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THE MIDSESSION REVERSAL TASK WITH PIGEONS: EFFECTS OF A BRIEF DELAY BETWEEN CHOICE AND REINFORCEMENT

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THE MIDSESSION REVERSAL TASK WITH PIGEONS:
EFFECTS OF A BRIEF DELAY
BETWEEN CHOICE AND REINFORCEMENT

THESIS

A thesis submitted in partial fulfillment of the
requirements for the degree of Master of Science in the
College of Arts and Sciences
at the University of Kentucky

By

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2020

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ABSTRACT OF THESIS

THE MIDSESSION REVERSAL TASK WITH PIGEONS: EFFECTS OF A BRIEF DELAY BETWEEN CHOICE AND REINFORCEMENT

During a midsession reversal task, the session begins with a simple simultaneous discrimination in which one stimulus (S1) is correct and the alternate stimulus (S2) is incorrect (S1+/S2-). At the halfway point, the discrimination reverses and S2 becomes the correct choice (S2+/S1-). When choosing optimally, a pigeon should choose S1 until the first trial in which it is not reinforced and then shift to S2 (win-stay/lose-shift). With this task pigeons have been shown to respond suboptimally by anticipating the reversal (anticipatory errors) and continuing to choose S1 after the reversal (perseverative errors). This suboptimal behavior may result from a pigeon's relative impulsivity due to the immediacy of reinforcement following choice. In other choice tasks, there is evidence that the introduction of a short delay between choice and reinforcement may decrease pigeons' impulsivity. In the present experiment, a delay was introduced between stimulus selection and reinforcement in the midsession reversal task to assess whether anticipatory and perseverative errors decrease. The results showed a significant difference between the no-delay and delay groups for overall accuracy only during Sessions 11-20, with the no-delay group performing better than the delay group. There was no significant difference in overall accuracy during any other block of ten sessions. These results imply that the insertion of a delay may result in slower learning of this task.

KEYWORDS: midsession reversal, delay to reinforcement, anticipatory errors, perseverative errors, impulsivity, pigeons

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02/19/2020

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CHAPTER 1. INTRODUCTION

A mid-session reversal task involves a simple simultaneous discrimination in which one stimulus (S1) is correct (S1+) for the first half of a session and another stimulus (S2) is incorrect (S2-). At the midpoint of the session, the stimuli switch roles so that S2 is now correct (S2+) and S1 is incorrect (S1-). The midsession reversal can be used to assess how an animal, human or non-human, adapts to the feedback it receives following each trial. In order to respond optimally, if the animal cannot accurately count half of the trials, an organism should utilize a win-stay/lose-shift strategy. For example, if reinforcement was provided (win), the same stimulus should be chosen on the next trial (stay). However, if there was no reinforcement (lose), the alternate stimulus should be chosen on the next trial (shift). Several animals have been shown to use a win-stay/lose-shift strategy when presented with a mid-session reversal task including apes and monkeys (Beran, Klein, Evans, Chan, Flemming, Harris et al. 2008), horses (Martin, Zentall & Lawrence, 2006), and birds (Bond, Kamil & Balda, 2007), but pigeons have shown suboptimal performance with this task.

A study examining mid-session reversal in both pigeons and humans was conducted by Rayburn-Reeves, Molet, and Zentall (2011). Experiment 1 involved a color discrimination between red and green lights. Subjects were trained for 50 sessions and each session consisted of 80 trials, with a reversal occurring after trial 40. S1 was correct for the first 40 trials (S1+/S2-) and S2 was correct for the last 40 trials (S2+/S1-). At the beginning of each trial, one key was illuminated red and the other was illuminated green. A single peck to either the red or green stimuli

turned off both keys and produced reinforcement together with an intertrial interval (ITI) for correct selections or just an ITI for incorrect selections. Over the course of the session, the colors were counterbalanced over the left and right keys to control for side preference. For half of the subjects, red was the S1 and for the other half green was the S1. The results showed that pigeons chose S1 almost exclusively during the early trials of a session, but choice of S1 began to decline as the reversal approached. Choice of S1 continued to decline until subjects were almost exclusively choosing S2 towards the end of the session. Subjects were approximately 70% accurate during the five trials preceding the reversal (36-40) and approximately 55% accurate during the five trials immediately following the reversal (41-45). These results indicate that pigeons were anticipating the reversal, by choosing S2 while S1 was still correct (anticipatory errors) and they continued to choose S1 even after the reversal when S2 was correct (perseverative errors). This indicates that pigeons did not use the feedback from each trial sufficiently and instead relied on the passage of time or an estimation of trial number.

To try to get the pigeons to avoid using the passage of time or trial number as the basis for switching choice, in Experiment 2, the same basic procedure was implemented except the reversal did not always occur after trial 40. Instead, the reversal varied from session to session. Each bird was trained for 100 sessions, with the reversal occurring unpredictably in the session at various points in the session: Following Trial 10, 25, 40, 55 or 70. With this procedure the pigeons showed few anticipatory errors when the reversal occurred early in the session, but many perseverative errors. Conversely, when the reversal occurred late in the

session, there were few perseverative errors, but a large number of anticipatory errors. The greatest accuracy was observed when the reversal occurred at the midpoint, after trial 40. The worst performance was observed when the reversal occurred near the end of the session. This result shows that even when the reversal is varied and unpredictable, pigeons still relied on timing- or trial-based reference memory as opposed to relying on immediate feedback from the preceding trial. In Experiment 3, the same procedure was used, except 20 pecks were required to make a selection and turn off the response keys. The only significant difference between Experiment 2 and 3 was there were significantly more anticipatory errors in Experiment 3, when 20 pecks were required to make a selection. As noted in previous experiments, pigeons still showed a time- or trial-based strategy instead of win-stay/lose-shift.

The purpose of Experiment 4 was to determine if humans were able to implement a win-stay/lose-shift strategy with a similar mid-session reversal task. In this experiment, participants completed a discrimination between cards (10 of spades and 10 of clubs). Participants were given 10 sessions of 24 trials each with the reversal occurring after Trial 12. During the first five sessions, there was a decrease in choice of S1 from Trial 13, 96%, to Trial 14, 18%. This result suggests that most subjects were adopting very close to a win-stay/lose-shift strategy. Experiment 5 involved the same task, however the reversal point in the session was varied, similar to Experiment 2. The reversal occurred equally often after Trials 5, 9, 13, 17, and 21. With this task, participants could no longer attempt to predict when the reversal would occur, and they all adopted a clear win-stay/lose-shift

strategy. These experiments show a difference between a pigeon's and a human's ability to implement the optimal strategy under similar conditions. In later studies, modifications to the mid-session reversal task were explored to attempt to decrease both anticipatory and perseverative errors.

Rayburn-Reeves, Laude and Zentall (2012) conducted a mid-session reversal study with pigeons using a spatial discrimination with varying ITI lengths. For example, for half the subjects S1 was the left key and S2 was the right key and for the other half S1 was the right key and S2 was the left key. The ITI was varied to assess its effect on accuracy. They hypothesized that shortening the intertrial interval (ITI) might increase accuracy by improving the pigeon's ability to use the stimulus (location) and outcome of the previous trial's selection to make its choice on the next trial. During the first phase of the study, birds were randomly assigned to one of three ITI durations: 1.5s, 5s, or 10s. Each pigeon had 40 sessions during the first phase that consisted of 80 trials run similarly to Experiment 1. However, this experiment utilized locations as the discriminative stimuli instead of color and the ITI varied between groups.

Phase 1 results showed significantly higher accuracy over the last ten sessions of training (31-40) in birds assigned to the 1.5s ITI and especially the five trials immediately before the reversal point as compared to both the 5s ITI group and the 10s ITI group. Thus, reducing the ITI duration improved anticipatory errors but did not influence perseverative errors.

Following Phase 1, two pigeons were randomly selected from the 5s ITI group and the 10s ITI group and moved to the 1.5s ITI group for Phase 2. An

additional 80 sessions, identical to Phase 1 were completed followed by 100 sessions in which the reversal point varied from session to session as in Experiment 2 above. During Phase 2, the pigeons that were transferred to the 1.5s ITI group showed the same responding pattern as the birds that were initially in the 1.5s ITI group. Phase 3 results continued to show fewer anticipatory errors with the shortest ITI, but no significant difference in perseverative errors across ITIs.

