and prospective coding in which to-be-visited keys were

remembered when a delay was interpolated late in a trial. An alternative explanation, the

criterion shift hypothesis proposed by Brown, Wheeler, and Riley (1989), suggests that

these data are consistent with dual coding because of an artifact of the correction

procedures used by Zentall et al. The criterion hypothesis suggests that retrospective

coding is used and that pigeons make choices more carefully after many choices have

been made on delay trials as compared to control trials, which creates the appearance of

prospective coding later in a trial. The present experiments tested this hypothesis using a

new testing trial procedure and new, more conservative control trials. In experiment 1,

the results of Zentall et al. were replicated using a fixed delay procedure instead of their

original progressive delay procedure. Experiment 2 used a forced choice procedure after

the delay to make the probability of making an error 50% on each trial type. Control trials also included a forced choice procedure to eliminate the assumptions required by the corrections procedure used by Zentall et al. The results were inconsistent with the retrospective coding account predicted by the criterion shift hypothesis and with the dual coding hypothesis. Instead, the results were consistent with a prospective coding account in which to-be-visited keys were remembered. These results were replicated in Experiment 3 using the pigeons from Experiment 1. The present findings have important implications for the field of comparative cognition.

KEYWORDS: Working Memory, Retrospective Coding, Prospective Coding, Radial Maze Analog Task, Pigeons

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RULES FOR THE USE OF DISSERTATIONS

DISSERTATION

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Chapter One

Introduction

The field of comparative cognition investigates parallels between behaviors that can be observed in humans and non-human animals. These behaviors are often measured in the laboratory under precisely controlled conditions. These conditions are unnatural in the sense that animals do not come in contact with testing chambers or water bottles under normal circumstances, however these conditions can be used to ask questions about how animals behave in a changing environment. For example, pigeons typically forage using a win-stay strategy, that is, they can consume large quantities of food at a central location. This strategy differs from that of rats, which is a win-shift strategy in which small quantities of food are consumed at many different locations. The laboratory can be used to ask questions about the flexibility of behavior such as how pigeons would behave in a task in which win-shift behavior is reinforced. In other words, could pigeons learn to use a more efficient strategy than their typical win-stay strategy? If so, it would suggest that there is some flexibility in their behavior that might be useful in a novel environment in which food is sparse and located in various places. One of the most studied processes in comparative cognition is memory. Of particular interest is whether flexible memory strategies can be used to solve tasks in the lab that are analogous to win-shift foraging environments. The present experiments address this issue by testing pigeons in a win-shift task.

Memory is usually divided into two broad categories, working memory and reference memory. Working memory includes memory that is being used at the current time or is stored only briefly. For example, a new phone number is typically stored in working memory until it can be written down. After it has been written down, it is often impossible to recall that number (e.g., even a minute later). Reference memory is memory that is stored for extended periods of time. One's home phone number is typically stored in reference memory and can be recalled at a later point in time (e.g., 24 hrs later).

Several different paradigms have been used to investigate memory processes in animals. In a delayed discrimination (DD) or delayed simple discrimination (DSD), an initial stimulus is presented (e.g., for pigeons, on a center key in an operant chamber) for

a fixed duration and upon stimulus termination, a test stimulus is presented. The initial stimulus predicts whether the test stimulus is followed by reinforcement or not. For example, red and green hues are initial stimuli and are followed by a white stimulus. For some pigeons, trials on which red initial stimuli are followed by the white stimulus would be followed by reward and trials on which green initial stimuli are followed by the white stimulus would not be followed by reward. In this paradigm, the initial stimuli predict on which trials reinforcement will occur and on which trials reinforcement will not occur. After reaching the training criterion, the testing phase begins. During testing, a delay is inserted between presentation of the initial stimulus and presentation of the test stimulus. The duration of the delay varies from trial to trial. The delay is expected to increase the error rate such that memory processes can be inferred from the retention function (the relation between matching accuracy and delay duration).

In a delayed matching-to-sample procedure (DMTS), an initial sample stimulus is presented. Upon completion of a response requirement (e.g., 10 pecks), the initial stimulus is terminated and is followed by the presentation of a test stimulus (comparison stimulus) on each of the side keys. A response to the positive test stimulus (as designated by the experimenter) produces reinforcement (e.g., feeder access). Upon reaching the training criterion, the testing phase begins. As with other paradigms, delays can be inserted between the sample and the comparison stimulus to increase the error rate and inferences can be made about memory processes.

In these paradigms, working memory consists of memory for events on a particular trial such as the identity of a stimulus that had been presented on that trial. This kind of memory differs from reference memory, which includes memory for information that is constant across trials. Response rules and task requirements are examples of items that could be stored in reference memory. For example, one rule might be to choose a red test stimulus after having seen a red initial stimulus. It is a rule that can be stored in reference memory and can be used over sessions.

Working Memory Codes

Many theories have been proposed and tested to explain animal working memory. Riley, Cook, and Lamb (1981) described two types of codes that can be used to achieve

accurate performance in the delayed matching-to-sample paradigm. Sample codes are representations of sample attributes that are formed during sample stimulus presentation and are recalled during test stimulus presentation to direct accurate performance. Sample codes are also called retrospective codes. Test codes are representations of the correct test stimulus that are activated upon sample presentation and are maintained through delays to guide correct responding during test stimulus presentation. Test codes are also called prospective codes. There is evidence that both retrospective and prospective codes can be used by pigeons (Grant, 1993; Honig, 1978, 1981; Honig & Thompson, 1982; Roitblat, 1993; Wasserman, 1986; Zentall, 1998; Zentall, Steirn, Jackson-Smith, 1990) and rats (Cook, Brown, Riley, 1985).

Retrospective Coding

Retrospective coding has been examined using the delayed matching-to-sample procedure (Grant, 1976, 2001; Grant & Kelly, 1998; Riley, Cook, & Lamb, 1981; Roberts & Grant, 1974; Spetch & Wilkie, 1983; Urcuioli & Zentall, 1986; Zentall, Sherburne, & Urcuioli, 1995). Two of the earliest retrospective coding theories were trace strength theory and temporal discrimination theory (Grant, 1976; Roberts & Grant, 1976). Roberts and Grant reviewed evidence that was relevant to these two theories. Trace strength theory states that a stimulus creates a memory trace that increases in strength with increasing presentation time and decreases after the stimulus has been terminated. Performance depends on the strength of the remaining memory trace at the time of testing. Temporal discrimination theory states that performance depends on the ability to discriminate which stimulus had been presented most recently. For example, if a red sample stimulus is presented on the first trial and the correct response is to choose the red test stimulus, the memory of the red sample stimulus could interfere with performance on upcoming trials in which a different sample is presented (e.g., a green sample). When a green sample stimulus has been presented and the correct test stimulus is green, the memory for the red sample could disrupt performance. According to temporal discrimination theory, performance depends on the ability to determine whether the red sample or the green sample has been presented most recently (on that trial) at the

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time of test. Both of these theories are retrospective coding theories in which memory for the sample is used to make a choice at the time of test.

Roberts and Grant (1974) tested several predictions of trace strength theory, a theory of sample coding, by manipulating sample presentation time. Trace strength competition theory suggests that matching accuracy should increase as the strength of the memory trace increases. Strength of the memory trace was expected to increase as sample presentation time increased and decrease with time since offset of the sample. During test stimulus presentation, the pigeon could make choices by comparing the current level of strength of each sample stimulus and choosing the test stimulus appropriate to the sample with the strongest trace. These predictions were supported by the results of three experiments. Matching accuracy increased as the fixed-ratio requirement increased and inserting a delay between the initial stimulus and test stimuli adversely affected performance (Experiments 1 and 2). Trace strength interaction was examined by presenting two different sample stimuli on some trials (Experiment 3). Choice of the test stimulus associated with the sample stimulus that had been presented second was reinforced. Manipulating the duration of the first sample stimulus was proposed to change its trace strength such that on some trials the memory trace of the first sample stimulus would be stronger than that of the second sample stimulus. This difference in trace strengths was expected to make pigeons more likely to choose the test stimulus associated with the first sample stimulus even though choosing the test stimulus associated with the second sample stimulus had been reinforced. The results suggest that as the duration of the first sample increased pigeons were more likely to choose the test stimulus associated with the first test stimulus. Roberts and Grant interpreted their results as support for trace strength competition theory.

Grant (1976) found additional evidence for trace strength theory by testing its predictions against predictions of temporal discrimination theory. Temporal discrimination theory predicts that the memory of conflicting sample presentations from earlier trials creates interference on the current trial. For example, performance on green sample trials would be adversely affected if the prior trial was a red sample trial in which the correct test stimulus is a red key light (conflicting trial) compared to a prior trial with a green sample on which the correct test stimulus is a green key light (non-conflicting

trial). Prior conflicting trials should create reduced matching accuracy on the current trial relative to trials that were preceded by a non-conflicting trial and the interference effect should be greater with increasing delay. Increasing sample presentation time should reduce this effect and no interference from the preceding trial is predicted when the memory from the previous trial is consistent with the correct test stimulus on the current trial. Therefore, temporal discrimination theory predicts more accurate performance on delay trials which were preceded by a non-conflicting trial. Eliminating interference from conflicting trials should reduce the rate of forgetting when tested with delays. Grant used a 2 min intertrial interval to eliminate interference from earlier trials (e.g., trial n-1 and trial n-2). Unlike temporal discrimination theory, trace strength theory predicts that testing with delays will produce reduced matching accuracy regardless of prior trial type because the memory trace will decay during the delay on all trials.

In contrast to predictions of temporal discrimination theory, matching accuracy was not affected by prior trial type. Rather, forgetting was observed on trials that were preceded both by conflicting and by non-conflicting trials. Accuracy decreased with increasing delays and increased on all trial types as sample duration increased, not just on trials that were preceded by a conflicting trial. These results support trace strength theory in which matching accuracy depends on the strength of the representation of the sample stimulus.

Another kind of code that could be used to perform delayed matching-to-sample is a test code or prospective code, for example, a representation of the correct test stimulus. Urcuioli and Zentall (1986) wanted to determine if pigeons used retrospective or prospective coding when performing delayed matching-to-sample. If pigeons are coding the sample stimuli and are using the representations of those sample stimuli to respond upon test stimulus presentation, then manipulating the discriminability of the sample stimuli should affect performance. If however, representations of the test stimuli are activated during sample presentation and are used to respond during test stimulus presentation, then manipulating discriminability of the test stimuli should affect performance. In Experiment 1, Urcuioli and Zentall showed that training pigeons with easy to discriminate hue samples facilitated acquisition and retention during delay testing relative to a group trained with line samples. In a second experiment, the results of a

between-groups design suggested that hue sample stimuli facilitated matching accuracy relative to line sample stimuli but that the test stimulus dimension did not affect performance. These results are consistent with a retrospective coding account in which sample stimuli were encoded during sample presentation and those representations were differentially forgotten during delay testing.

Further evidence for retrospective coding comes from many-to-one (MTO) DMTS procedures. MTO matching pairs more than one sample stimulus with a single comparison stimulus. For example, red and vertical line samples might be paired with a vertical line test stimulus and green and horizontal line samples might be paired with a horizontal line test stimulus. Urcuioli, Zentall, Jackson-Smith, & Steirn (1989, Experiment 1) trained pigeons to match four sample stimuli to two comparison stimuli. Group Hue learned to match red, green, vertical line, and horizontal line samples to red and green comparisons and Group Line learned to match the same samples to vertical line and horizontal line comparisons. Both groups were trained to criterion and were then tested with delays. Pigeons could form a representation of the common comparison upon sample presentation and use that representation to choose that comparison during testing. Urcuioli et al. referred to this strategy as the comparison-response hypothesis, a prospective code. If this strategy were being used, one would expect the comparison dimension to affect delayed matching accuracy (i.e., there should be better performance by Group Hue during delay testing as hues are more salient than line stimuli). Alternatively, samples that are associated with the same comparisons could evoke one retrospective representation that directs comparison choice. Urcuioli et al. referred to this strategy as derived-sample coding or common coding. Because this code is based on the relationship between samples and not comparisons, this hypothesis predicts no group differences during delay testing. The results of delay testing support a retrospective coding account. There was no effect of group on performance during delay testing, which suggests that the codes do not contain comparison stimulus information. These results support the common coding hypothesis.

Experiment 2 was designed to provide additional evidence for common coding using a transfer task. In Phase 1, pigeons were trained with red, green, vertical, and horizontal line samples and vertical and horizontal line comparisons. After reaching

criterion, pigeons were trained to match red and green samples to new comparisons, circle and dot (Phase 2). Once stable performance was reached, the pigeons were trained on a transfer task in which vertical and horizontal line samples were followed by circle and dot comparisons. For pigeons in Group Consistent these pairings were consistent with the common coding relationship that was established in Phase 1. For example, in Phase 1, red and vertical samples were paired with the vertical comparison. In Phase 2, red was paired with circle and in the transfer task, and choice of the circle comparison was reinforced after presentation of the vertical line sample. If red and vertical samples were commonly represented in Phase 1, then this common code could have been used in the acquisition of the new pairing (red and circle) in Phase 2. This pairing, common code for red and vertical with circle, could facilitate performance in the transfer task.

For Group Inconsistent, the pairings in the transfer task were inconsistent with the presumed common codes. For example, choice of the dot comparison was reinforced after vertical line sample presentation. If the red and vertical samples were commonly coded in Phase 1, then for Group Inconsistent, the common code would predict negative transfer (but see Urcuioli (1996) for a prospective coding account). Urcuioli et al. (1989) found evidence for positive transfer for Group Consistent and negative transfer for Group Inconsistent which suggests that pigeons commonly coded pairs of samples in Phase 1 based on their relationship to a single comparison.

The results of Urcuioli et al. (1989) suggested that samples associated with the same comparison are commonly represented. Zentall, Sherburne, and Urcuioli (1995) were interested in determining the exact nature of the retrospective codes. Were the samples coded independently or was one sample represented in terms of the other sample associated with the same comparison? Zentall et al. (1995) used a MTO design with food, no-food, and two hue samples to determine the nature of the relation between sample pairs. The sample stimuli were chosen because of the differences in retention functions observed when each kind of sample is used independently. When two hue sample stimuli are used parallel retention functions are typically found during delay testing (i.e., the functions for each sample decrease at the same rate over delays). However, food and no-food samples typically produce divergent retention functions in which performance on food sample trials decreases rapidly over delays, but performance on no-food sample

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trials remains high. They paired one hue and a food sample stimulus with one test stimulus and a second hue and the no-food sample with the other test stimulus. For example, some birds had to choose the circle test stimulus after food and red hue sample stimuli and the dot test stimulus after no-food and green hue sample stimuli. Hue, food, and no-food stimuli were counterbalanced across groups. The pigeons were then tested with delays. If pigeons code food and no-food samples as their hue counterparts, then delay testing should produce parallel retention functions for both sample sets. However, if pigeons code hue samples in terms of food and no-food sample stimuli, then delay testing should reveal divergent retention functions for both sample sets.

Zentall et al.(1995) found that delay testing produced divergent retention functions for both sets of sample stimuli. These results are consistent with a retrospective coding account in which hue samples are coded as the corresponding food and no-food sample stimuli. A second experiment confirmed this conclusion using a transfer design. Pigeons were first trained with food and no-food sample stimuli and the hue sample stimuli were added after achieving stable performance on food/no-food sample stimuli. After establishing accurate performance on hue sample trials, pigeons began interim training in which only hue sample stimuli were associated with new test stimuli. Pigeons were then tested with food and no-food sample stimuli and the test stimuli used during interim training. In the final test phase, pigeons were tested with delays using food and no-food sample stimuli and the original test stimuli (not those used during interim training). In the consistent condition, pigeons were trained with hue and food/no-food samples paired with test stimuli such that commonly coding the sample pairs could facilitate performance during the transfer test. Pigeons in the inconsistent condition could not use the commonly coded samples to facilitate performance in the transfer phase. If pigeons commonly coded the hue and food and no-food sample stimuli, the consistent group would transfer at a higher rate than the inconsistent group. In fact, pigeons in the consistent condition did perform better in the transfer test than those in the inconsistent condition. Performance on the transfer test suggests that pigeons commonly coded the hue and food/no-food stimulus pairs. Furthermore, divergent retention functions were found in delay testing, with performance on no-food and the no-food hue trials remaining high and flat across delays and performance on food and the food hue trials decreasing

across delays. These results suggest that the hue sample stimuli were coded as their food/no-food sample counterparts and they support a retrospective coding account in which pigeons use memory for the sample to choose a comparison after the delay.

Prospective Coding

Several lines of evidence suggest that under certain conditions, pigeons use prospective coding. Unlike retrospective coding in which the sample stimuli are coded and remembered for accurate performance at test, prospective coding involves forming a representation of the test stimulus. There are two kinds of prospective coding strategies. The first kind of prospective coding is that which is directed by the consequences of test stimulus choice. This kind of coding, referred to as the differential outcomes effect, facilitates acquisition and performance over delays. The second kind of prospective coding is the representation of the test stimuli themselves. The former will be described first.

Differential Outcomes Effect

In addition to the properties of the initial stimuli, the consequences of test stimulus choice (i.e., the rewards) can also influence learning and performance. Typically correct stimulus choices are reinforced with a common outcome. However when different outcomes follow correct choices of each test stimulus, there is evidence that the outcomes are represented prospectively. Brodigan and Peterson (1976) used a matching-to-sample procedure with red and green hues for initial stimuli and vertical and horizontal lines as test stimuli. Pigeons were rewarded with peas for a correct response following presentation of one sample stimulus and were rewarded with water for a correct response following the other sample stimulus. Pigeons were trained with this differential outcomes procedure and were then tested with delays. The group that trained with differential outcomes for each trial type performed better during delay testing than a group that was rewarded with peas and water on both kinds of trials. These results suggest that when the outcome for a correct response on one trial type differs from the outcome for a correct response on the other trial type, pigeons perform better over delays. The result implies that the differential outcomes serve as a cue for stimulus choice during delay testing. These results have been replicated and extended by others (Fedorchak & Bolles, 1986;

Peterson & Trapold, 1980; Peterson, Wheeler, & Armstrong, 1978; Peterson, Wheeler, & Trapold, 1980).

Edwards, Jagielo, Zentall, and Hogan (1982) tested whether a common outcome could form the basis of an association between a sample and a test stimulus with which it had never been paired. Pigeons were trained to match two hue samples and two shape samples to their matching comparison stimuli. In the experimental group they paired choice of the "plus" stimulus and choice of the red hue stimulus with corn reinforcement and choice of the "circle" stimulus and choice of the green hue stimulus with wheat reinforcement. This procedure was expected to create the expectation of corn after a correct response on plus and red trials and the expectation of wheat after a correct response on circle and green trials. The control group experienced corn or wheat after correct responses on all trials in an unpredictable manner. Thus it was impossible to predict which outcome would occur on a given trial. Edwards et al. used a transfer design to test whether the experimental group had formed expectations of the predictable outcomes. In the transfer phase, initial shape stimuli were paired with hue test stimuli and initial hue stimuli were paired with shape test stimuli. These pairings had never been presented in the training phase, but if the experimental group had formed expectations about the outcome, they should be able to use these expectations to choose correctly. For example, if a red hue is presented with circle and plus test stimuli, the expectation of corn produced by the red sample could produce positive transfer because in training, when pigeons in this group expected corn, they chose the plus test stimulus. The expectation of corn or wheat is a type of prospective code and positive transfer in the experimental group would support a prospective coding account of performance. In fact, the pigeons in the experimental group did show positive transfer relative to the control group. These results suggest that initial stimuli produce outcome expectancies that can serve as a cue for test stimulus choice and are evidence for prospective coding (see also Sherburne & Zentall, 1995; Zentall & Sherburne, 1994).

Honig and Wasserman (1981) examined the effect of the training procedure on the type of coding strategy. Experiments conducted using a delayed simple discrimination (DSD) procedure often reveal faster acquisition and better retention than in delayed conditional discriminations (DCD) (Honig & Wasserman, 1981). Honig and Wasserman

used equivalent DSD and DCD training procedures to ask whether the procedural differences between the tasks encourage either retrospective or prospective coding. In Experiment 1, they used a between-subjects design with red and green hue initial stimuli and vertical and horizontal line test stimuli. In the DSD group, responses to any test stimulus (vertical and horizontal lines) following one initial stimulus (e.g., red) were always reinforced and responses to either test stimulus (vertical and horizontal lines) following the other initial stimulus (e.g., green) were never reinforced. In the DCD group, reinforced responses to each test stimulus were contingent on the initial stimulus. For example, responses to vertical test stimuli were reinforced after red initial stimuli and responses to horizontal test stimuli were reinforced after green initial stimuli. The procedures encourage different types of coding in each group. In a DSD procedure the sample stimulus dictates the response to the test stimulus, however a DCD procedure requires sample and test stimulus information to respond appropriately to the test stimulus. If pigeons code retrospectively, both groups need information about the initial stimuli to respond appropriately to the test stimulus. If both groups use information about the initial stimulus to perform during delay testing, the retention functions for both groups should be similar. However, prospective coding would predict divergent retention functions for the two groups. Specifically, the DSD group could plan their responses to test stimuli upon initial stimulus presentation. They could code "respond when the test stimulus appears" to one test stimulus and "do not respond when the test stimulus appears" to the other test stimulus. These would be prospective codes. The DCD group could also use prospective coding, but the prospective codes for this group would need to include information about the test stimuli. For example, prospective codes could be "respond to the vertical test stimulus" and "respond to the horizontal test stimulus". Using this strategy, the memory load would be greater for the DCD group and should adversely affect performance during delay testing. Both groups were tested with retention intervals and the pigeons in the DSD group performed better than the DCD group. These results suggest that the DSD group used a prospective code and the DCD group used a different kind of code, either a retrospective code of the initial stimulus or a prospective code that included test stimulus information.

However, the difference in coding strategies found by Honig and Wasserman (1981) could have been caused by the ability to predict reinforced and nonreinforced trials in the DSD procedure upon initial stimulus presentation. This procedural difference makes it possible to code prospectively (plan to respond) using only sample information in DSD procedures instead of retrospectively (remembering the sample) or prospectively using sample and test information as in DCD procedures. Thus, it could have been the differential outcomes expectancies that formed upon sample presentation rather than the differential response intentions that accounted for the facilitation of the DSD group relative to the DCD group. Urcuioli and Zentall (1990, Experiment 1) tested for this possibility by using trial outcomes that were equivalent in both designs. Instead of using food outcomes on only half of the trials in the DSD procedure, they used food outcomes on both kinds of trials but manipulated the response intentions as before. They used a fixed interval 5 sec schedule on half of the trials (pigeons were reinforced for the first peck after 5 sec) and a DRO 5 sec (differential reinforcement of other behavior) schedule on the other trials (pigeons were reinforced for refraining from pecking for 5 sec). These schedules provided potential rewards on both trial types thereby making it impossible to use trial outcome in the DSD procedure to facilitate performance. When differential outcomes were eliminated, Urcuioli and Zentall found parallel retention functions for the DSD and DCD groups. Having a food outcome on both trial types eliminated the superior performance in the DSD group found by Honig and Wasserman (1981). Urcuioli and Zentall's results suggest that differential trial outcomes mediated the differences in retention functions observed by Honig and Wasserman. Thus, in their experiment, the pigeons were not prospectively coding the test stimuli.

Cohen, Galgan, and Fuerst (1986) used a similar procedure with rats. They predicted that retrospection would be more affected by the initial stimuli and that prospection would be more affected by the difficulty of the response requirements. They relied on rats' ability to remember light and tone stimuli differently to test their predictions by manipulating the initial stimulus dimension. They used both symmetrically reinforced and asymmetrically reinforced procedures (within-subjects) to measure the effect of predictable reinforced and nonreinforced trials in the DSD and DCD groups. In the symmetrically reinforced procedures of each task, omitting a response on the

appropriate trial was reinforced. For example, in the DSD symmetrically reinforced procedure, rats were reinforced on trials in which a response was made when the visual initial stimulus was presented and on trials in which a response was withheld when the auditory initial stimulus was presented. Rats in Experiment 1 were better at remembering auditory initial stimuli than they were at remembering visual stimuli in the DCD procedure, but rats performed equally well with auditory and visual initial stimuli when trained using the DSD procedure. These results were replicated in Experiment 2 using the symmetrically reinforced procedure in a within-subjects design. Cohen et al. concluded that rats used a retrospective coding strategy in the DCD procedure and they used a prospective coding strategy in the DSD procedure.

Evidence for Prospective Coding Using Non-differential Outcomes

In addition to designs that use differential trial outcomes, there are designs using non-differential outcomes that can be used to demonstrate prospective coding. Roitblat (1980, Experiment 3) tested for evidence of prospective coding by manipulating stimulus similarity. Three sample stimuli and three test stimuli were used. Two stimuli in each pair were more similar to each other than they were to the third stimulus, for example, hue stimuli: red, orange, and blue (orange is more similar to red than to blue), and line stimuli: 0, 12.5, and 90 deg. The similar sample stimuli were paired with the dissimilar test stimulus pair and the dissimilar sample stimuli were paired with the similar test stimulus pair. For example, if choice of the 90 deg line test stimulus was reinforced after the red sample then choice of the 12.5 deg line test stimulus would be reinforced after the orange sample had been presented and choice of the 0 deg line test stimulus would be reinforced after the blue sample had been presented. This arrangement would pair the similar samples, red and orange, with dissimilar test stimuli, 90 and 12.5 deg, respectively, and the dissimilar samples, blue and orange, would be paired with similar test stimuli, 0 deg and 12.5 deg, respectively.

The pigeons were tested with delays and the pattern of errors was expected to reveal more confusion either between similar sample stimuli or between similar test stimuli. If pigeons code sample stimuli, they should be more likely to make errors to test stimuli associated with the similar sample stimulus (i.e., between red and orange) during delay testing than to dissimilar sample stimuli (i.e., between orange and blue) and the

proportion of those similar sample stimulus errors should increase with increasing delay. If pigeons code test stimuli, they should be more likely to make errors to test stimuli that are more similar during delay testing (i.e., between 0 deg and 12.5 deg), than to test stimuli that are dissimilar (i.e., between 12.5 deg and 90 deg) and the proportion of those similar test stimulus errors should increase with increasing delay. Two out of the three pigeons tested were significantly more likely to confuse a set of similar test stimuli than similar sample stimuli, with errors increasing with increases in delay. Roitblat (1980) interpreted these results in terms of a prospective coding account in which a representation of the test stimulus is activated upon sample presentation.

Grant (1982) used a different approach to investigate coding processes. Instead of using stimulus similarity, he used three pairs of two sample stimuli (20 pecks vs. 1 peck, red vs. green, food vs. no food) to ask whether pigeons were using retrospective or prospective codes to maintain accurate performance. One member of each pair of samples was paired with each test stimulus. For example, a red hue, 20 sample pecks, and food samples were paired with the red test stimulus while a green hue, 1 sample peck, and no-food samples were paired with the green test stimulus. On each trial, between one and three sample stimuli were presented before presentation of the test stimuli. On some trials with multiple samples, the samples were identical (e.g., red, red, red) and on other trials the samples were different, but were from the same set (e.g., red, 20 pecks, food). Because of the relatively large number of different samples, a prospective code for each set of samples might facilitate performance by reducing the number of codes from six (one code for each sample) to two (one for each set of samples). A prospective coding account predicts that the code for that sample set will be activated for each sample on trials on which multiple samples are presented. A retrospective coding account predicts that each sample stimulus will be coded on all trials, thus six codes would be required to acquire the task. On trials in which one sample is presented more than once (i.e., red, red, red), a retrospective coding account suggests that the representation of that sample will be more salient due to extended exposure time and when tested with delays should therefore be remembered better than on different sample trials (in which each sample would create its own code). When performance on same sample trials and on different sample trials (from the same set) was compared, Grant found parallel retention functions for same and

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different sample trials. These results are consistent with prospective coding of the test stimuli. However, they are also consistent with common coding proposed by Urcuioli et al. (1989; see also Urcuioli, DeMarse, & Zentall, 1994) and as already noted Zentall et al. (1995) found evidence for retrospective common coding.

It can be argued that prospective coding should be used when it promotes a more efficient memory strategy. If true, then in a DMTS task, manipulating the number of sample and test stimuli should affect the coding strategy. Zentall, Jagielo, Jackson-Smith, and Urcuioli (1987) manipulated the number of sample and test stimuli in a between-groups design. Pigeons were trained with either two or four sample stimuli and with either two or four test stimuli so that all possible combinations of number of sample and test stimuli were formed. Lines and shapes were the sample and test stimuli. The trial types for each group are presented in Table 1. All groups were tested with delays. If pigeons were coding retrospectively, groups trained with two sample stimuli should perform better than groups trained with four sample stimuli because the four-sample groups have more sample codes and therefore more potential for confusion during testing. If pigeons were coding prospectively, pigeons trained with two test stimuli should perform better than those trained with four test stimuli because the four-test-stimuli groups have more items to interfere with memory. The acquisition data suggest that more stimuli, either samples or test stimuli, extended the number of sessions needed to reach criterion. The results of delay testing however suggest that pigeons trained with two samples and two test stimuli and pigeons trained with four samples and two test stimuli performed better during delay testing than pigeons trained with four test stimuli. Because pigeons trained with two test stimuli performed better than those trained with four test stimuli during delay trials the delay testing results are consistent with a prospective coding account.

Zentall et al.'s (1987) results suggest that pigeons can code prospectively in a DMTS task. The characteristics of the task may have made the use of prospective coding more likely than retrospective coding. Specifically, Jackson-Smith, Zentall, & Steirn (1993) noted that in the DMTS task, the correct test stimulus is always present during testing. When using a retrospective code, the memory for the sample could be correct or incorrect, but the only cue is the representation from the sample on that trial. Because of

this difference, the presence of the correct test stimulus on every test trial may make prospective coding a more efficient coding mechanism for the task. Taking this asymmetry into consideration, Jackson-Smith et al. manipulated number of stimuli using a successive delayed matching-to-sample task. In a successive matching-to-sample procedure, an initial stimulus is presented on a center response key and is followed by a single test stimulus. Certain sequences are reinforced as determined by the experimenter. For example, a vertical line stimulus followed by a triangle might be reinforced, but a horizontal line stimulus followed by a triangle would not be reinforced. Retrospective coding predicts that pigeons trained with fewer sample stimuli will perform better during delay testing because there will be fewer items to cause interference than there will be for pigeons trained with more sample stimuli. Similarly, prospective coding predicts that the number of sample stimuli should not affect performance, but the number of test stimuli should affect performance. Specifically, pigeons trained with fewer test stimuli should perform better during delay testing than pigeons trained with more test stimuli. They found that groups trained with two test stimuli performed better during delay testing than groups trained with four test stimuli. These results suggest that memory load for test stimuli was different for these groups (greater for the group trained with more test stimuli) and that this difference adversely affected performance in the group trained with four test stimuli. Their results offer further support for a prospective coding account.