These results indicate that pigeons can implement a win-stay/lose-shift strategy when the ITI is relatively short. However, with a spatial discrimination, a short ITI allows the bird to anticipate a quick move from the feeder to the correct location (right or left) with little pause. This repeated anticipatory movement may account for the decreased anticipatory errors with the short ITI because the improvement in accuracy was not found when the discrimination involved colors, the location of which could not be anticipated (Laude, Stagner, Rayburn-Reeves & Zentall, 2014). Additionally, since all three groups had almost identical accuracy on the trials following the reversal, the ITI duration seems to reduce only anticipatory errors.

The question that remains is why pigeons continue to make anticipatory and perseverative errors even after many sessions of training. Smith, Beckmann, and Zentall (2017) hypothesized that pigeons may defer to a time-based strategy to predict the reversal, thus making anticipatory and perseverative errors, because they are unable to remember what stimulus was chosen on the previous trial and what the outcome of the selection was. In that study they tested whether cueing pigeons, with the use of houselights during the ITI, to indicate the stimulus that

was selected on the previous trial and whether the response was correct, might serve as a reminder and decrease errors. The experimental group received feedback during the ITI intended to remind the subjects of the cue selected on the previous trial and the outcome, while the control group received no relevant cue. When the experimental group pecked the S1 or S2 key, a houselight (panel light or ceiling light) corresponding to that stimulus illuminated. If the pigeon selected the correct stimulus, the feeder light was illuminated during the reinforcement and it stayed on during the ITI. In this way the houselights could serve as a reminder of what stimuli was chosen, and the feeder light could indicate if reinforcement had occurred or not. For the control group, during the ITI either the panel light or the ceiling mounted light would illuminate randomly. The results indicated that the experimental group was more accurate and was more sensitive to the reversal than the control group. Although the relevant cues improved accuracy, both groups continued to show anticipatory and perseverative errors. That is, neither group showed evidence of a win-stay/lose-shift choice pattern, suggesting that even the cued group was still relying on a time-based strategy.

To determine the extent to which the two groups were relying on temporal cues, in Experiment 2a, the duration of the ITI was manipulated. On every fourth session the ITI was either doubled to 10.0s or halved to 2.5s. The results showed that the cued group and control group were still relying on temporal cues. During the 2.5s ITI sessions an increase in perseverative errors was observed, while an increase in anticipatory errors was observed during the 10s ITI sessions.

Thus, several studies highlight the difficulty that pigeons have in learning to adopt a win-stay/lose-shift strategy. Laude, Beckmann, Daniels and Zentall (2014) conducted a suboptimal choice task in which pigeons were presented with a choice between a vertical line or a horizontal line. A single peck to the vertical line changed the stimulus to a red hue 20% of the time followed by a 10 pellet reinforcement. However, 80% of the time the stimulus changed to a green hue and no reinforcement followed. A single peck to the horizontal line changed the stimulus to yellow 20% of the time and to blue 80% of the time, but with either hue the reinforcement was 3 pellets. Pigeons tended to prefer the vertical line as compared to the horizontal line, despite it resulting in less reinforcement overall. These results indicated that pigeons' tendency to choose suboptimally in a gambling-like task was correlated with their level of impulsivity as shown by a delay-discounting task. It is hypothesized that the pigeons' impulsivity may hinder their acquisition of win-stay/lose-shift behavior.

1.1 Delay between choice and reinforcement

Interestingly, a number of studies have found that tasks that should be relatively easy to learn have proven to be quite difficult when the choice response involves a single peck followed immediately by reinforcement. In those studies, learning has been facilitated, paradoxically, by increasing the time between the choice response and reinforcement. This increase in time may encourage pigeons to choose more carefully and thus reduce impulsive choice.

For example, in the ephemeral choice task, the animal is given a choice between two stimuli, S1 and S2, choice of either one results in an identical reinforcer. If the animal chooses S1, it gets the reinforcer and the trial is over. However, if the animal chooses S2, it gets the reinforcer but S1 remains and it can also get the reinforcer associated with S1. In this task, it is always optimal to choose S2. Research has found that wrasse (cleaner fish) quickly learn to choose optimally, an ability that was attributed to their natural foraging strategy (Salwiczek et al., 2012). Most primates, however, were not able to learn to choose optimally within the same number of trials (Salwiczek et al., 2012). Interestingly, however, grey parrots did learn to choose optimally (Pepperberg & Hartsfield, 2014), even though their natural foraging strategy is quite different from that of wrasse and like that of primates. Pepperberg and Hartsfield hypothesized that wrasse and parrots both make selections with their mouths, while primates make selections with their hands, which may account for the differences in species with this task. However, despite making selections with their beak, pigeons tend to choose suboptimally when presented with the ephemeral choice task (Zentall, Case, & Berry 2016).

Zentall et al. (2016) hypothesized that pigeons might not be associating their choice with the second reinforcement because the immediate reinforcement was not differential. Using a technique developed by Rachlin and Green (1972) they introduced a delay between the choice response and reinforcement (what Rachlin & Green referred to as “making a prior commitment”). For the prior commitment group, an initial choice between a yellow and blue stimulus started a 20s timer and the first response following the delay provided reinforcement. If the

optimal choice had been selected, pigeons received reinforcement and were able to select the other stimulus and receive an additional reinforcement. If the suboptimal choice had been selected a single reinforcement was provided and the trial ended. For the no prior commitment group, the trial duration was initiated for an equal 20-s duration *prior to the choice* to control for the duration of the trial and a single peck to the yellow or blue stimulus immediately turned off the stimuli and the experiment proceeded as for the prior commitment group.

The differences between the prior commitment and no prior commitment group began to become evident at about Session 7. The prior commitment group began to choose optimally, while the no prior commitment group continued to choose suboptimally. This study illustrates how a forced prior commitment (delay) increases optimal choice as compared to pigeons that do not make a prior commitment. Additionally, this study illustrates that impulsivity might be the reason there are differences among species in reference to the ephemeral choice task. Pigeons appear to learn the optimal response with an inserted delay between choice and reinforcement because of the immediacy of reinforcement independent of their choice. That is, the delay may reduce their tendency to respond impulsively and therefore increases accuracy for the optimal choice.

A similar finding was reported by Zentall and Raley (2018) for pigeons trained on an object permanence task using a procedure similar to that in previous research with dogs (Miller, Gipson, Vaughan, Rayburn-Reeves, & Zentall, 2009). The study used a rotating beam with cups on either end of the beam. For the first experiment, pigeons were trained on visible displacement task in which an object

(or reinforcer in this experiment) is evident to the subject and placed inside an opaque container. A subject is tested to determine if it will look inside the container for the object.

During the first phase, visible displacement testing, trials began with the beam aligned so that there was a cup on the right or left side, in view of the pigeon. On each trial, the pigeon observed as one cup was baited. The pigeon selected a cup and if correct, received reinforcement. During the initial session of 30 testing trials, pigeons showed no statistical difference from chance in correct selections. Following the initial visible displacement testing, there were 30 sessions of training with the same procedure. While pigeons did better than chance, there was considerable variability among the pigeons and as a group they never exceeded 80% correct.

As previously suggested by Zentall et al. (2016) the immediacy of reinforcement following choice may have resulted in impulsive choice and the implementation of a prior commitment might decrease impulsivity and in turn increase accuracy. In the next experiment, a delay of 5 s was introduced between when the cup was baited and access to the cups to determine if this would increase the accuracy in the object permanence task. Aside from the 5 s delay, the procedure was the same as Experiment 1. With the introduction of the 5 s delay the visible displacement task showed improved accuracy. These results show that the delay facilitated learning of the visible displacement. Thus, introducing a delay between choice and reinforcement for pigeons can help to counteract what is

presumed to be their apparent impulsive choice and significantly improve accuracy.