Instead of manipulating number of stimuli as Jackson-Smith et al. (1993) did, Grant & MacDonald (1990) used a cueing paradigm to determine whether pigeons used retrospective coding, prospective coding, or both types of coding in delayed matching. In their cueing paradigm, red and green hue samples were paired with two pairs of test stimuli, hue stimuli and line stimuli, in a one-to-many design. No-cue trials were typical delayed-matching trials in which either hue or line stimuli served as test stimuli. On cue trials, a cue, presented simultaneously with the sample stimulus, indicated which test stimulus pair (hues or lines) would be presented on that trial. For example, a triangle would predict hue test stimuli and a circle would predict line stimuli. On occasionally incorrectly cued trials, a cue was presented, but was followed by the test stimuli that usually followed the other cue. For example, the test stimuli would be lines instead of hues on triangle trials. On cue trials the pigeons could use the cue to prepare to choose

the correct test stimulus, a prospective code. However, on incorrectly cued trials, using this strategy would dictate choice of a test stimulus that was not present. Using a retrospective code upon test stimulus presentation would allow pigeons to choose the correct test stimulus on these trials. This dual-code assumes that a prospective code is formed on cued trials, which dictates choice of the appropriate test stimulus on correctly cued trials and on incorrectly cued trials, the prospective code must be ignored in favor of a retrospective code that dictates choice of the appropriate test stimulus. In this way, a dual-code would facilitate accurate performance on incorrectly cued trials during delay testing. Grant and MacDonald argued that if pigeons use this dual coding strategy, the prospective code would be used on correctly cued trials and the retrospective code would be used on incorrectly cued trials. Grant and MacDonald examined performance on delay trials to determine if dual coding was being used. Retrospective coding on incorrectly cued and no-cue trials would result in less accurate performance during delay testing (vs. an immediate test) as the representation of the sample is assumed to be less durable over retention intervals than a prospective code would be. If pigeons code only prospectively, performance should be at chance on incorrectly cued and no-cue trials (immediate and delayed tests).

Performance on incorrectly cued trials was worse than on correctly cued trials, but did not differ from performance on no-cue trials. Furthermore, performance on incorrectly cued trials was no different on immediate and delayed tests. Grant and MacDonald (1990) concluded that these results are inconsistent with a dual coding strategy in which a prospective code is used on correctly cued trials and a retrospective code is used on incorrectly cued and no-cue trials. According to Grant and MacDonald, the failure to find a difference between performance on immediate and delayed tests on incorrectly cued and no-cue trials is inconsistent with dual coding because a retrospective strategy predicts decreased performance with delays vs. an immediate test. They favor a purely prospective account in which sample presentation elicits the prospective code for both comparison pairs and is responsible for performance on incorrectly cued and no-cue trials.

Although Grant and MacDonald (1990) argue for prospective coding, these results are also consistent with a general disruption of performance on incorrectly cued

and no-cue trials. During training, the sample and cue could be represented together as a complex stimulus. For example, instead of a red sample, the red center key plus the triangle side keys could be thought of as the sample. This sample is usually followed by a particular set of test stimuli and pigeons are trained to choose correctly. During testing, correctly cued trials are just like training trials and pigeons should be expected to perform accurately. However, sample stimuli on incorrectly cued and no-cue trials are novel and a performance decrement would be expected. For example, a red center key with triangle side keys is now followed by the other test stimuli. This novel sequence of stimuli could explain the performance decrement on incorrectly and no-cue trials.

Evidence for Flexible Coding

Several factors including stimulus dimension, procedural factors, and task requirements affect the likelihood that retrospective and prospective coding strategies will be used by animals in matching-to-sample tasks. Grant (1991) used present/absent sample stimuli to investigate flexible coding strategies in pigeons. Pigeons typically code food/no-food samples asymmetrically as shown by divergent retention functions. This finding suggests that pigeons are using a strategy in which the present sample is coded and responses to the absent sample are made by default, a single-code default strategy. This strategy reduces the number of codes from two (one for the present sample and one for absent sample) to one (one for the present sample). Grant predicted that using a MTO matching procedure would make a prospective coding strategy more efficient than the retrospective strategy typically observed in a present/absent task. If pigeons use a prospective coding strategy with present/absent samples in a MTO design, then retention functions should be parallel instead of divergent.

Grant's (1991) Experiment 1, was designed to replicate the divergent retention functions typically observed when pigeons are trained with a present/absent sample design. Separate groups were trained with one present sample (food, hue, or triangle) and one no-sample (no-food, no-hue, no-triangle). Testing with retention intervals revealed that memory for the present sample declined at a steady rate with increasing retention intervals but performance on no-sample trials did not decrease – they remained high and flat. These divergent retention functions are consistent with a retrospective single-code/

default strategy in which pigeons choose the comparison associated with the absent sample unless a memory for the present sample exists at the time of test.

A MTO procedure was used in Experiment 2 with present and absent samples. In the MTO procedure, the food sample and one line sample was associated with one of the test stimuli. The no-food sample and the other line stimulus were associated with the other test stimulus. In the one-to-one (OTO) control procedure, pigeons were trained with four samples and two pairs of test stimuli such that each sample was paired with its own test stimulus. Both groups were tested with delays. Grant (1991) hypothesized that if MTO training encourages a prospective coding strategy, the delay testing should reveal parallel retention functions. Delay testing revealed that the MTO training procedure produced parallel retention functions whereas the OTO training procedure produced the typical divergent retention function pattern. Although it is possible to produce parallel retention functions using a retrospective coding strategy (i.e., food and no-food samples are coded as their line sample stimuli counterparts), Grant concluded that parallel retention functions are evidence for prospective coding. A third experiment revealed that this pattern of results is only produced when the no-food sample shares a test stimulus with another sample. Divergent functions are produced when the no-food sample is paired with its own test stimulus.

The results of all three experiments suggest that pigeons are capable of choosing the most efficient coding strategy as determined by the task. In Experiment 1, a retrospective single-code default strategy reduced the number of codes necessary to complete the OTO task. In Experiment 2, a prospective code was used in the MTO task even though the present/absent samples that were included in the task are typically coded using a retrospective single-code default strategy. Experiment 3 revealed that divergent retention functions, suggestive of retrospective coding, are produced when the no-food sample is associated with its own comparison, but parallel retention functions, suggestive of prospective coding, are produced when the no-food sample shares its comparison with another sample. These results suggest further that the task demands (OTO or MTO procedure) and the sample characteristics (e.g., present/absent) determine which coding strategy will be used by pigeons.

Zentall, Urcuioli, Jagielo, Jackson-Smith (1989) investigated coding strategies by manipulating both the number and discriminability of the sample and comparison stimuli. There were four groups of pigeons. Groups were either trained with two samples (Groups 2-2 and 2-4) or four samples (Groups 4-2 and 4-4) and either two comparisons (Groups 2-2 and 4-2) or four comparisons (Groups 2-4 and 4-4). Stimulus dimension was counterbalanced within groups. For example, half of the pigeons in Group 2-2 were trained with hue samples and hue comparisons and half were trained with line samples and line comparisons. All groups were tested with delays. Retrospective and prospective coding strategies make different predictions about performance during delay testing. Retrospective coding predicts that sample stimulus dimension will affect performance due to differences in stimulus salience, but comparison stimulus dimension will not affect performance. Prospective coding predicts that groups with two comparisons (Groups 2-2 and 4-2) will perform better than groups with four comparisons (Groups 2-4 and 2-4).

The results were more complicated than any of the predicted group differences and the data were presented by sample type. In general, performance was better with hue samples than with line samples. This finding suggests that hue samples were coded retrospectively. However, further analysis of line-sample trials revealed between-group differences that support prospective coding. Zentall et al. (1989) suggested that the less discriminable line samples might encourage prospective coding. On line-sample trials, groups trained with two comparisons performed better than those trained with four comparisons. This difference was not present on hue-sample trials. These results suggest that the type of coding may be affected by the stimulus dimensions and task demands.

Flexible Within-trial Coding Processes

Much of the evidence for flexible coding processes comes from experiments that have used between group differences in training procedures or task demands, however Cook, Brown, and Riley (1985) found within-subject evidence for flexible coding processes by rats. Cook et al. used a radial arm maze in which 12 baited arms radiate out from a center platform. The rats are placed in the center platform and are allowed to make arm choices to retrieve a small amount of food that has been placed at the end of each arm. The most efficient strategy to complete a trial is to enter each arm once until all 12 arms have been entered. Cook et al. analyzed the pattern of errors (revisits) that were

created by inserting delays, to make inferences about the coding strategy that was being used at different points in the trial. They used a procedure in which a 15 minute delay was inserted after 2, 4, 6, 8, or 10 correct choices had been made. After the delay, rats were allowed to complete the trial. Errors were plotted for each point of delay interpolation (PDI) and were corrected for opportunity to make an error. This correction for opportunity was necessary because the probability of making an error by chance increases as more correct choices have been made and thus is confounded with PDI. For example, if the rat chooses arms 3 and 6 before the delay, then only errors to arms 3 and 6 are possible after the delay, however, if the rat chooses arms 1, 2, 3, 4, 5, and 6 before the delay, then the rat could make errors to any of those six arms after the delay. To correct for the increase in probability of making an error with increases in PDI, errors were calculated on control trials as if a delay had been inserted at each point that corresponded to the PDI on delay trials. For example, to obtain errors due to the "delay" for PDI 2, the first two correct choices would be noted and errors would be recorded for revisits to those arms after that point in the trial. In the following example of a list of choices: 1, 2, 3, 4, 5, 6, 7, 8, 9, 2, 10, 5, 11, 12, the first two correct arms are 1 and 2. The list of choices beyond that point in the trial would be examined for revisits to those arms. In that example, errors for PDI 2 would include revisits to arms 1 and 2 because they are the first two correct choices. Arm 2 has been revisited after the point at which the "delay" has been interpolated and would count as an error due to the "delay" for PDI 2. The calculation for PDI 4 would include any revisits to arm 1, 2, 3, or 4 because these were the first four correct choices, therefore the "delay" would be inserted after the choice of arm 4. Only arm 2 was revisited making one error at PDI 4 for that trial. Calculations for PDI 6 would include revisits to arms 1, 2, 3, 4, 5, or 6 therefore revisits to arms 2 and 5 would be included for PDI 6. Similarly, at PDI 8, revisits to arms 1 through 8 would be included as errors. Revisits to arms 1 through 10 would be included as errors for PDI 10. Errors due to the "delay" were calculated on control trials at each PDI and these errors were subtracted from errors made on delay trials to yield errors attributed to the actual delay.

There are several possible strategies that rats could use to complete this task. Rats could use a retrospective strategy in which visited arms are remembered and avoided.

Alternatively, they could use a prospective strategy in which a "list" of to-be-visited arms is stored and as each arm is visited it is removed from the list. In the radial arm maze, a retrospective coding strategy would result in more errors later in the trial because memory load would increase as more arms are chosen. A prospective coding strategy would create more errors early in the trial because memory load would decrease as arms are chosen. These strategies make different predictions about the effect of a delay on the number of errors made. If the rat is using a retrospective strategy, the delay should be more disruptive when the memory load is greater and should therefore affect performance more at the end of a trial than at the beginning of a trial. If rats are using a prospective coding strategy, the delay would be more disruptive at the beginning of a trial.

These strategies also make different predictions about the serial position functions for errors. The serial position functions represent the relationship between the order of arm choices before the delay and the tendency for the rats to revisit them. A primacy effect is the ability to remember items at the beginning of a list better than items at the end of the list whereas a recency effect is the ability to remember items at the end of a list better than items in the beginning of the list. These serial position effects are believed to be caused by the greater salience of first and last list items and due to similar contexts during encoding of last list items and recall. A retrospective coding account in which a list of previously visited arms is remembered predicts serial position effects. A prospective coding account predicts that there will not be any relationship between order of arm choices before the delay and the tendency to revisit those arms because the previously visited arms are presumably not what is represented in memory.

The results of Cook et al.'s (1985) Experiment 1 revealed an increase in errors as the PDIs increased from 2 to 6 and a decrease in errors as the PDIs further increased from 6 to 10. These results suggest that rats used a dual-coding strategy. They used retrospective codes during the first half of the trial and prospective codes during the second half of the trial. The serial position curves also support a dual coding account. The data from PDIs 4, 6, 8, and 10 show a recency effect for PDIs 4 and 6, but neither a primacy nor a recency effect for 8 or 10. These serial position curves are consistent with a retrospective coding account early in the trial and a prospective coding account late in the trial.

In Experiments 3 and 4, Cook et al. used a modified procedure to determine whether or not the results of Experiment 1 were due to the asymmetrical effect of the delay on a preferred response strategy. For example, the rat could have a particular preferred sequence of choices and inserting a delay in the middle of the trial could be more detrimental to the accurate completion of this choice sequence. In Experiment 3, they used a forced choice procedure before the delay in which the rat made a sequence of randomly determined arm choices until the delay. After the delay, all arms became available and rats were free to make choices until all arms had been visited. A forced choice procedure was used to prevent the rats from using a preferred sequence of choices. For example, rats could have arms that they prefer to choose in the beginning of the trial and arms that they prefer to choose at the end of the trial. These preferences could cause the rats to perform well at early PDIs because the most preferred arms would have been chosen before the delay and can be avoided. Similarly, rats could do well at later PDIs because the least preferred choices are more likely to have food late in the trial than more preferred arms. Arms in the middle of the preferred sequence (non-preferred) would be easily confused at middle PDIs because the most preferred and least preferred arms are probably more salient than these non-preferred arms. If the delay is more disruptive in the middle of the trial because it is harder to remember which non-preferred arms have been chosen, the rats would appear to do better at earlier and later PDIs, thus appearing to be a dual coding strategy.

To eliminate this possibility, a two-alternative forced choice procedure was used in Experiment 4. Rats were forced to choose between one previously visited arm and one previously unvisited arm after the delay. This procedure makes the probability of choosing the correct arm equal (50%) at all PDIs, thus performance across PDIs can be compared. The results of forced choice trials were consistent with a dual coding account because functions similar to those in Experiment 1 were found. Serial position curves support a retrospective coding account at PDIs 4 and 6 (Experiment 4, PDI 6) and a prospective coding account at PDIs 8 and 10. The results from their experiments support a dual-coding account in the radial arm maze. These results represent a highly flexible strategy in rats that minimizes errors at all points in the trial.

To test the generality of the flexible coding strategy used by rats, Kesner and DeSpain (1988) tested human subjects with lists that consisted of 2, 4, 6, 8, 10, 12, or 14 Xs. Each X was presented alone in a specific location on a grid of 16 squares. Subjects were tested by presenting one X that had been presented in the list on that trial and one X that had not been presented on that trial. Subjects were judged to be correct if they chose the X that had not been presented on that trial. Kesner and DeSpain found individual differences in strategies for completing the task. They found that some subjects used a retrospective coding strategy, which was supported by an increase in errors from early to late PDIs. They also found that some subjects used a dual coding strategy. These subjects made more errors from PDIs 2 to 8 and fewer errors from PDIs 8 to 14. These results suggest that some subjects preferred to remember the list of Xs that had been presented on each trial while others preferred to remember the set of fewer items, Xs that had been presented at early PDIs and empty grid spaces at later PDIs.