Zentall, Andrews & Case (2017) also showed evidence that introducing a delay can increase optimal choice for a task in which pigeons were choosing suboptimally without a delay. The experiment involved a gambling-like task in which pigeons were presented with a spatial discrimination (left and right). Choosing optimally resulted in a signal indicating reinforcement 100% of the time, while the suboptimal selection resulted in one of two equally probable signals: one indicating reinforcement and the other indicating no reinforcement (thus, overall, 50% reinforcement). For the experimental group there was a 20s delay (a fixed interval 20-s schedule) between the initial selection and the presentation of the signal for reinforcement. For the control group there was no delay between initial selection and the signal for reinforcement. The results indicated that a majority of the experimental group (4/5 birds) showed a tendency to choose optimally, while the majority of the control group (4/5 birds) showed a tendency to choose suboptimally.

The results of the preceding experiments on the effect of inserting a delay between choice and reinforcement (or conditioned reinforcement) on suboptimal choice, ephemeral reward, and object permanence suggest that such a delay can facilitate the learning of several tasks. In the present study, I explored the possibility that in the mid-session reversal task, errors prior to and following the reversal may result at least in part from impulsive choice and much like the results of earlier research in which a delay was inserted between choice and

reinforcement, inserting such a delay may reduce anticipatory and perseverative errors. Alternatively, it is possible that the errors made by pigeons performing the midsession reversal are not produced by impulsive choice. Because pigeons appear to time the interval from the start of the sessions to the reversal, errors may result from the variability in the pigeons' ability to time the occurrence of the reversal. If this is the case, inserting a delay between choice and feedback may not lead to fewer anticipatory and perseverative errors. This study included two groups: one with a 5s delay inserted between stimulus choice and reinforcement and with a 5s ITI and the other with 5 s added to the ITI to control for total session time.

CHAPTER 2. METHODS

2.1 Subjects

The subjects were 12 non-naïve unsexed pigeons that had participated in unrelated color discrimination learning experiments. All subjects were retired breeders from the Palmetto Pigeon Plant (Sumter, SC). During the experiment, the birds were kept at 85% of their free-feeding body weight to ensure motivation in the experiment. They were individually housed in wire cages (28 x 38 x 30.5 cm) with free access to water and grit in a colony room that was maintained on a 12:12-hr light:dark cycle. The pigeons were maintained in accordance with a protocol approved by the Institutional Animal Care and Use Committee at the University of Kentucky.

2.2 Apparatus

The experiment was conducted in a BRS/LVE (Laurel, MD) sound-attenuating standard operant test chamber measuring 34 cm high, 30 cm from the response panel to the back wall, and 35 cm across the response panel. Three circular response keys (2.5 cm diameter) were aligned horizontally on the response panel and separated from each other by 6.0 cm, but only the left and right-side keys were used in this experiment. The bottom edge of the response keys was 24 cm from the wire-mesh floor. A 12-stimulus in-line projector (Industrial Electronics Engineering, Van Nuys, CA) with 28-V, 0.1-A lamps (GE 1820) that could project blue and yellow hues (Kodak Wratten Filters Nos. 38 and 9, respectively) was mounted behind each response key. Mixed-grain reinforcement

(Purina Pro Grains, a mixture of corn, wheat, peas, kafir, and vetch) was provided from a raised and illuminated grain feeder located behind a 5.1 × 5.7 cm aperture horizontally centered and vertically located midway between the response keys and the floor of the chamber. Reinforcement consisted of 1.5 s access to mixed grain. White noise was generated from outside the chamber and the apparatus was controlled by a computer in the adjacent room running Med-PC IV (Tatham & Zurn, 1989) with a 10-ms resolution.

2.3 Procedure

Each experimental session began with one side key illuminated blue and the other side key illuminated yellow. For the experimental group, a single response to either stimulus turned off the stimulus not selected and started a 5s delay. Following the delay, a correct response resulted in 1.5s access to grain followed by a 3.5s ITI. An incorrect response resulted in a 5s ITI with no reinforcement. For the control group, reinforcement occurred immediately following a correct response. To account for the increased trial duration resulting from the delay, the control group had a 10s ITI. Each session consisted of 80 trials in which during the first 40 trials (1-40) S1 was correct (S1+/S2-) and during the last 40 trials (41-80) S2 was correct (S1-/S2+), reversing the contingencies. For half of the subjects the blue hue was S1 and for the other half of the subjects the yellow hue was S1. The location of the blue and yellow hues was counterbalanced over trials to control for possible side preferences. Pigeons completed 60 sessions of training.

2.4 Analysis

Data from each bird was averaged across blocks of ten sessions (Sessions 1-10, 11-20, 21-30, 31-40, 41-50, and 51-60). Overall accuracy (Trials 1-80), first half accuracy (Trials 1-41), and second half accuracy (Trials 42-80) for each group for each ten-session block, was assessed. Because individual differences in asymptotic accuracy at the start and end of each session may be unrelated to the ability to detect the reversal, the data in close proximity to the reversal were analyzed. Anticipatory errors just prior to the reversal were analyzed using trial-by-trial data for the 4 trials prior to the reversal (Trials 38 to 41; note, the feedback from the reversal occurred only after choice on Trial 41, so choice on Trial 41 was included in anticipatory errors) while perseverative errors just after the reversal were analyzed using the 4 trials immediately following the reversal (Trials 42 to 45) now referred to as pre-reversal and post-reversal errors respectively. The four trials immediately preceding and following the reversal were chosen because these trials are most likely to be affected by impulsive choice and therefore most likely to be affected by a delay. Additionally, the number of sessions to various criteria 60%, 70%, 80% and 90% were analyzed for each pigeon. Statistical significance was set at $p = .05$ level for all statistical tests.

CHAPTER 3. RESULTS

A two-way 2 (Session Half: first-half or second-half) x 2 (Group: delay or no-delay) mixed ANOVA on percent correct was conducted for each ten-session block. Another two-way 2 (Error Type: pre-reversal errors or post-reversal errors) x 2 (Group: delay or no-delay) mixed ANOVA on percent correct was conducted for each block of ten sessions on the errors immediately before and after the reversal. Additionally, an independent samples t-test was conducted to compare the delay group with the no-delay group for criterion accuracy (60%, 70%, 80%, 90% correct).

3.1 Sessions 1-10

First-Half vs. Second-Half

The data from the first 10 training sessions plotted by choice of the first correct stimulus (S1) as a function of trial number appears in Figure 1. There was no significant main effect of session half, $F(1, 10) = 0.220$, $p = 0.649$ on percent correct regardless of group type. There was also no main effect of group type on percent correct regardless of session half, $F(1, 10) = 1.01$, $p = 0.339$. No significant interaction between session half and group type, $F(1, 10) = .038$, $p = 0.849$, was observed for Sessions 1-10.

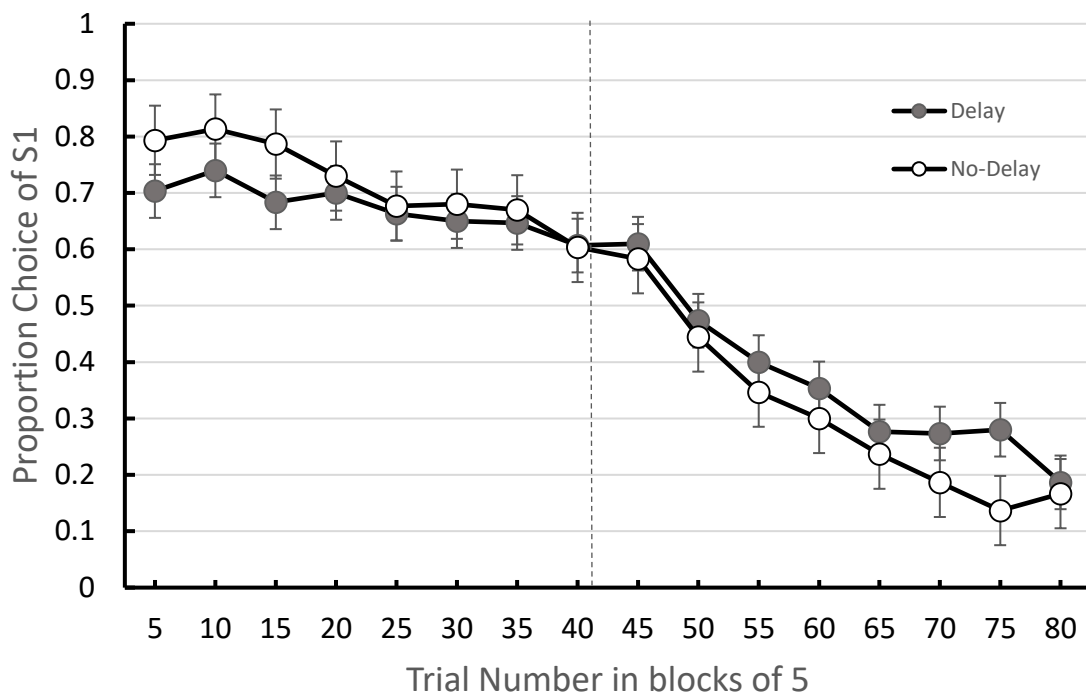


Figure 1 The average % choice of S1 grouped by blocks of five trials for Sessions 1-10 for the delay and no-delay groups. The midsession reversal point is denoted by a dashed vertical line. Error bars = ± 1 SEM