Zentall, Steirn, and Jackson-Smith (1990) used a radial maze analog task to look for evidence of a dual coding strategy in pigeons. Their task consisted of five response keys. The first completion of an FR5 requirement produced reinforcement. An additional 5 responses to the same response key did not produce reinforcement, but resulted in a 2.5 sec period of darkness. Each trial continued until all five keys had been chosen. The most efficient way to complete a trial was to perform the FR5 for each key one time and avoid revisits. In Experiment 1, although the pigeons learned to avoid revisits to keys above chance level, they showed a strong bias to make revisits early in training. In Experiment 3, they used a PDI procedure similar to that used by Cook et al. (1985). A delay was inserted after the pigeon made 1, 2, 3, or 4 correct choices. They used a progressive system of delays, beginning with 15 sec and increasing up to 3600 sec. When the pattern of errors was examined at each PDI, the pigeons were found to perform better at PDIs 1 and 4 than at 2 and 3, a pattern consistent with the dual coding strategy found for rats. Similar results were reported by Steirn, Zentall, and Sherburne (1992).

An alternative to the dual coding account of the results obtained by Cook et al. (1985) and Zentall et al. (1990) is the criterion shift hypothesis. This hypothesis states that the animal makes choices more carefully at the end of a trial than at the beginning. This strategy is compatible with the trial structure in that the probability of making an

error increases as more correct choices are made. Making choices more carefully as the probability of making an error increases (i.e., a criterion shift) facilitates accurate performance. This hypothesis predicts that errors should decrease relative to chance in the later PDI conditions, however, it does not predict an increase in errors at earlier PDIs. A retrospective code combined with a criterion shift at later PDIs could create the pattern of errors consistent with dual-coding. Although neither the serial position curves obtained by Cook et al. nor the results of their forced choice testing procedure used in Experiment 4 support the criterion shift hypothesis, the present experiments extended the findings of Zentall et al. by using forced choice procedures to provide a better test of the dual coding hypothesis in pigeons.

Purpose of the Present Experiments

The purpose of Experiment 1 was to replicate the results of Zentall et al. (1990) using fixed delays of 15 sec and 30 sec in the testing phase. Experiment 2 tested the dual coding hypothesis using a forced-choice two-alternative procedure to control for the change in response criterion produced by the increasing probability of making an error with increasing PDI. This procedure avoided the problems of having to correct for opportunity to make errors as is the case when five keys are available after the delay. In the forced-choice procedure, two response keys were presented after the delay. One alternative was correct (had not been chosen before the delay) and one alternative was incorrect (had been chosen before the delay). With this procedure, the probability of making an error by chance was the same at all PDIs, 50%. Control trials with forced choices, but no delay were also included to measure any systematic changes in errors over the course of the trial that might not be attributed to the delay. These procedures provided a test of the hypothesis that the results obtained by Zentall et al. were due to a criterion shift (due to the changing probability of making an error by chance). The dual coding hypothesis predicts that pigeons should do better at PDIs 1 and 4 compared to PDIs 2 and 3. The criterion shift hypothesis together with retrospective coding can produce the pattern of results obtained by Cook et al. (1985) and Zentall et al., but the forced choice two-alternative procedure eliminated the change in the probability of making an error by chance (it was 50% at all PDIs). Thus, if the criterion shift plus

retrospective coding is responsible for the effect found by Zentall et al., the forced choice procedure will remove the effect of the criterion shift and will leave the effect of retrospective coding and errors should increase with increasing PDI. Therefore the criterion shift hypothesis predicts that performance should decrease from PDI 1 to PDI 4 using this procedure (i.e., only evidence for retrospective coding will be found).

In addition to holding the probability of making an error constant at 50% at each PDI, Experiment 2 used a more conservative control trial procedure than that used in Experiment 1 when control trial errors were subtracted from delay trial errors as a correction procedure. While the subtraction method used in Experiment 1 is an appropriate control procedure and has been used by other investigators (Cook et al., 1985; Zentall et al., 1990), the use of separate control trials allowed performance on delay and control trials to be compared directly. This procedure eliminated the need for the assumptions made with the use of the subtraction method. Specifically, the subtraction method assumes that the same factors that direct choices on control trials are exactly the same as those affecting choices on delay trials. In this way, it is believed that subtracting control trial errors from delay trial errors reveals only the effect of the delay on memory without being affected by any other factors that could possibly affect choice across PDIs. However, using a procedure in which control trials are exactly like delay trials, except for the delay, is a more conservative approach. Experiment 2 used control trials for each PDI in which a stopping point occurs before the forced choice, but a 0 sec delay is interpolated. For example, on PDI 1 control trials, the first correct choice was followed by reinforcement and then instead of a delay, the forced choice was presented. These trials eliminated all differences between control trials and delay trials except for the actual delay. This procedure provided a more conservative control procedure than the subtraction that was used in Experiment 1.

Experiment 3 was designed to clarify the results of the first two experiments by using the birds from Experiment 1 and the testing procedure from Experiment 2. Because a novel forced choice procedure was used in Experiment 2, Experiment 3 aimed to replicate the results with a new group of birds to validate the procedure.

Experiment 4 attempted to test the dual coding hypothesis while preventing the pigeons from making a preferred sequence of choices before the forced choice. In this

design, pigeons made between 1 and 4 responses. The sequence of responses was randomly determined, with only one response key available at any given time before the two-alternative forced choice. Performance on each trial type (one for each PDI) was measured.

Trial Types for Each of the Four Groups					
Group					
2-2	2-4			4-2	4-4
V(VH)	V(VH)			V(VH)	V(VH)
H(HV)	H(HV)			H(HV)	H(HV)
	V(TC)			T(VH)	T(TC)
	H(CT)			C(HV)	C(CT)
		OR			
T(TC)	T(TC)			T(TC)	T(TC)
C(CT)	C(CT)			C(CT)	C(CT)
	T(VH)			V(TC)	V(VH)
	C(HV)			H(CT)	H(HV)

Chapter Two

Experiment 1

Method

  Subjects. Six unsexed White Carneaux pigeons were used as subjects. They were
purchased as retired breeders from the Palmetto Pigeon Plant (Sumter, SC). The pigeons
were free-fed until their weights had stabilized and were then put on a restricted diet to
reduce them to 85% of their free-feeding weights. This weight was maintained
throughout the experiment. The pigeons were housed with free access to water and grit in
a colony room on a 12-12 light-dark schedule.

  Apparatus. A standard operant chamber (BRS/LVE, Beltsville, MD) was used.
The operant chamber was 35 cm high, 30 cm wide, and 35 cm across the intelligence
panel. A houselight was located in the ceiling 13 cm from the intelligence panel and 16
cm from the door of the chamber. There were 25 keys on the intelligence panel which
were arranged in a 5 X 5 matrix. Five keys were utilized 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 by one hue
[blue, (top left), red, (top right), green, (bottom left), yellow, (bottom right), and white
(center)] consistently throughout the experiment. A feeder provided mixed grain through
an opening 5.7 cm high and 5.1 cm wide. The feeder opening was located 6 cm above the
floor of the chamber.

Procedure

  Pre-training and Training. During the first phase of pre-training one response key
was illuminated at a time. The pigeons were trained to peck the illuminated key and were
reinforced with 1.5 s of access to mixed grain (the type and duration of reinforcement
used throughout the experiment). They were required to peck the illuminated key one
time for reinforcement with a 10 s intertrial interval (ITI) during which the houselight
was illuminated. Once they completed 4 sessions of 50 trials per day, they began the next
phase of pre-training. The pigeons were trained six days a week throughout the
experiment.

During the second phase of pre-training, all five keys were illuminated at the beginning of each trial. The first response to any key was reinforced. Keys were not lit during the reinforcement interval. The chosen key remained dark after reinforcement, but keys that had not been chosen were re-illuminated. Any response to the remaining keys turned off that key and provided access to reinforcement. This process continued until each of the five keys had been pecked. Trials were separated by a 60 s lit ITI. The pigeon completed 2 sessions of 24 trials per day, then the response requirement was increased to an FR3 for two sessions and finally to an FR5 for two sessions. After completing these phases of pre-training the pigeons moved on to the training phase.

The first phase of training was similar to the last phase of pre-training in that all five keys were illuminated at the beginning of each trial. Five pecks to any key was considered a choice and initial choices to each key produced access to reinforcement, but unlike in pre-training, that key was not turned off after it had been chosen. Because all five keys were re-illuminated after the reinforcement interval, the pigeon was able to choose keys that had been chosen earlier in the trial. These choices were considered errors and resulted in the offset of all keys for 2.5 s. The trial ended when all five keys had been chosen at least once. Trials were separated by a 60 s lit ITI. The pigeons completed 15 trials per day. They were trained until they completed three consecutive sessions with an average of fewer than three errors per trial.

Delay Testing. After reaching criterion in the training phase, the pigeons began testing trials with delays. There were ten trials in each delay session. On two control trials, pigeons were able to make choices until all five keys had been chosen at least once, just as in training. The other eight trials began with all five keys illuminated and included a delay. The point at which the delay was inserted, the point of delay interpolation (PDI), was randomly chosen by the computer program with the constraint that there were two trials for each point of delay interpolation after 1, 2, 3, or 4 reinforced choices. On these trials, pigeons made choices according to the contingencies established in training until the delay began. The delay began after the last correct choice for that particular PDI and consisted of 15 sec of darkness. After the delay, all keys were re-illuminated and the trial continued until the pigeon chose all keys that had not been chosen before the delay. For example, on a PDI2 trial, the pigeon made choices until two correct choices had been

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made. After reinforcement had been given for the second correct choice, the chamber was darkened for 15 sec. After 15 sec had passed, all five keys were re-illuminated and the pigeon continued to make choices until the three keys had been chosen that had not been chosen before the delay. Reinforcement was given for all initial choices and 2.5 sec of darkness followed all incorrect choices as in training. There was 1 block of ten sessions with a 15 sec delay and then pigeons began testing sessions with a 30 sec delay. Pigeons completed 9 blocks of 10 sessions with a 30 sec delay.

Results

     Training. Pigeons made about 9 errors per trial during the first block of 10 sessions. Errors decreased to about 4 errors per trial by the third block of 10 sessions and leveled off at 3 errors per trial by block 7. Mean number of errors per trial are presented in blocks of 10 sessions in Figure 1. The number of sessions to reach criterion was recorded for each pigeon. Mean sessions to criterion was 34.16 (SE = 8.36).

     Delay Testing. The mean number of total errors is shown for control trials and delay trials separately in Figures 2 (control trials in 10 blocks of 10 sessions) and 3 (delay trials in 10 blocks of 10 sessions) respectively. Errors are reported in 10 blocks of 10 sessions. Pigeons made an average of 2 -3 errors on control trials and slightly more, an average of between 2.5 and 3.5 errors, on delay trials. A Block X Trial Type (control vs. delay) analysis of variance ANOVA was performed using the error data. A significant effect of trial type was obtained, $F(1, 5) = 43.61$, $p < .05$. No effects of block or the Block X Trial Type interaction were found, $F(9, 45) = 1.74$, $p > .05$ and $F(9, 45) = .71$, $p > .05$.

     Errors on delay trials were analyzed further to determine whether a dual coding strategy was used on delay trials. The first step in this analysis was to compare number of errors across PDIs. On delay trials, the number of errors attributable to the delay were calculated. Errors attributable to the delay are choices made after the delay to response keys that had been chosen before the delay. These errors were summed for each PDI. This total was divided by the number of possible errors that could have been made for that PDI. For example, on PDI 2 trials, two correct choices are made before the delay so there are two possible ways to make an error after the delay. If the pigeon makes one of

these errors, the proportion of errors attributable to the delay would be .5. These proportions represent the errors attributable to the delay for each PDI.

Errors were also corrected for the potential changing tendency to make errors throughout the trial because of a criterion shift in responding. This calculation was obtained using errors made on control trials as a baseline. A measure of control errors was calculated for each PDI as if a delay, or a pseudodelay, had been interpolated. For each control trial, the number of errors was calculated for each PDI by counting the number of errors made after the pseudodelay to keys that had been chosen before that point. For example, when calculating errors for a PDI 2 trial, the sequence of choices on a control trial from that session were analyzed by examining choices made after the second correct choice, the pseudodelay. The number of choices made after the second correct choice to those keys chosen correctly before the pseudodelay were calculated. If the first two correct choices were to the green and red keys, later responses were examined for choice of either the green or the red key. If responses were made to green or red, one error was counted against that color regardless of how many revisits to that response key were made. Using this method, the number of possible errors equals the number of correct pre-delay choices. This number was divided by the number of opportunities to make an error. In the previous example, if the pigeon chose green or red after the pseudodelay it was included as an error. Choices to one of those two keys resulted in a proportion of .5. These calculations are shown for control trials and delay trials in Figure 4. The adjusted (for opportunity to make an error) errors on control trials were subtracted from the adjusted (for opportunity to make an error) errors on delay trials. These proportions were calculated for each PDI and are shown in Figure 5. The last 50 sessions was analyzed because earlier sessions involve acquisition of the delay testing task and no effect was predicted for these sessions. The errors attributable to the delay increased from PDI 1 to PDI 2 and decreased from PDI 3 to PDI 4. A repeated measures ANOVA was conducted with PDI as the factor. The ANOVA showed a main effect of PDI, $F(3, 15) = 5.05$, $p < .05$. The errors attributable to the delay function were also analyzed for linear and quadratic components. There was a significant quadratic trend, $F(1, 5) = 30.48$, $p < .05$. There was no linear trend, $F(1, 5) = .517$, $p > .05$.

<u>Discussion</u>

The results of Experiment 1 replicated the results of Zentall et al. (1990) using a fixed delay procedure. Pigeons made many errors in the early stages of training, but learned to avoid previously visited keys. During Delay Testing 1, they made more errors on delay trials than on control trials. In blocks 6 – 10, the difference in adjusted errors between control trial and delay trial performance was greater at PDIs 2 and 3 than at PDIs 1 and 4. Specifically, errors increased from PDIs 1 to 2 and decreased from PDIs 3 to 4. This pattern of errors is consistent with a dual coding strategy in which pigeons use retrospective coding at the beginning of a trial and prospective coding at the end of a trial. These results suggest that the evidence for a dual coding strategy is not an artifact of the progressive delay procedure that was used by Zentall et al. (1990).

Experiment 1 used a pseudodelay as a control procedure in which errors on control trials were subtracted from errors on delay trials. The pseudodelay procedure is designed to correct for artifacts that are associated with differential care in making choices at different PDIs. This subtraction method makes the assumption that the care with which choices are made on delay trials is the same as the care with which choices are made on control trials. For example, non-memorial factors (e.g., impulsivity) could affect choices more on control trials than on delay trials. That is, if they take greater care after a delay than at the same point in the trial without a delay, the subtraction method may not be appropriate. Although there is no evidence that there is a difference between the choice strategies on delay and control trials, it is possible that this assumption is not correct. Experiment 2 addresses this issue.
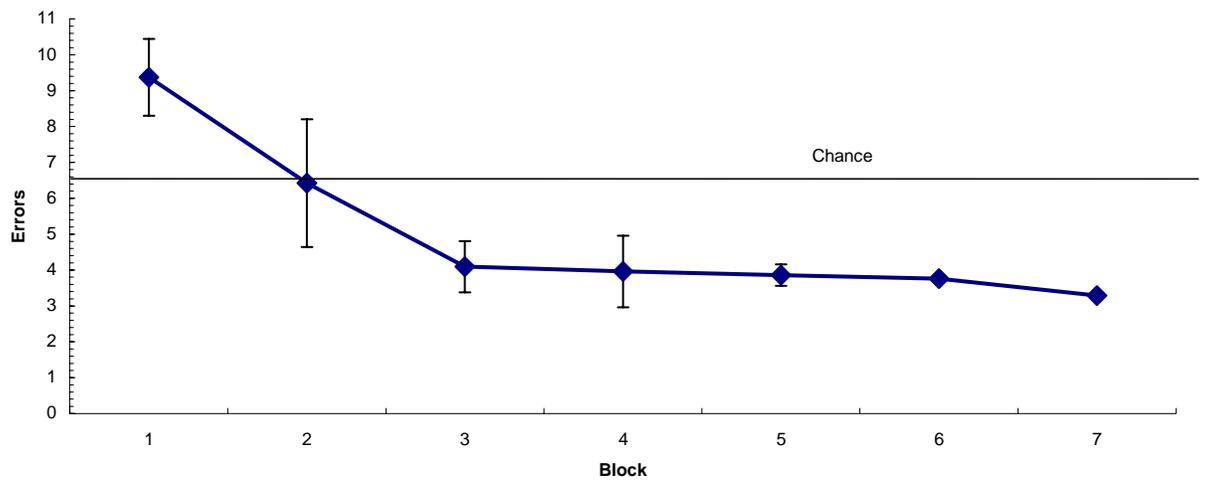
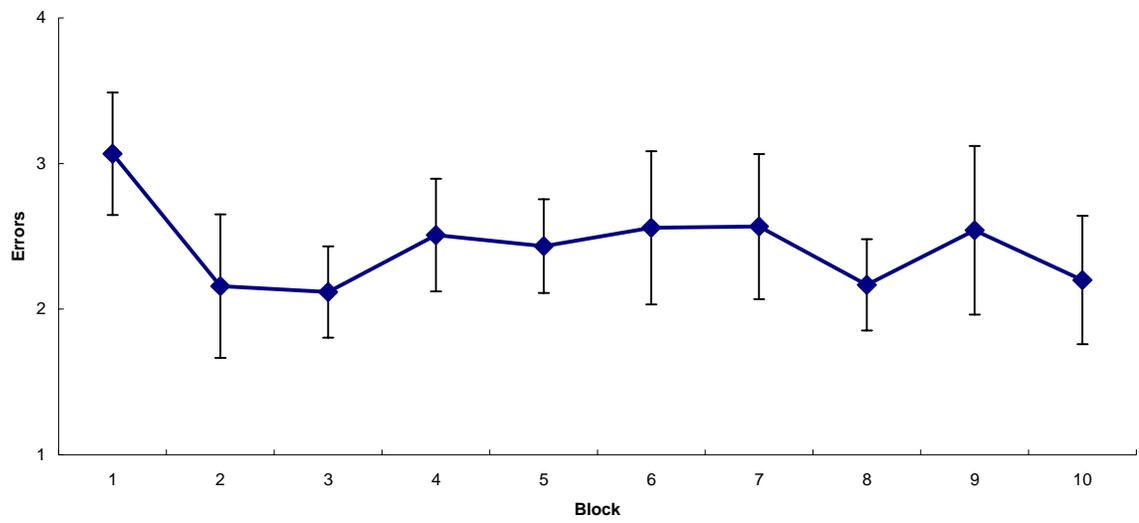Figure 1. Errors on Training Trials in Experiment 1.

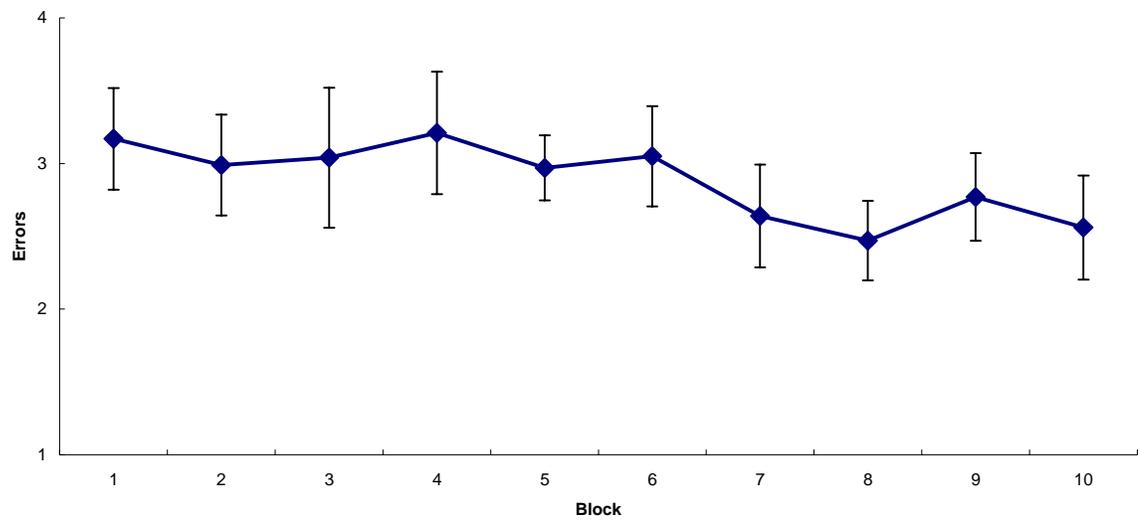Figure 2. Control Trial Errors in Delay Testing in Experiment 1.

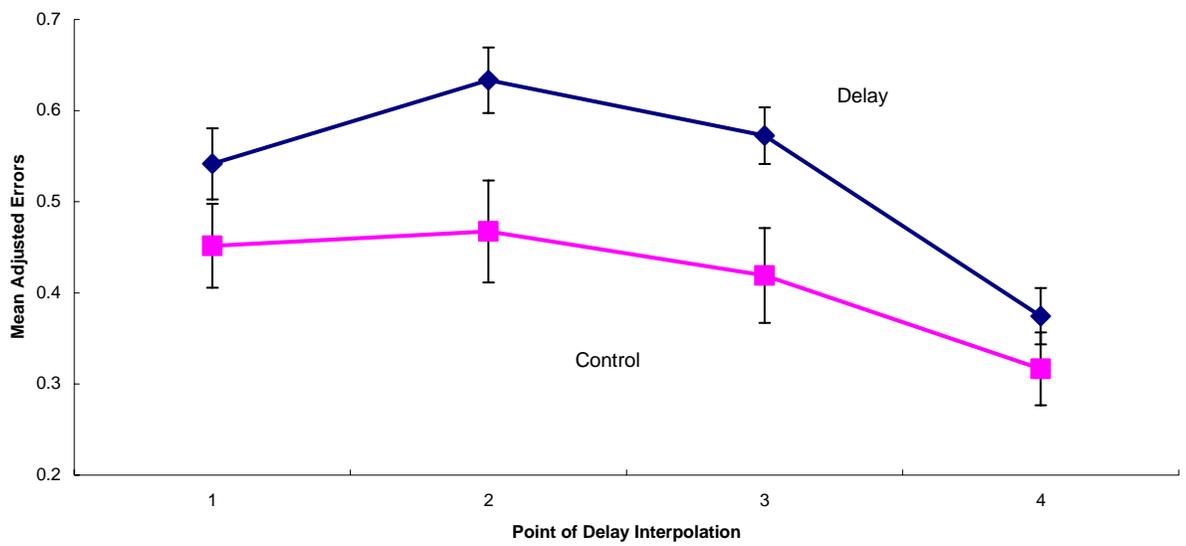Figure 3. Delay Trial Errors in Delay Testing in Experiment 1.

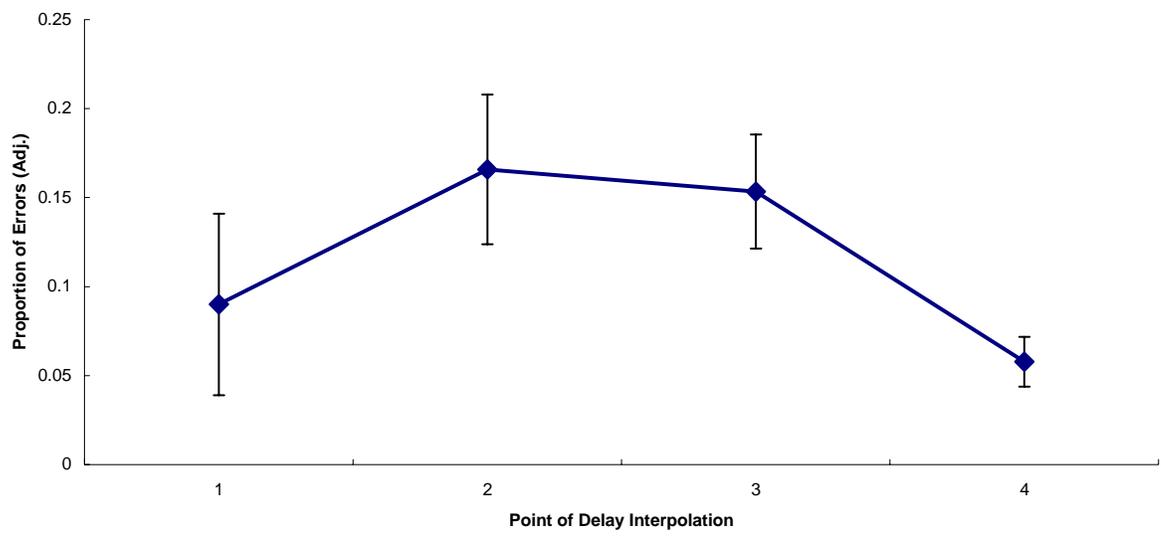Figure 4. Control and Delay Trial Errors in Experiment 1.

Figure 5. Errors Attributable to the Delay in Experiment 1.

Chapter Three

Experiment 2

In Experiment 1, a procedure was required to adjust for the changing opportunity to make an error. This correction procedure made it possible to make comparisons across PDIs. Experiment 2 used a testing procedure that did not require correction for opportunity to make an error created by the presence of all five keys being re-illuminated after the delay. Instead of re-illuminating all five response keys after the delay, two response keys were presented. One key had been chosen prior to the delay and one had not been chosen before the delay. The computer program randomly chose these keys from the previously chosen and the previously not chosen arrays. With this procedure, the probability of being correct by chance was 50% at all PDIs. This change in procedure allowed for the direct comparison of performance as a function of PDI.

As mentioned above, there may be differences in the non-memorial factors that affect choices on control and delay trials. To control for the possibility that there may be changes in choice unrelated to the delay, separate control trials were included in Experiment 2. These control trials included a stopping point in the trial but no delay. Performance on delay trials was compared to performance on these control trials at each PDI to subtract all errors that are not attributable to the delay.

Method

Subjects. Six pigeons of the same type and maintained in the same way as in Experiment 1 were subjects in Experiment 2.

Apparatus. The same operant chamber used in Experiment 1 was used in Experiment 2.

Procedure.

Pre-training and Training. Pigeons in the second experiment experienced the same pre-training and training phases as the pigeons in Experiment 1.

Testing 1. Their first testing phase was similar to that used in the first experiment. As in Experiment 1, there were five types of trials. Control trials were exactly like training trials. Five keys were available until the pigeons had chosen each key at least

once. Errors were defined as choice of a key after reinforcement had been given on that trial (for the initial choice). On the other four trial types, a dark 15 sec delay was inserted. There was one trial type for each PDI. For example, on PDI 3 trials, a delay began after the third correct choice had been reinforced. After the delay, instead of all five keys becoming available, the computer program chose one key that had been chosen previously on that trial and one key that had not yet been chosen. The pigeons were allowed to choose between these keys and were reinforced for choosing the key that had not been chosen. Choices of the previously chosen key were not reinforced. All choices were followed by the 60 sec lit ITI. There were ten trials in early test sessions, two of each type (control, PDI 1, PDI 2, PDI 3, and PDI 4). After ten sessions, the delay increased to 30 sec and testing continued for 30 additional sessions.

　　　　Testing 2. Beginning with testing session 41, control sessions (one for each PDI) were used in addition to delay sessions. Control sessions and delay sessions were alternated daily. Delay sessions consisted of three delay trials at each PDI. Control sessions included 3 control trials of each type. The control trials were exactly like delay trials at each PDI except that no delay was interpolated. For example, pigeons made choices until the predetermined number of choices had been made and then pigeons were presented with one previously chosen response key and one previously unchosen response key. Pigeons were reinforced for choosing the previously unchosen response key. These trials were used to ensure that errors made on delay trials could be attributed to the delay instead of using the pseudodelay procedure used in Experiment 1.

　　　　A correction procedure was used during this testing phase to promote accurate performance. The correction procedure occurred on control and delay trials in which pigeons had chosen incorrectly on the forced choice portion of the trial. After an incorrect choice, the chamber was darkened for 2.5 s after which the same two keys were re-illuminated. This correction procedure was repeated until the pigeon chose correctly. Pigeons were reinforced for correct choices on these trials. The number of repeats was recorded for each PDI. This procedure was used for 60 sessions.

　　　　Testing 3. Beginning with session 101, the correction procedure was discontinued because it failed to facilitate performance. Control sessions and delay sessions in Phase 3 were identical to those in Phase 2 except that an incorrect choice during the forced choice

portion of the trial terminated the trial without reinforcement. This procedure was continued for 60 sessions.

Results

Training. Mean number of errors per trial were reported in 4 blocks of 10 sessions and are shown in Figure 6. Pigeons made about 7 errors per trial in the first block of 10 sessions and declined sharply to about 3 errors per trial in block 2 and remaining flat for blocks 3 and 4. The number of sessions to reach criterion was recorded for each pigeon and averaged, 19.5 (SE = 2.64).

Testing 1. The percentage of correct choices was calculated for each PDI for each pigeon for each block of ten trials and is shown in Figure 7. The mean percent correct did not exceed 55% correct at any PDI and therefore statistical analyses are not reported for these data.

Testing 2. Percent correct at each PDI was calculated for control and delay sessions for each pigeon for each block of 10 trials and is shown in Figure 8. Performance on delay sessions was subtracted from performance on control sessions and the difference function is shown in Figure 9. As in Testing 1, performance was poor at each PDI and therefore statistical analyses are not reported for these data.

Testing 3. One pigeon died before beginning Testing Phase 3 and therefore no data was collected for that bird. Performance at each PDI was calculated for the remaining birds for control and delay sessions and is shown in Figure 10. Performance on control sessions was on average better than performance on delay trials. Performance on delay sessions was subtracted from performance on control sessions and the difference function is shown in Figure 11. The difference function suggests that errors decrease with increasing PDI.