Pre-Reversal vs. Post-Reversal Errors

The average percent correct of the delay group and no-delay group for Sessions 1-10 are plotted for pre-reversal and post-reversal accuracy in Figure 2. There was a significant main effect of error type, $F(1,10)= 16.83$, $p=0.002$, with significantly fewer pre-reversal errors ($M=0.546$, $SD=0.045$) as compared to post-reversal errors ($M=0.417$, $SD=0.087$). However, there was no significant main effect of group type, $F(1,10)= 0.382$, $p=0.55$, nor was there a significant interaction between error type and group type, $F(1,10)= 0.280$, $p= 0.608$.

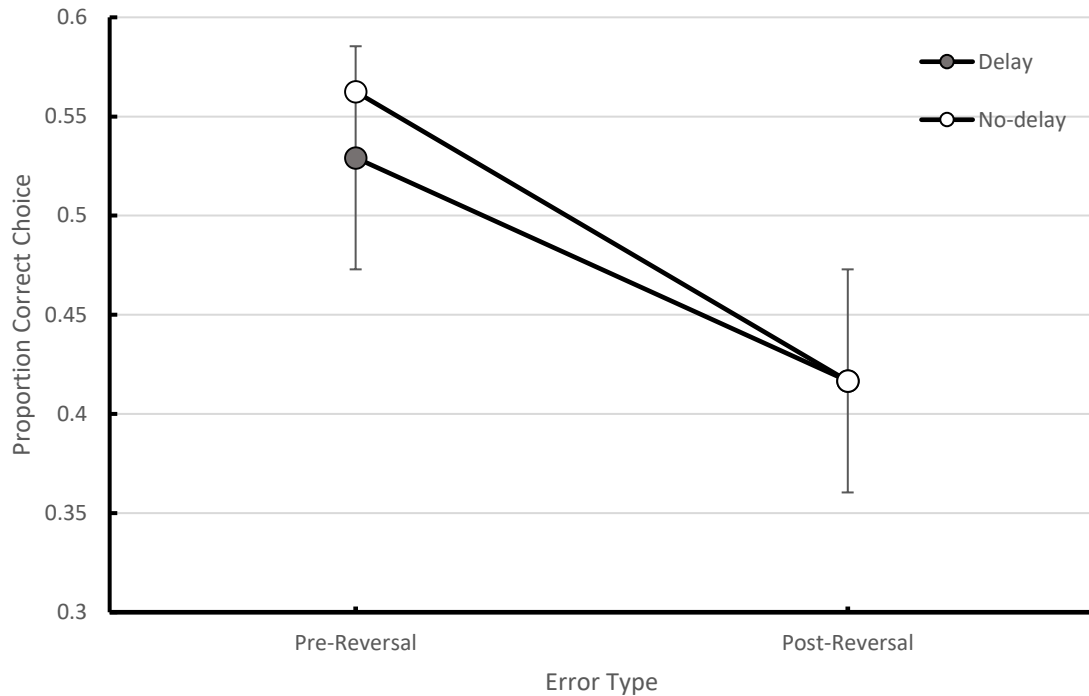


Figure 2. The average proportion correct choice for pre-reversal (Trials 38-41) and post-reversal errors (Trials 42-45) for Sessions 1-10. Error bars = ± 1 SEM

3.2 Sessions 11-20

First-Half vs. Second-Half

The data from Sessions 11-20 plotted by choice of S1 as a function of trial number appears in Figure 3. There was no significant difference between first-half accuracy and second-half accuracy $F(1,10)= 3.586$, $p=0.088$, but there was a significant difference between the delay group ($M=0.795$, $SD=0.069$) and no-delay group ($M=0.873$, $SD=0.027$), $F(1,10)= 6.531$, $p=0.029$, with the no-delay group having significantly better accuracy as compared to the delay group. No significant

interaction between session half and group type was observed, $F(1,10)= 2.270$, $p=0.163$.

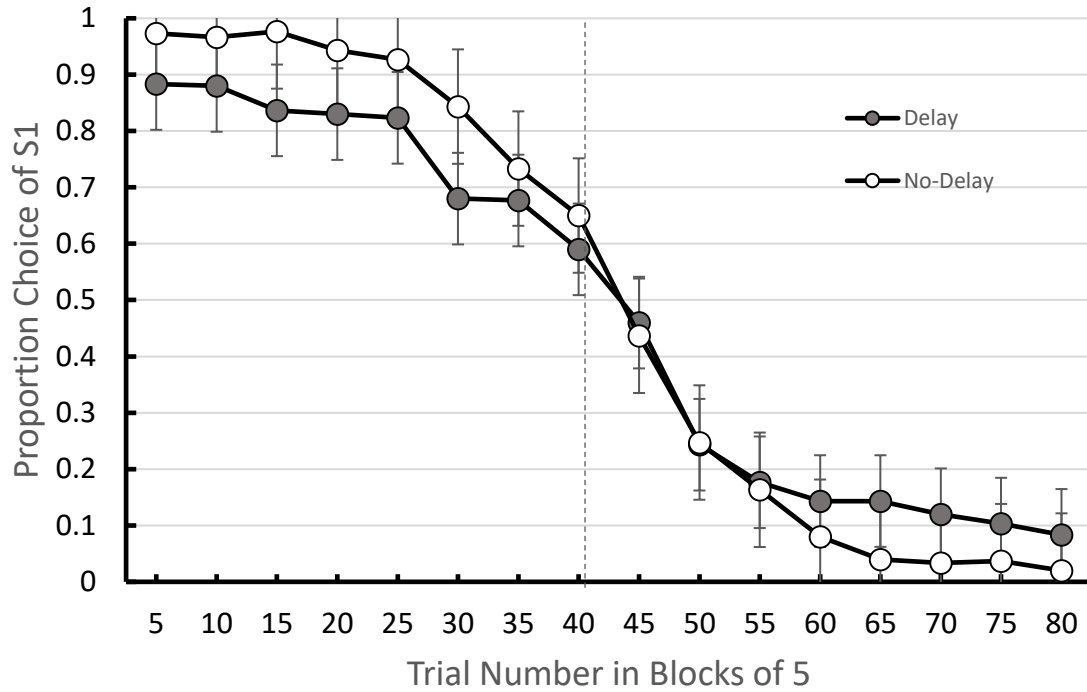


Figure 3. The average % choice of S1 grouped by blocks of five trials for Sessions 11-20 for the delay and no-delay groups. The midsession reversal point is denoted by a dashed vertical line. Error bars = ± 1 SEM

Pre-Reversal vs. Post-Reversal Errors

The average percent correct of the delay group and no-delay group for Sessions 11-20 are plotted for pre-reversal and post-reversal accuracy in Figure 4. There was no significant main effect for error type, $F(1,10)= .098$, $p= 0.761$, or

for group type, $F(1,10)= 2.538$, $p= 0.142$ on accuracy. There was also no significant interaction between error type and group type, $F(1,10)= 0.011$, $p= 0.919$.

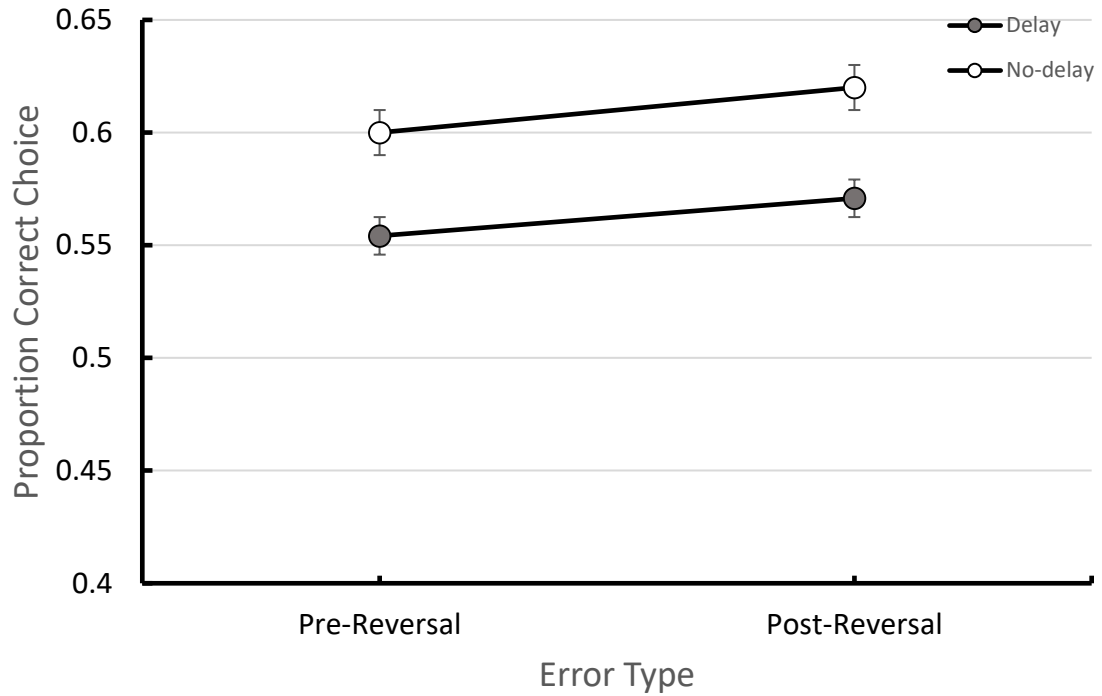


Figure 4. The average proportion correct choice for pre-reversal (Trials 38-41) and post-reversal errors (Trials 42-45) for Sessions 11-20. Error bars = ± 1 SEM

3.3 Sessions 21-30

First-Half vs. Second-Half

The data from Sessions 21-30 plotted by choice of S1 as a function of trial number appears in Figure 5. There was no significant main effect of session half,

$F(1,10)= 0.94$, $p= 0.0354$, but there was a marginally significant main effect of group type, $F(1,10)= 4.674$, $p= 0.056$, with the no-delay group ($M=0.869$, $SD=0.039$) responding more accurately overall than the delay group ($M=0.808$, $SD=0.056$). There was no significant interaction between session half and group type, $F(1,10)= 0.412$, $p= 0.536$.

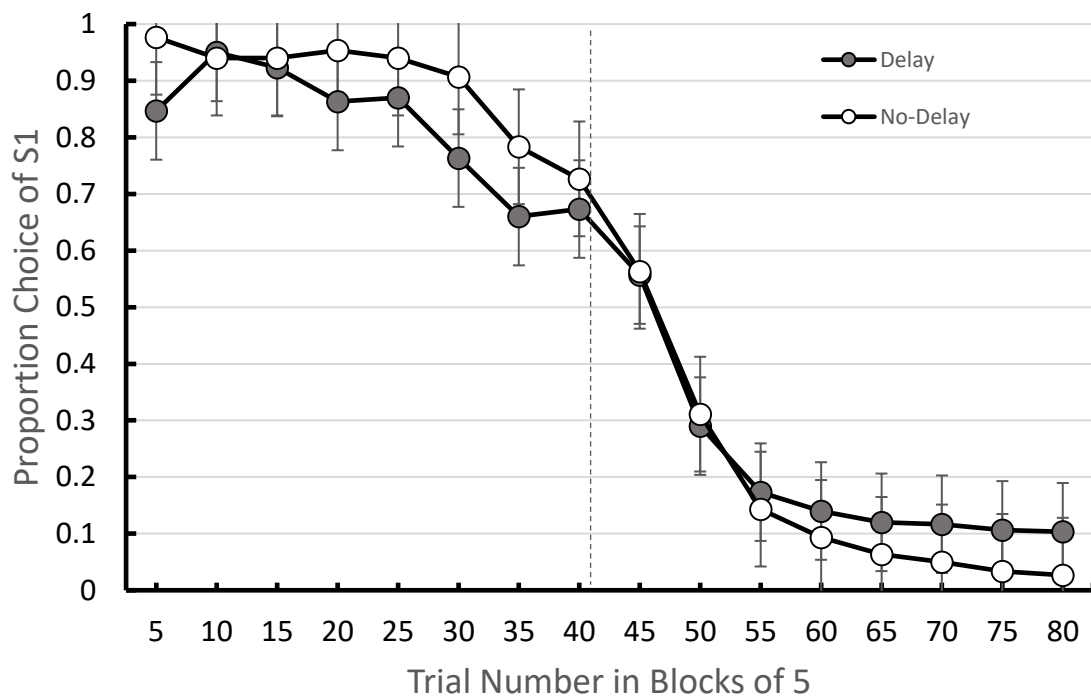


Figure 5. The average % choice of S1 grouped by blocks of five trials for Sessions 21-30 for the delay and no-delay groups. The midsession reversal point is denoted by a dashed vertical line. Error bars = ± 1 SEM

Pre-Reversal vs. Post-Reversal Errors

The average percent correct of the delay group and no-delay group for Sessions 21-30 are plotted for pre-reversal and post-reversal accuracy in Figure 6. Subjects had significantly fewer pre-reversal errors ($M=0.606$, $SD=0.058$) as compared to post-reversal errors ($M=0.465$, $SD=0.076$), $F(1,10)= 17.462$, $p= 0.002$, but there was no main effect of group type, $F(1,10)= 0.033$, $p= 0.860$, on accuracy. Furthermore, there was no interaction between error type and group type, $F(1,10)= .000$, $p= 1.00$.

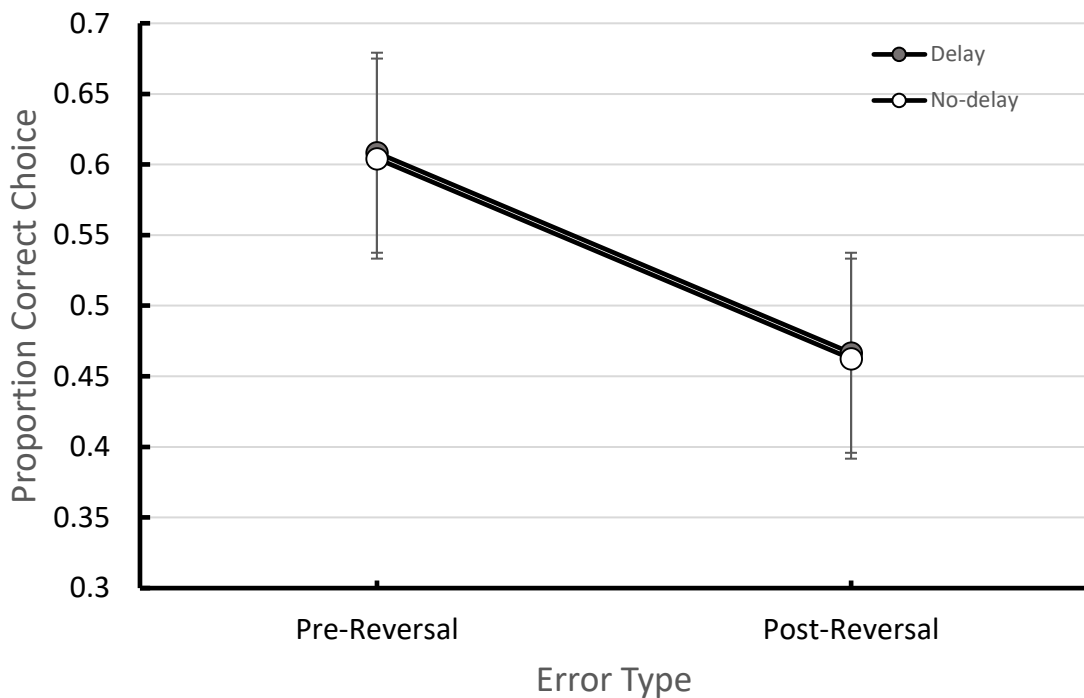


Figure 6. The average proportion correct choice for pre-reversal (Trials 38-41) and post-reversal errors (Trials 42-45) for Sessions 21-30. Error bars = ± 1 SEM