A 2 (trial type) X 4 (PDI) ANOVA was conducted using percent correct at each PDI. The ANOVA showed a significant effect of trial type, $F(1, 10) = 48.94$, $p < .05$. Neither the effect of PDI, $F(3, 12) = 2.19$, $p > .05$ nor the PDI X Trial Type interaction was significant, $F(3, 12) = .729$, $p > .05$, but the contrasts for the Trial Type X PDI interaction revealed a nearly significant linear trend, $F(1, 4) = 6.09$, $p = .06$.

Discussion

As in Experiment 1, the pigeons in Experiment 2 made many errors in the first few sessions of training, but quickly learned to avoid previously visited keys. During the first phase of delay testing, performance was poor across PDIs. In Testing 2, the introduction of repeats facilitated performance slightly on control and delay sessions. In Testing 3, control session accuracy reliably exceeded delay session performance.

The purpose of the testing phase was to determine whether the errors attributable to the delay were most consistent with a retrospective, prospective, or dual coding strategy. Retrospective coding predicts that errors would increase with increases in PDI as memory load (responses made) increases. Prospective coding predicts that errors would decrease with increases in PDI as memory load (responses to be made) decreases. Dual coding predicts that errors will increase from PDIs 1 to 2 and decrease from 3 to 4 as they did in Experiment 1. Unlike in Experiment 1 however, the difference function for Testing 3 suggests that errors decreased as PDI increases. These results are consistent with a prospective coding strategy in which to-be-visited places are remembered. These results are inconsistent with the results of Experiment 1 in which the error function suggested that the pigeons were using a dual coding strategy. These results are also inconsistent with the criterion shift hypothesis, which predicted that the error function would be consistent with retrospective coding.

There are two hypotheses that could explain the differences between Experiments 1 and 2. First, the pigeons in Experiments 1 and 2 were using different coding strategies due to the particular requirements of each testing procedure. For example, the testing trials in Experiment 1 included a delay followed by the re-illumination of all response keys and the pigeons were required to choose the remaining keys that had not been chosen before the delay. This task is presumably more difficult than testing trials in Experiment 2 in which the delay was followed by the two-alternative forced choice. If the pigeons chose incorrectly on these two-alternative forced choice trials, the trial ended, but in Experiment 1, the pigeon was forced to choose correctly in order to move onto the next trial. The testing procedure used in Experiment 1 may have encouraged a dual coding strategy in order to minimize errors on the more difficult task. In Experiment 2, the testing procedure did not require that the pigeons choose all remaining unchosen keys

after the delay and therefore, a prospective coding strategy may have been sufficient to support accurate performance. If pigeons in Experiment 1 were using dual coding and pigeons in Experiment 2 were using prospective coding, it would suggest that the type of coding is quite flexible and is probably dictated by the specific task that is used. Specifically, it would suggest that dual coding is used when the task is very difficult for pigeons, thus requiring the most efficient strategy in order to perform accurately.

Alternatively, the correction for opportunity and errors not attributable to the delay used in Experiment 1 is an inadequate control procedure because the assumption that non-memorial factors that affect choices are the same on control and delay trials may not be valid. In Experiment 2, using the two-alternative forced choice procedure and subtracting errors on delay trials from those on comparable control trials should have more effectively eliminated errors not attributable to the delay. Specifically, the assumption violated in Experiment 1 is the assumption that all factors that affect choices on control trials are the same as those that affect choices on delay trials except that on delay trials memory load causes additional errors. For example, factors that affect choices on control trials after the first correct choice has been made (the point analogous to PDI 1 trials) are identical to those that affect choices on delay PDI 1 trials except that additional errors are created by the delay due to memory load. The assumption is that factors other than memory load (e.g., impulsivity, the care with which choices are made) are identical at each point on control trials (at each pseudodelay) and delay trials.

This critical assumption could have been violated in several ways using the testing procedure in Experiment 1. First, control trials may be more conducive to impulsivity than delay trials especially on early PDIs. Pigeons needed extensive training to inhibit errors on training trials to 3 or fewer errors per trial (the training criterion). During delay testing, impulsive pecking on control trials is likely to remain at this level (3 or fewer errors per trial). Delay trials include a stopping point during which responses will not provide reinforcement and may extinguish impulsive pecking especially at early PDIs when impulsivity might be reinforced. In Experiment 1, as mentioned in the context of the criterion shift hypothesis, the consequences of choosing impulsively early in the trial, when the probability of reinforcement by chance is 80%, are usually positive (reinforcement) compared to choosing impulsively later in the trial (no reinforcement)

when the probability of reinforcement by chance is 20%. Pigeons tend to be impulsive early on control and delay trials, but on delay trials these errors may be attenuated because the delay may break up the impulsive response pattern. On control trials, pigeons make choices until each key has been chosen once. The psuedodelay control procedure mimics each PDI, but there is no stopping point on these trials as on delay trials. Thus, control errors may be inflated. The inflated control errors would be subtracted from delay PDI 1 and PDI 2 errors, making that number lower than it should be. The erroneously low PDI 1 (and PDI 2) value for errors attributable to the delay would be consistent with a dual coding strategy, thus perhaps masking a prospective coding strategy.

If the subtraction method that was used in Experiment 1 produced data consistent with dual coding, then changing the control procedure to that used in Experiment 2 with the pigeons that were used in Experiment 1 may reveal prospective coding. The testing procedure used in Experiment 2 avoids the problems of the correction procedures in Experiment 1. First, all trials in Testing 3 of Experiment 2 included a two-alternative forced choice in which the probability of choosing correctly by chance was always 50%. This procedure made it equally likely for impulsive choices to end without reinforcement at all PDIs (i.e., it was not better for pigeons to be impulsive at the beginning vs. the end of a trial). These trials included a stopping point (a 0 sec delay on control trials and a 30 sec delay on delay trials), which should also minimize impulsive responses. Incorrect choices were followed by the ITI and no reinforcement was provided on that trial.
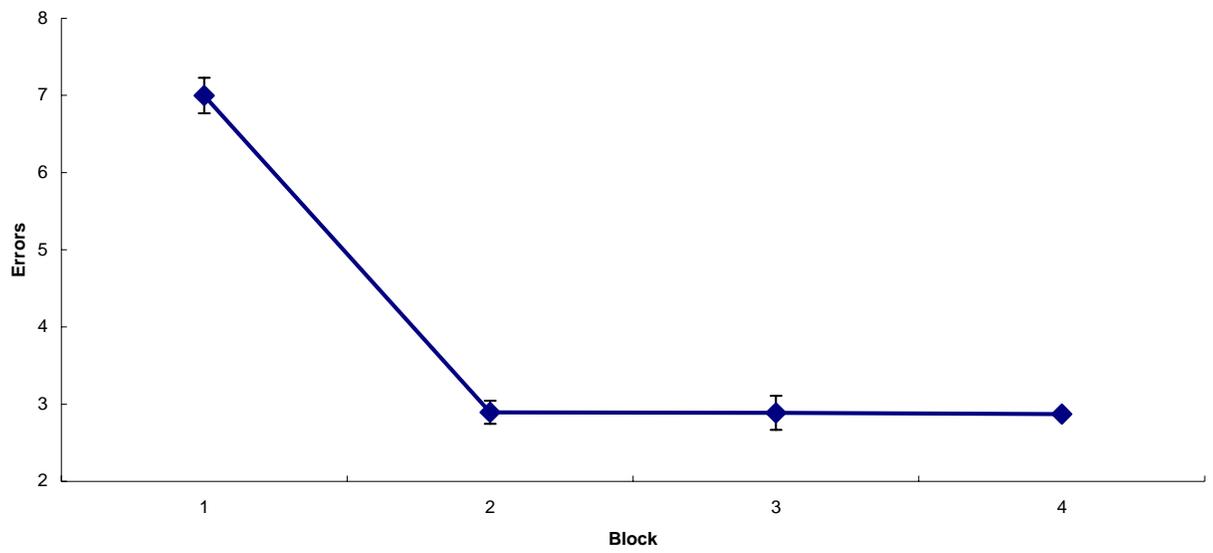
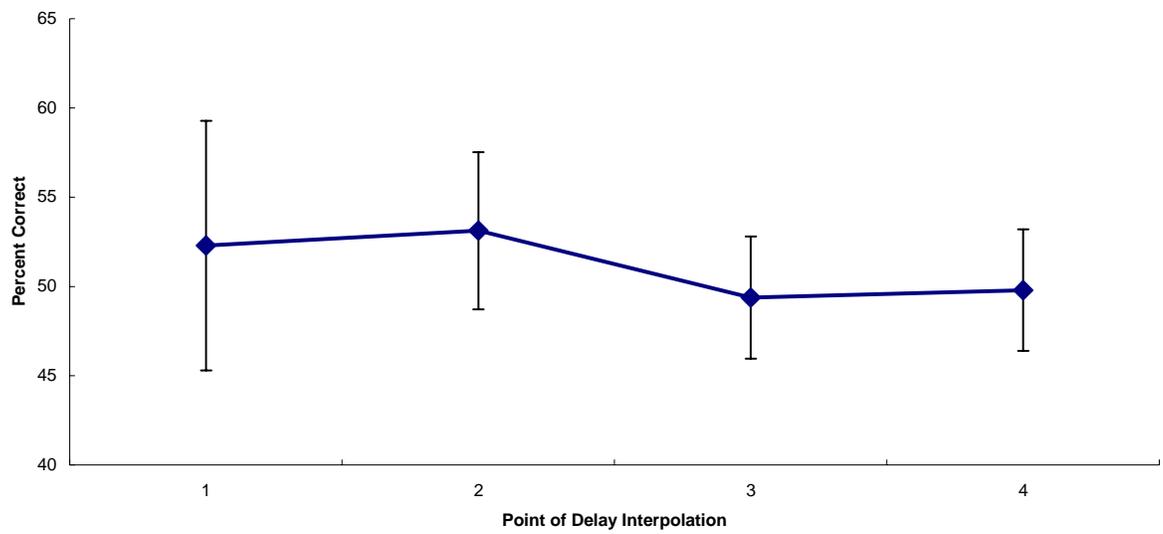Figure 6. Errors on Training Trials in Experiment 2.

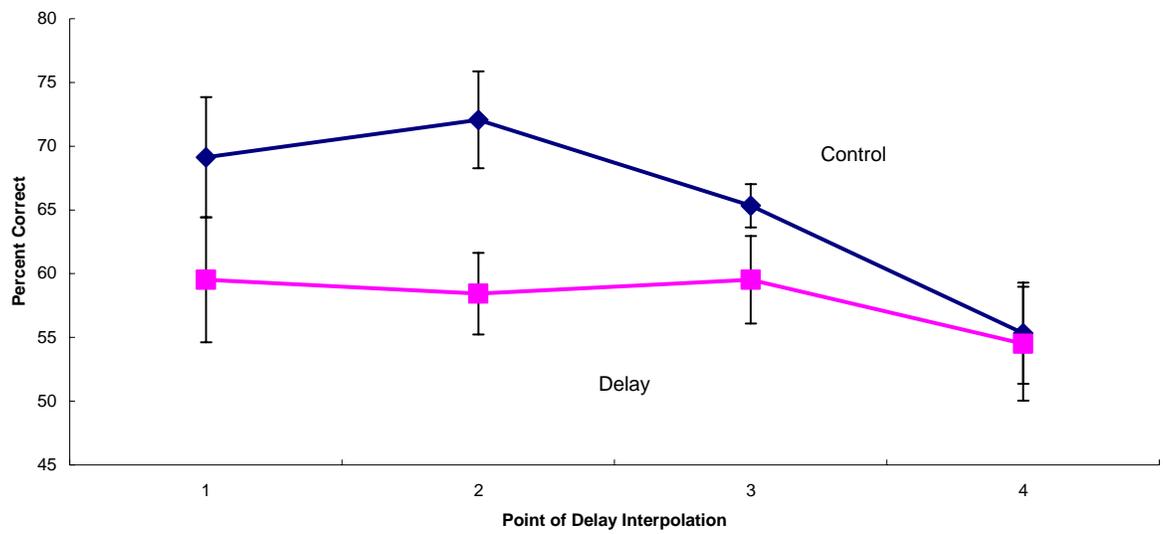Figure 7. Performance on Delay Trials (Testing 1) in Experiment 2.

Figure 8. Control and Delay Performance (Testing 2) in Experiment 2.
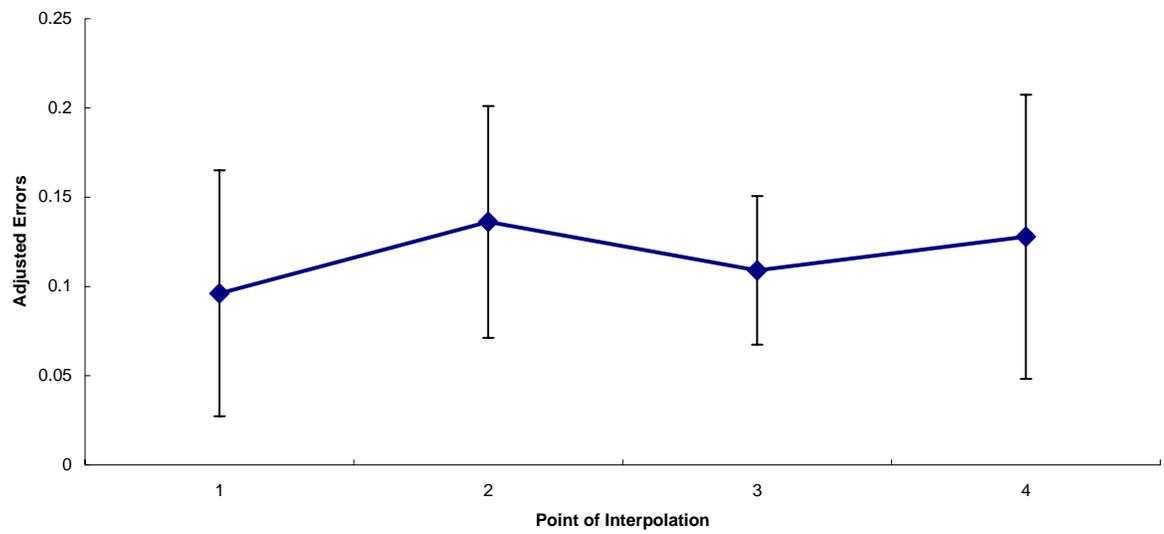
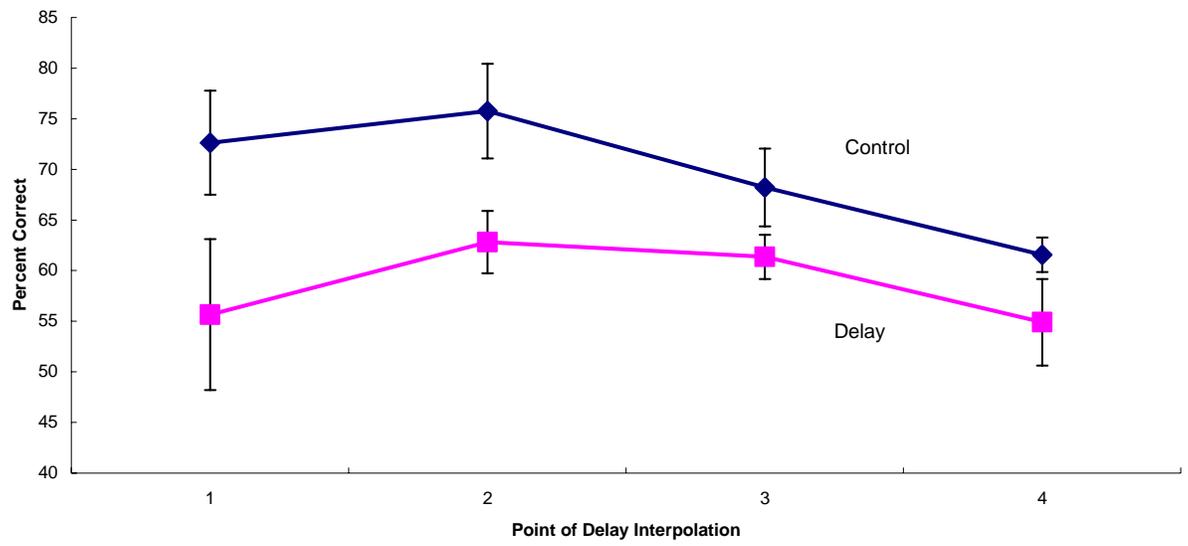Figure 9. Errors Attributable to the Delay (Testing 2) in Experiment 2.