3.4 Sessions 31-40

First-Half vs. Second-Half

The data from Sessions 31-40 plotted by choice of S1 as a function of trial number appears in Figure 7. No significant main effect was observed for sessions half, $F(1,10)= 2.388$, $p= 0.153$, however there was a nearly significant main effect of group type, $F(1,10)= 4.681$, $p= 0.056$, with the no-delay group performing better than the delay group.

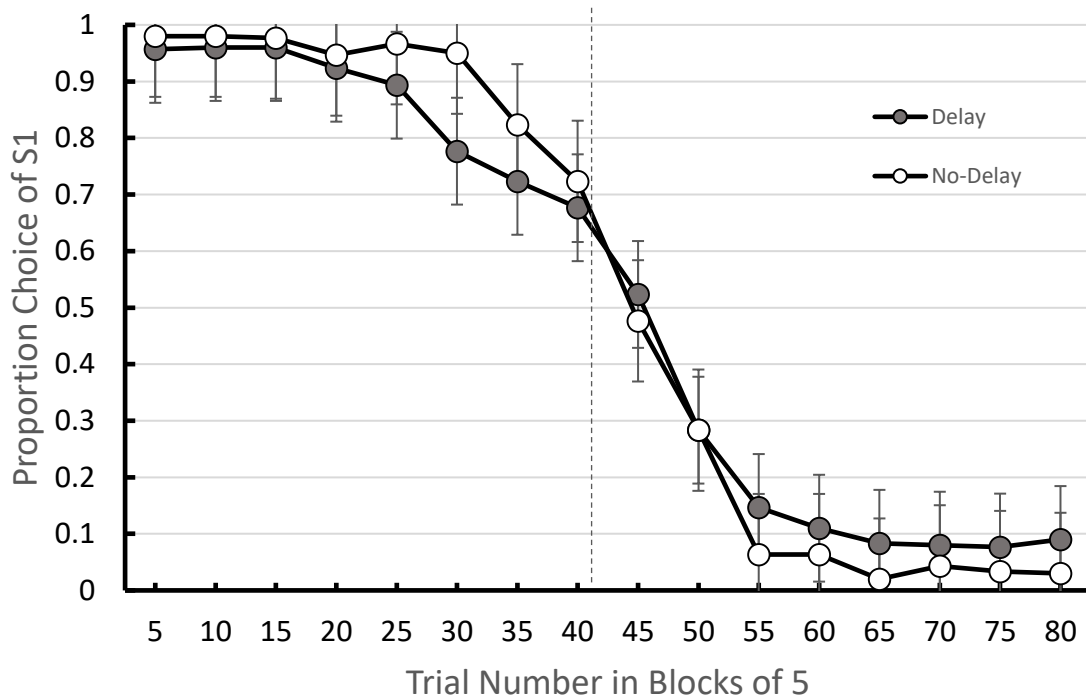


Figure 7. The average % choice of S1 grouped by blocks of five trials for Sessions 31-40 for the delay and no-delay groups. The midsession reversal point is denoted by a dashed vertical line. Error bars = ± 1 SEM

Pre-Reversal vs. Post-Reversal Errors

The average percent correct of the delay group and no-delay group for Sessions 31-40 are plotted for pre-reversal and post-reversal accuracy in Figure 8. Error type had no significant main effect on accuracy, $F(1,10)= 4.239$, $p=0.067$. Similarly, there was no main effect of group type, $F(1,10)= 2.282$, $p= 0.162$. There was also no interaction between error type and group, $F(1, 10)= 0.087$, $p= 0.775$.

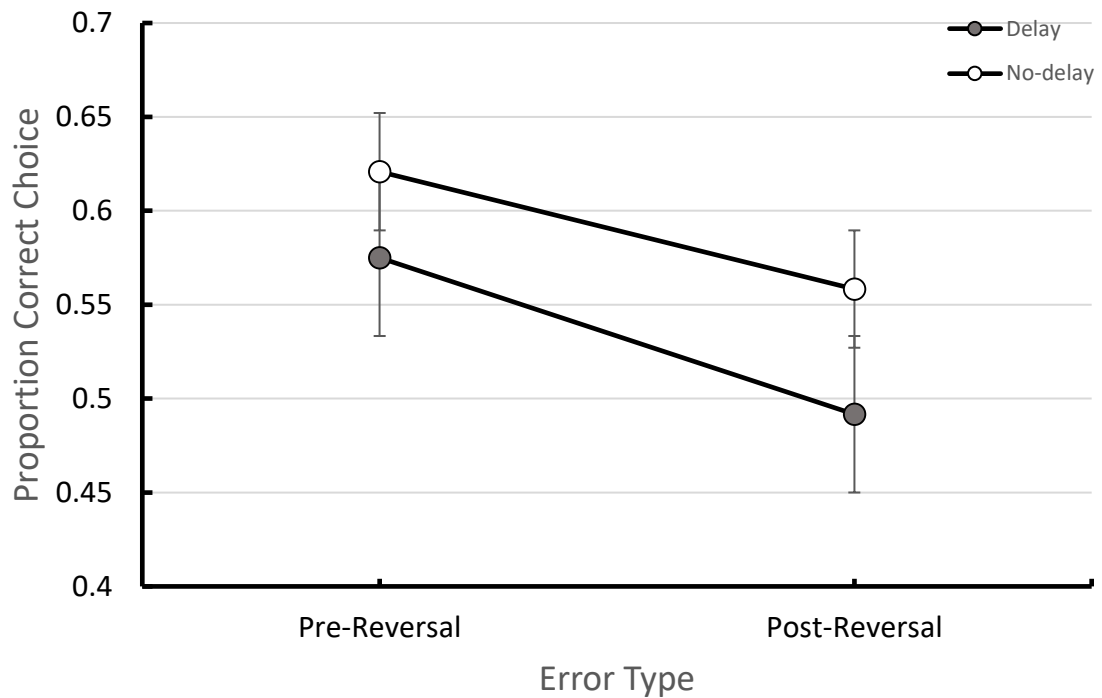


Figure 8. The average proportion correct choice for pre-reversal (Trials 38-41) and post-reversal errors (Trials 42-45) for Sessions 31-40. Error bars = ± 1 SEM

3.5 Sessions 41-50

First Half vs. Second-Half

The data from Sessions 41-50 plotted by choice of S1 as a function of trial number appears in Figure 9. For both session half, $F(1,10)= 2.021$, $p=0.186$ and group type, $F(1,10)= 2.332$, $p= 0.158$ there were no significant main effects. Additionally, there was no significant interaction between session half and group type, $F(1,10)= 0.162$, $p=0.696$.

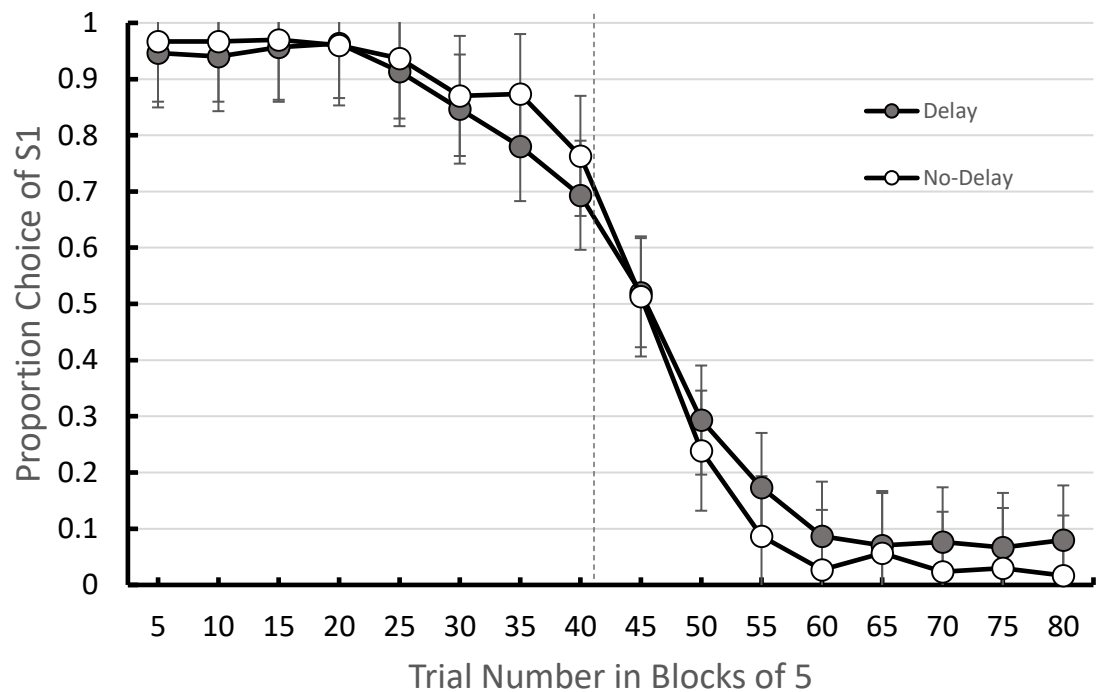


Figure 9. The average % choice of S1 grouped by blocks of five trials for Sessions 41-50 for the delay and no-delay groups. The midsession reversal point is denoted by a dashed vertical line. Error bars = ± 1 SEM

Pre-Reversal vs. Post-Reversal Errors

The average percent correct of the delay group and no-delay group for Sessions 41-50 are plotted for pre-reversal and post-reversal accuracy in Figure 10. There was a significant main effect of error type, $F(1,10)= 7.25$, $p= 0.023$, with fewer pre-reversal errors ($M=0.627$, $SD=0.063$) than post-reversal errors ($M=0.506$, $SD=0.127$). However, there was no main effect of group type on accuracy, $F(1,10)= 0.171$, $p= 0.688$. There was also no significant interaction between error type and group type $F(1,10)= 0.078$, $p= 0.786$.

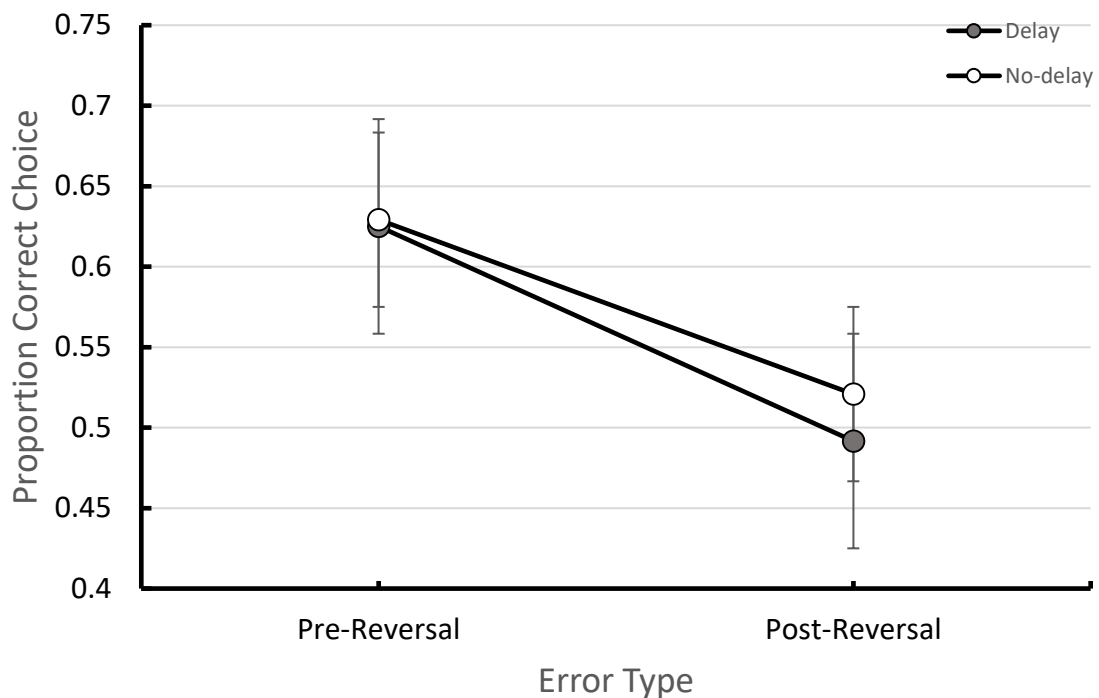


Figure 10. The average proportion correct choice for pre-reversal (Trials 38-41) and post-reversal errors (Trials 42-45) for Sessions 41-50. Error bars = ± 1 SEM

3.6 Sessions 51-60

First-Half vs. Second-Half

The data from Sessions 51-60 plotted by choice of S1 as a function of trial number appears in Figure 11. No main effects were observed for session half, $F(1,10)= 0.004$, $p= 0.954$ or for group type, $F(1,10)= 0.701$, $p= 0.422$. Furthermore, no significant interaction was observed between session half and group type, $F(1,10)= 0.107$, $p= 0.750$. For comparison, data from the last ten sessions of a traditional mid-session reversal with a 5s ITI and no-delay is plotted alongside the current data.

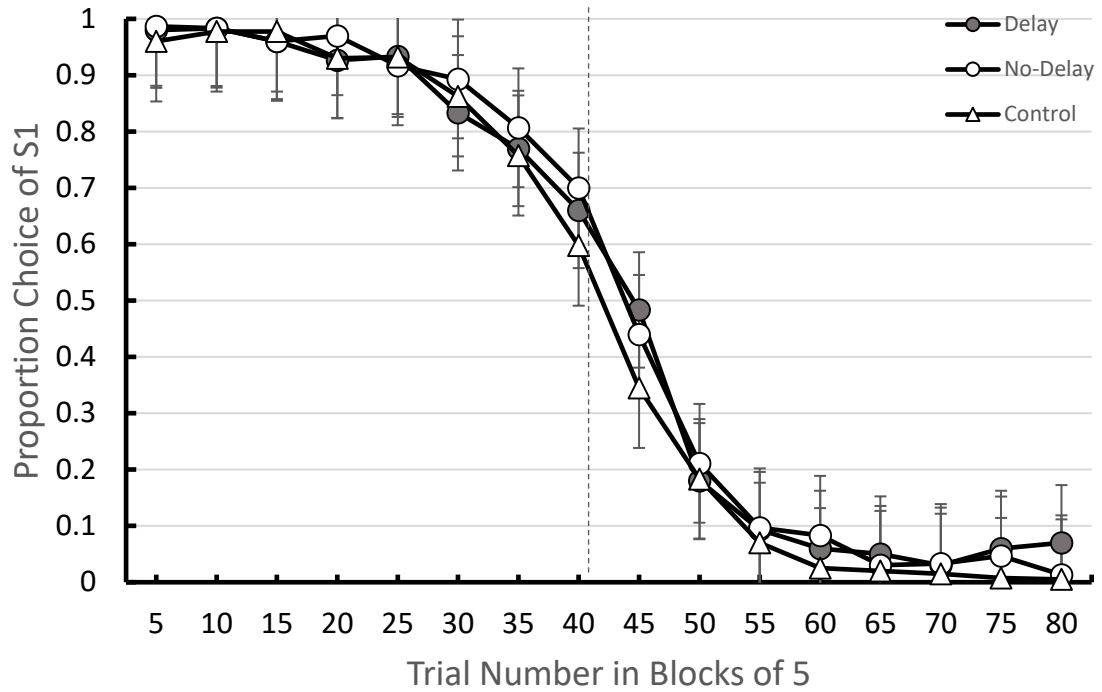


Figure 11. The average % choice of S1 grouped by blocks of five trials for Sessions 51-60 for the delay and no-delay groups as well as the 5s ITI no-delay control group from Rayburn-Reeves et. al. (2013). The midsession reversal point is denoted by a dashed vertical line. Error bars = ± 1 SEM