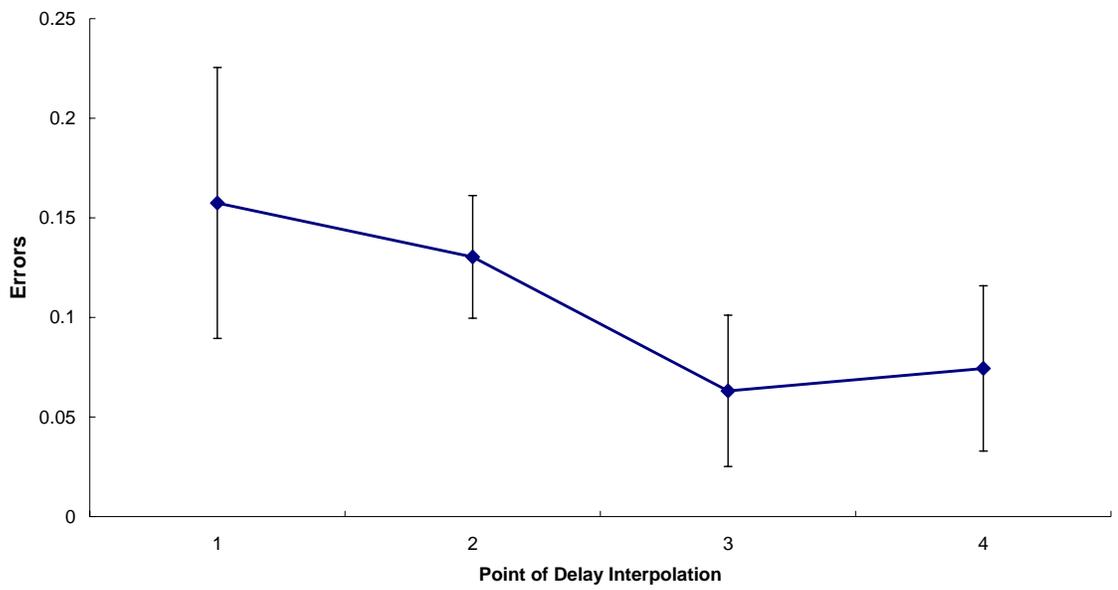Figure 10. Control and Delay Performance (Testing 3) in Experiment 2.

Figure 11. Errors Attributable to the Delay (Testing 3) in Experiment 2.

Chapter Four

Experiment 3

Experiment 3 was conducted to determine whether the pigeons in Experiments 1 and 2 were using different coding strategies or if the correction procedure used in Experiment 1 was responsible for the differences found. This experiment also tested the reliability of the procedure used in Experiment 2. The pigeons that were used in Experiment 1 were tested with the two-alternative forced choice procedure used in Experiment 2. If the pigeons in Experiment 1 were using dual coding then testing them with the two-alternative forced choice procedure with separate control trials should reveal an error function that increases from PDI 1 to PDI 2 and decreases from PDI 3 to PDI 4. If they were using prospective coding, the two-alternative forced choice procedure with separate control trials will reveal an error function that starts out high at PDI 1 and decreases as PDI increases.

Therefore the results are expected to be consistent with either dual coding or prospective coding. If the results are consistent with dual coding, it would suggest that these pigeons were using a different strategy than those birds used in Experiment 2. If the results are consistent with prospective coding, it would suggest either that these pigeons switched from dual coding to prospective coding or that they were coding prospectively in Experiment 1 and the correction procedure gave the illusion of dual coding in Experiment 1. It is also possible that the results of Experiment 3 will be consistent with prospective coding even though these pigeons were using dual coding in Experiment 1 (the former hypothesis). That is, pigeons used the most efficient strategy in Experiment 1 and switched to a less efficient strategy, prospective coding, in Experiment 3.

Method

Subjects

The six pigeons that were used in Experiments 1 were subjects in Experiment 3.

Apparatus

The same operant chamber used in Experiments 1 and 2 were used in Experiment 3.

Procedure

After completing Delay Testing in Experiment 1, the pigeons were immediately tested using the two-alternative forced choice procedure that was used in Testing 3 of Experiment 2. Specifically, there were 3 trials at each PDI per session. Because of the large number of delay and control trial types, delay and control sessions were alternated daily. On control trials, pigeons made the number of correct choices as determined by PDI then a 0 sec delay was interpolated. At this point a two-alternative forced choice was presented in which pigeons were rewarded for choosing the key that had not been chosen earlier during that trial. Delay trial sessions were identical except that a 30 sec delay was interpolated instead of a 0 sec delay. Pigeons were tested for a total of 60 sessions (30 delay sessions and 30 control sessions, 12 trials per session).

Results

Performance at each PDI was calculated for control and delay sessions separately and is shown in Figure 12. Performance on control sessions was on average higher at each PDI than performance on delay sessions. Control session performance decreased with increasing PDI. Delay session performance was higher at PDIs 2 and 3 than at PDIs 1 and 4. Performance on delay sessions was subtracted from performance on control sessions to obtain a difference score at each PDI. The difference function represents errors attributable to the delay. This function suggests that errors decrease with increases in PDI and is shown in Figure 13.

A 2 (trial type, control vs. delay) X 4 (PDI) ANOVA was conducted using the percent correct on each trial type. The ANOVA showed a significant main effect of trial type, $F(1, 5) = 25.75$, $p < .05$ and a significant main effect of PDI, $F(3, 15) = 3.59$, $p < .05$. Finally, there was a significant interaction, $F(3, 15) = 12.33$, $p < .05$. Contrasts revealed a significant linear trend for the Trial Type X PDI interaction, $F(1, 5) = 32.00$, $p < .05$.

Discussion

Using the two-alternative forced-choice procedure, pigeons performed better on control sessions than on delay sessions. The difference in performance between control

and delay sessions decreased from PDI 1 to PDI 4. As in Experiment 2 these results are consistent with a prospective coding strategy in which to-be-chosen keys are remembered throughout the trial.

These results suggest that the error correction (correction for opportunity with control trial errors subtracted from delay trial errors at each PDI) used on the data in Experiment 1 may have been responsible for the shape of the error function (consistent with dual coding). Specifically, the assumption that factors that affected choices on control trials were the same at each PDI to those that affected choices on delay trials may not be valid. Although pigeons may make impulsive choices early on control trials, a delay could make impulsive errors less likely on delay trials. This non-memorial factor is a plausible cause for an inflated PDI 1 (and possibly PDI 2) control trial error rate, which would make low errors attributable to the delay at PDI 1 an artifact of this procedure. The procedure used in Experiments 2 and 3 provided a more appropriate control procedure in which non-memorial factors should have the same effect on delay trials at all PDIs and on control trials as compared with delay trials. For example, errors on one trial type had no effect on errors on other trial types because data were collected for control and delay trials at each PDI separately (i.e., one control trial did not provide data for all PDIs). Using this procedure, control and delay trials included a stopping point after which the two-alternative forced choice was presented. These characteristics made control and delay trials as similar as they could be while still including a delay on delay trials. This procedure ensured that non-memorial factors (e.g., impulsivity) were more similar on control and delay trials than in Experiment 1. When this procedure was used the results suggested that prospective coding was used. The results of Experiment 3 provide further support for prospective coding, which predicted that errors attributable to the delay would start out high and decrease with increasing PDI.
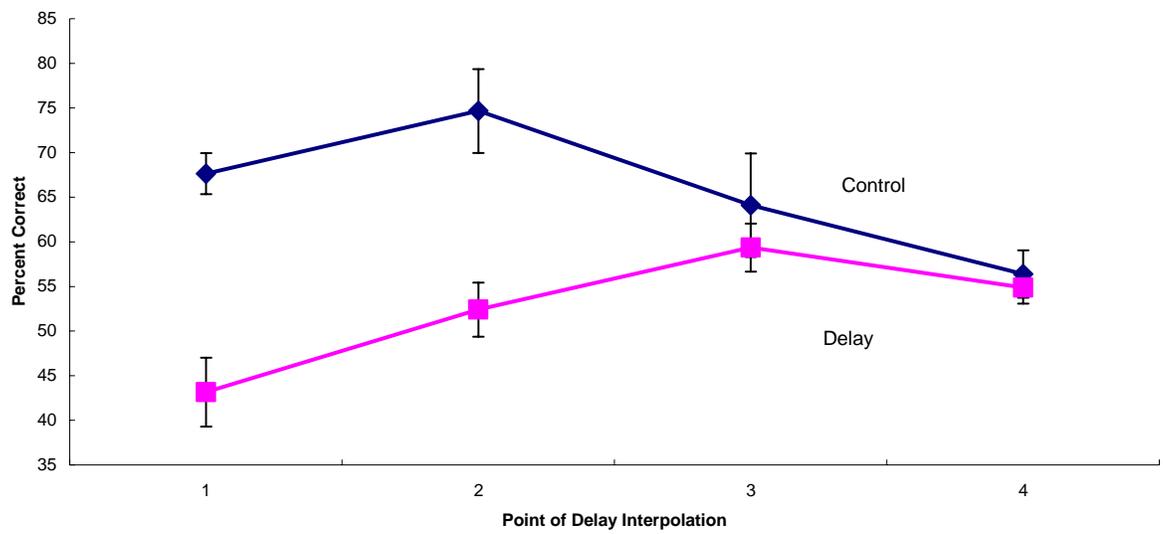
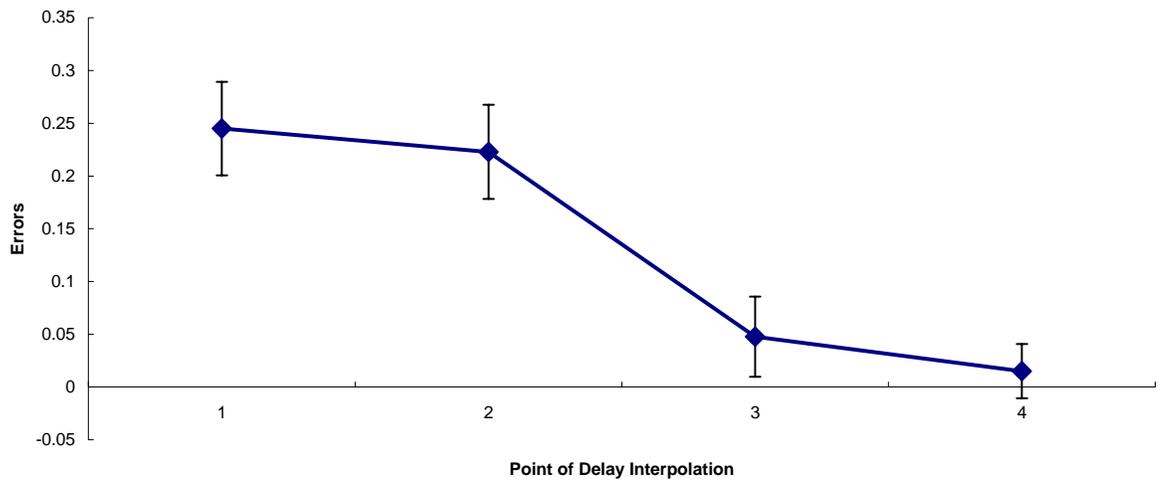Figure 12. Control and Delay Performance in Experiment 3.

Figure 13. Errors Attributable to the Delay in Experiment 3.

Chapter Five

Experiment 4

Experiments 2 and 3 were designed to test the dual coding strategy without having to make assumptions about the way choices were affected by the changing probability of making an error by chance. The results of these experiments support a prospective coding account. Examination of the trial-by-trial data did not suggest that any of the pigeons used a preferred sequence of choices to complete control or delay trials however, a relative preference could have affected their choice strategy. For example, if a pigeon preferred to choose certain response keys later in the choice sequence they would have been placed in the "to be chosen" array by the computer on late PDI trials. If a least preferred key at the start of the trial was green, the pigeon could have learned to avoid the green response key on late PDI trials and could have performed using this strategy until given a two-alternative choice. A pigeon with strong least preferred key preferences could have performed better at late PDIs than at early PDIs with this strategy. If this type of strategy directed choice behavior, the results could reflect an artifact instead of differences in memory load across PDIs. Experiment 4 attempted to rule out this remote possibility by using a forced response procedure before and a forced choice procedure after the delay to make it impossible for pigeons to perform based on a preferred choice sequence. It used the same procedure as in Experiments 2 and 3 after the delay, but it forced pigeons to make a randomly selected sequence of responses before the delay. Using a forced choice sequence before the delay would eliminate the use of this strategy.

Method

Subjects

Six pigeons of the same type and maintained in the same way as in Experiments 1, 2, and 3 were subjects in Experiment 4.

Apparatus

The same operant chamber used in Experiments 1, 2, and 3 were used in Experiment 4.

Procedure

Pre-training and Training. Pigeons in Experiment 4 were not trained like the pigeons in Experiments 1, 2, and 3. They began the experiment with the same pre-training procedures, but instead of beginning training as pigeons in Experiments 1, 2, and 3, they experienced four types of forced choice trials. On each trial the computer randomly chose a previously not pecked key to be presented. Just as in Experiments 1, 2, and 3, there was one trial type for each PDI. Response keys were illuminated individually until the predetermined number of correct responses had been made. After the pre-determined number of responses had been made, the computer program presented one key that had been pecked previously on that trial and one key that had not yet been pecked. The pigeons chose between these two keys and were reinforced for choosing the key that had not been pecked earlier in the trial. Choice of the key that had not yet been pecked was reinforced. Incorrect choices were followed by the correction procedure described in Experiment 2 in which the same two response keys were presented until a key had been chosen. Correct choices were followed by reinforcement and incorrect choices were followed by a 2.5 sec period of darkness. Following the 2.5 sec of darkness, the same two keys were re-illuminated for a choice. This procedure was repeated until the correct choice had been made. Reinforcement was followed by the 60 sec lit ITI. There were twelve trials, three at each PDI. Pigeons were trained with this procedure for 60 sessions. Beginning with session 61, pigeons began training without the correction procedure for 20 sessions.

Results

Percent correct at each PDI was calculated for each pigeon and is shown in Figure 14. Although performance was poor overall, performance at early PDIs was better than performance at later PDIs. A two-way ANOVA was conducted using these data with PDI and block as the factors. There was a main effect of PDI, $F(3, 15) = 4.55$, $p < .05$, with a significant linear trend, $F(1, 5) = 11.59$, $p < .05$. There was no effect of block, $F(5, 25) = 2.02$, $p > .05$ and no PDI X Block interaction, $F(15, 75) = 1.35$, $p > .05$.

Performance at each PDI was calculated for training sessions without repeats and is shown in Figure 15. As in training sessions with repeats, performance in training sessions without repeats was poor overall. An ANOVA was conducted with PDI and

block as the factors. There was no effect of PDI, $F(3, 15) = 1.74$, $p > .05$, no effect of block, $F(1, 5) = .192$, $p > .05$, and no interaction, $F(3, 15) = .52$, $p > .05$.

Discussion

The results of Experiment 4 suggest that this training procedure is qualitatively different from the training procedure used in Experiments 1 and 2. Unlike the training procedure used in previous experiments in which revisits could be made, this training procedure presented one key at a time before the forced-choice. The inability to make revisits during training apparently hindered accurate performance. Performance did not improve in the first 6 blocks of training. The use of repeats was discontinued after 6 blocks in order to discourage impulsivity at choice, but performance remained poor in the 2 blocks of training without the repeat procedure. Pigeons were unable to achieve a high level of accuracy using this training procedure.

These results are surprising because the errorless training procedure was expected to remove the factor that presumably made it difficult to learn the training task used in Experiments 1 and 2, namely the tendency to return to previously chosen keys. These unexpected results suggest that the pigeon's role in choosing a sequence of keys could be important in the ability to remember that sequence. That is, it could be easier for the pigeon to remember a sequence of keys that it had chosen as compared to a series of keys that had been chosen by the computer. This hypothesis suggests that key preferences may play a significant role in memory for choices in this task. Even though this experiment was unsuccessful, the testing procedure could be used in the future to rule out preferred choice sequences by including probe trials in testing sessions for pigeons already familiar with avoiding previously visited keys.
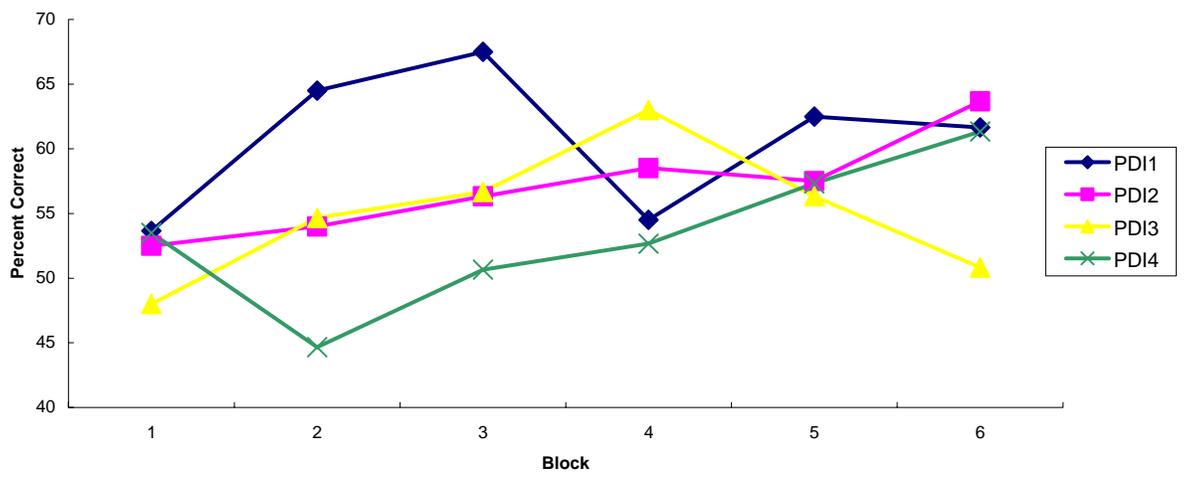
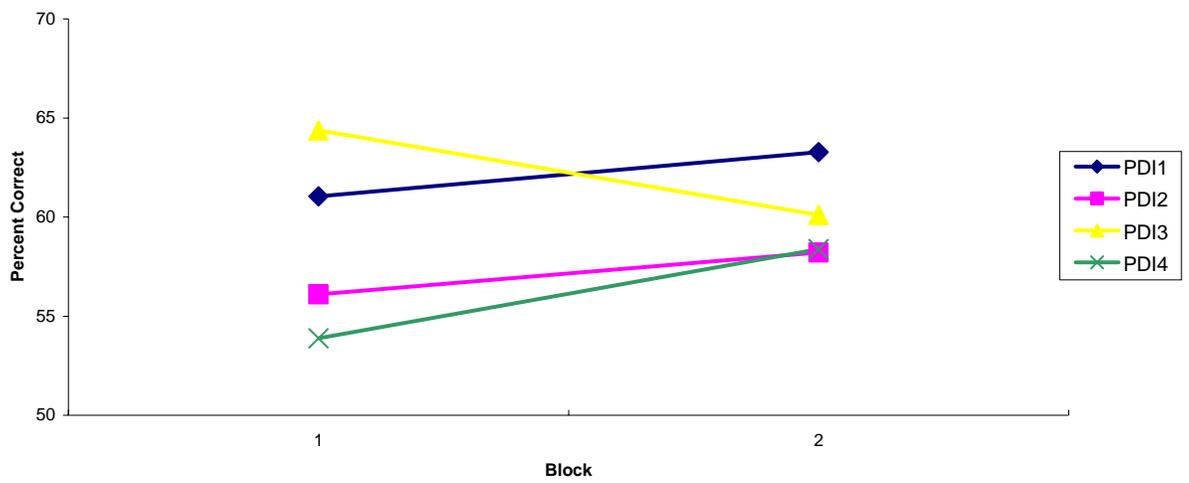Figure 14. Performance During Training (With Repeats) in Experiment 4.

Figure 15. Performance During Training (Without Repeats) in Experiment 4.

Chapter Six

General Discussion

These experiments were designed to replicate and extend the results of Zentall et al. (1990) by providing a test of the criterion shift hypothesis. The criterion shift hypothesis states that pigeons code retrospectively and that they make choices more carefully at later PDIs when the probability of making an error by chance increases. More specifically, they choose more carefully on delay trials than they do on control trials. The present results suggest, however, that pigeons use a prospective coding strategy to acquire the radial maze analog task, and not a dual coding strategy as previously found by Zentall et al. This novel finding in Experiment 2 was replicated in Experiment 3 with the same pigeons that were used in Experiment 1. The results of Experiments 1, 2, and 3 are inconsistent with the criterion shift hypothesis, which predicted that retrospective coding would be used. Instead, Experiments 2 and 3 suggest that pigeons in Experiment 1 were making choices less carefully at earlier PDIs on control trials than on delay trials.

There are two explanations for the types of coding found in Experiment 1 (dual coding) and Experiments 2 and 3 (prospective coding). First, it is possible that pigeons were using dual coding in Experiment 1 and prospective coding in Experiments 2 and 3. In this case, the testing procedure would encourage the specific coding strategy that was used. While it is possible that the testing procedure used in Experiment 1 encouraged dual coding and the testing procedure used in Experiments 2 and 3 encouraged prospective coding, it is an unlikely explanation considering the fact that the same pigeons were used in Experiments 1 and 3. If this explanation is correct, it would mean that the pigeons in Experiment 1 switched from using a more efficient coding strategy, dual coding, to a less efficient coding strategy, prospective coding, upon testing in Experiment 3.

An alternative is that pigeons in Experiments 1, 2, and 3 were coding prospectively, but the correction procedures used in Experiment 1 altered the results to appear consistent with a dual coding strategy. The subtraction method used in Experiment 1 is an adequate control procedure when certain assumptions are met. Specifically, it is assumed that the only factor affecting choices on delay trials as compared to control trials is the actual delay. If this assumption is met, the error function

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that is produced represents errors that are attributable to the delay. This correction uses control trials to represent non-memorial factors at each PDI. For example, impulsivity is a non-memorial factor that could affect choices on control and delay trials. The subtraction method assumes that impulsivity affects choices on PDI 1 delay and PDI 1 control trials equally. Unfortunately, this procedure does not accommodate irregularities in the way non-memorial factors could affect choices across PDIs. If some non-memorial factors affect control trials differently from delay trials, the procedure would not be an adequate control procedure.

There are many ways in which non-memorial factors could affect control trials differently from delay trials. The testing procedure used in Experiment 1 allowed pigeons to make free choices before and after the delay. The control trials did not have a delay, but a pseudodelay was used in which choices were examined for repeats as if a delay had been interpolated at each PDI. However, on control trials, there is no stopping point in the trial as on delay trials. This procedural difference may have created differences in the way these kinds of trials are completed. For example, the tendency to make impulsive choices could have been exaggerated on early (PDI 1 and 2) control trials as compared to delay trials (PDI 1 and 2) because on delay trials the delay may have inhibited impulsivity. In this case there would be more errors on early control trials than on early delay trials that are due to non-memorial factors. These errors will be subtracted from errors on delay trials providing an erroneously low difference score between PDI 1 and 2 control and delay trial errors. These results would give the appearance of dual coding instead of prospective coding. The combination of prospective coding and making choices more carefully at later PDIs on control trials in Experiment 1 explains the differences between this error function and those from Experiments 2 and 3.

Experiment 4 used a training procedure that was very difficult for the pigeons to learn and they never met the training criterion. There were many differences between this procedure and that used in Experiments 1 and 2. Most notably, the pigeons could not make errors before the test. This difference could have made it more difficult to learn to avoid previously chosen keys when presented with the forced choice. Furthermore, the repeat procedure, while meant to facilitate learning, may have reduced the cost of making an error. A follow-up experiment could train pigeons using the same procedure as

Experiments 1 and 2 and test with the control trials used in Experiment 4 and delay trials that are identical except for the delay. For example, these pigeons could be trained to avoid revisits to previously visited keys until the training criterion had been met, fewer than three revisits per trial. Then they could be tested using control trials in which keys are presented randomly as dictated by PDI before the test. Delay trials would be identical except that a 30 sec delay would be interpolated prior to the test. Using this procedure, performance on control trials and delay trials can be compared.

While the results of Experiments 2 and 3 provide evidence for prospective coding, additional tests would confirm these findings and could eliminate alternative accounts. Brown, Wheeler, and Riley (1989) used signal detection analysis to ask whether rats use retrospective, prospective, or dual coding in the radial arm maze. They wanted to extend Cook et al.'s (1985) findings by measuring two processes independently, the choice criterion and the coding strategy. They trained rats on a 12 arm radial maze. The testing phase consisted of forced choices according to PDI. They used the same PDIs as Cook et al., 2, 4, 6, 8, and 10. After a 15 minute delay, one maze arm was made available along with a center manipulandum. On half of these trials, the available maze arm had not been visited prior to the delay and choice of this arm was reinforced. Choice of the center manipulandum was not reinforced. On the other trials, the available maze arm had been visited prior to the delay and choice of the center manipulandum was reinforced, while choice of the maze arm was not reinforced. This procedure allowed analysis of two kinds of errors. First, a failure to choose the maze arm when it had not been visited before the delay (miss) and second, incorrectly choosing the maze arm when it had been visited before the delay (false alarm). This procedure, which allows the rat to accept or reject a single maze arm, provides a measure of the ability to determine which arms have been visited prior to the delay and a measure of the criterion used to make choices. The authors found that the ability to discriminate between visited and unvisited arms decreased with increasing PDI. These results are consistent with retrospective coding. They also found that rats were more likely to reject already visited maze arms as the PDI increased, suggesting that rats make choices more carefully at later PDIs. These results support the criterion shift hypothesis in which a retrospective coding strategy is used and the care with which choices are made increases as the probability of making an error increases.

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Brown et al.'s (1989) findings are of note in light of the current findings because similar tasks would be expected to elicit the same coding strategy in rats and pigeons. Both the radial maze and the radial maze analog task used in the current experiments require that each arm/key be chosen once and revisits are to be avoided. There are obvious differences that are necessary due to the different species being tested. Rats acquire the radial maze task easily because it is similar to their natural foraging strategy, a win-shift strategy. Rats visit each maze arm once and eat the food that is located at the end of each arm. Revisits to previously chosen arms are not reinforced because the food has already been removed. This strategy is easy to use for animals, like rats, that naturally find small amounts of food in various places and must avoid those places visited most recently while the food is replenished. On the other hand, pigeons are naturally win-stay animals that often find large amounts of food in a particular location. Their radial maze analog task requires many sessions of training to discourage their natural tendency to revisit previously chosen keys. Perhaps this difference in natural foraging behavior makes retrospective coding more likely in rats and prospective coding more likely in pigeons. Rats are capable of using retrospective coding in the radial arm maze with much success, however, because pigeons have difficulty in learning the analogous task, using a retrospective code may lead to more errors. For example, a retrospective code (remembering previously chosen keys) may encourage revisits during the training phase by focusing attention on previously visited (incorrect) keys. By remembering previously visited keys, pigeons may be more tempted to make revisits than they would if they used a prospective code. Their tendency to make many revisits early in training may make prospective coding a better strategy for pigeons because only to-be-visited keys are remembered. In this task, these keys are the correct keys, whereas, a retrospective strategy dictates memory for the incorrect keys. Prospective coding may promote accuracy during acquisition of the task.

It is assumed that before the delay pigeons represent the whole sequence of five keys. As choices are made, those keys are marked or flagged in some way. After extensive experience with the delay testing procedure, pigeons learn that they are less likely to be reinforced after the choice point on delay trials. Because of this, pigeons need to develop a memory strategy in order to receive more reinforcement on delay trials. The

error data suggest that during the delay, they remember the to-be-chosen keys. The finding of prospective coding has important cognitive implications. These findings are important because they suggest that unlike with a retrospective code, pigeons remember choices that have not been completed yet. Retrospective coding is somewhat less complex because in its simplest form it requires memory for choices that have been made or stimuli that have already been presented. The pigeon could merely remember a list of previously chosen keys. Prospective coding, however, suggests that pigeons remember the set of choices that have not been made, or choices that they plan to make. In other words, they must represent events that have not yet taken place. Suddendorf and colleagues (Busby & Suddendorf, 2005; Suddendorf & Busby, 2005; Suddendorf & Corballis, 1997) argue that humans are capable of a more complex type of planning for future events called mental time travel. While they suggest that non-human animals are incapable of the level of mental time travel that humans possess, the present findings suggest that pigeons are able to represent choices that they plan to make, which consists of a more complicated representation than that required by retrospective coding.

Using a go/no-go procedure with pigeons as Brown et al. (1989) did with rats could provide additional evidence for prospective coding in pigeons. The signal detection method, with separate "miss" and "false alarm" scores, could test for prospective coding without using separate control trials. Pigeons could be tested with one response key following the delay. A response to previously unchosen keys would be reinforced, while responses to previously chosen keys would not be reinforced. Withholding responding to previously chosen keys would be reinforced, while withholding responding to previously unchosen keys would not be reinforced. Analysis of misses and false alarms would provide information about the ability to discriminate between visited and unvisited keys and the criterion used to reject keys. Prospective coding would predict that it would be easier to discriminate between visited and unvisited keys as PDI increases. With a go/no-go response at each PDI, the criterion used to choose keys is not expected to change over PDIs. The results of this follow-up experiment could provide converging evidence for prospective coding in this task.

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