Pre-Reversal vs. Post-Reversal Errors

The average percent correct of the delay group and no-delay group for Sessions 51-60 are plotted for pre-reversal and post-reversal accuracy in Figure 12. There was a nearly significant main effect of error type, $F(1,10)= 4.909$, $p= 0.051$, with fewer pre-reversal errors ($M=0.608$, $SD=0.044$) as compared to post-reversal errors ($M=0.571$, $SD=0.077$). There was no main effect of group type on

accuracy, $F(1,10)= 0.595$, $p= 0.458$. Also, there was no significant interaction between error type and group type, $F(1,10)= 2.182$, $p= 0.170$.

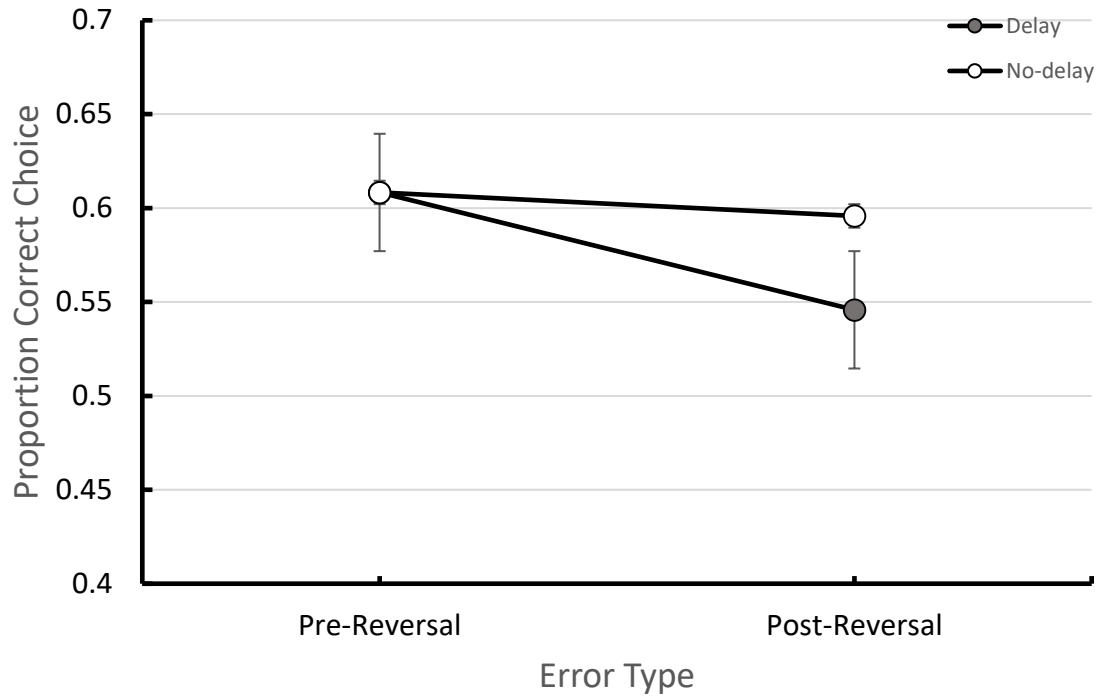


Figure 12. The average proportion correct choice for pre-reversal (Trials 38-41) and post-reversal errors (Trials 42-45) for Sessions 51-60 Error bars = ± 1 SEM

3.7 Sessions to Criteria

Additionally, there was no significant differences between the delay and no-delay groups in the sessions to 60% correct criterion ($M_{\text{delay}} = 2.67$, $SD_{\text{delay}} = 2.66$; $M_{\text{no-delay}} = 2.33$, $SD_{\text{no-delay}} = 1.37$), $t(10) = 0.27$, $p= 0.793$; sessions to 70% correct criterion ($M_{\text{delay}} = 5.67$, $SD_{\text{delay}} = 4.41$; $M_{\text{no-delay}} = 4.17$, $SD_{\text{no-delay}} = 2.99$), $t(10)=$

0.69, $p= 0.506$; sessions to 80% correct criterion ($M_{\text{delay}} = 8.0$, $SD_{\text{no-delay}} = 3.79$; $M_{\text{no-delay}} = 7.0$, $SD_{\text{no-delay}} = 3.1$), $t(10)= 0.5$, $p=0.628$; or sessions to 90% correct criterion ($M_{\text{delay}} = 18.83$, $SD_{\text{delay}} = 13.72$; $M_{\text{no-delay}} = 11.67$, $SD_{\text{no-delay}} = 3.5$), $t(10)= 1.24$, $p= 0.243$.

The results suggest that subjects in the delay group acquired the midsession reversal task slower than those in the no-delay group, but performed similarly to the no-delay group by the end of the study this is illustrated in Figures 13, 14 and 15.

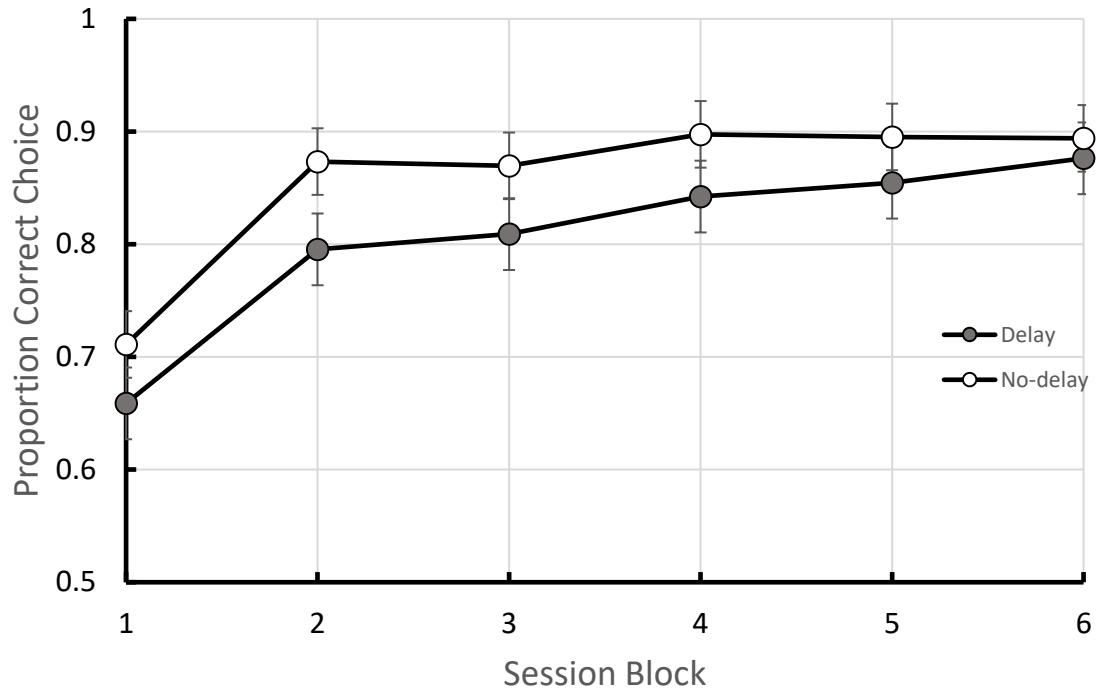


Figure 13. The overall average proportion correct choice for the delay and no-delay groups across 10-session blocks (1: Sessions 1-10, 2: Sessions 11-20, 3: Sessions 21-30, 4: Sessions 31-40, 5: Sessions 41-50, 6: Sessions 51-60). Error bars = ± 1 SEM

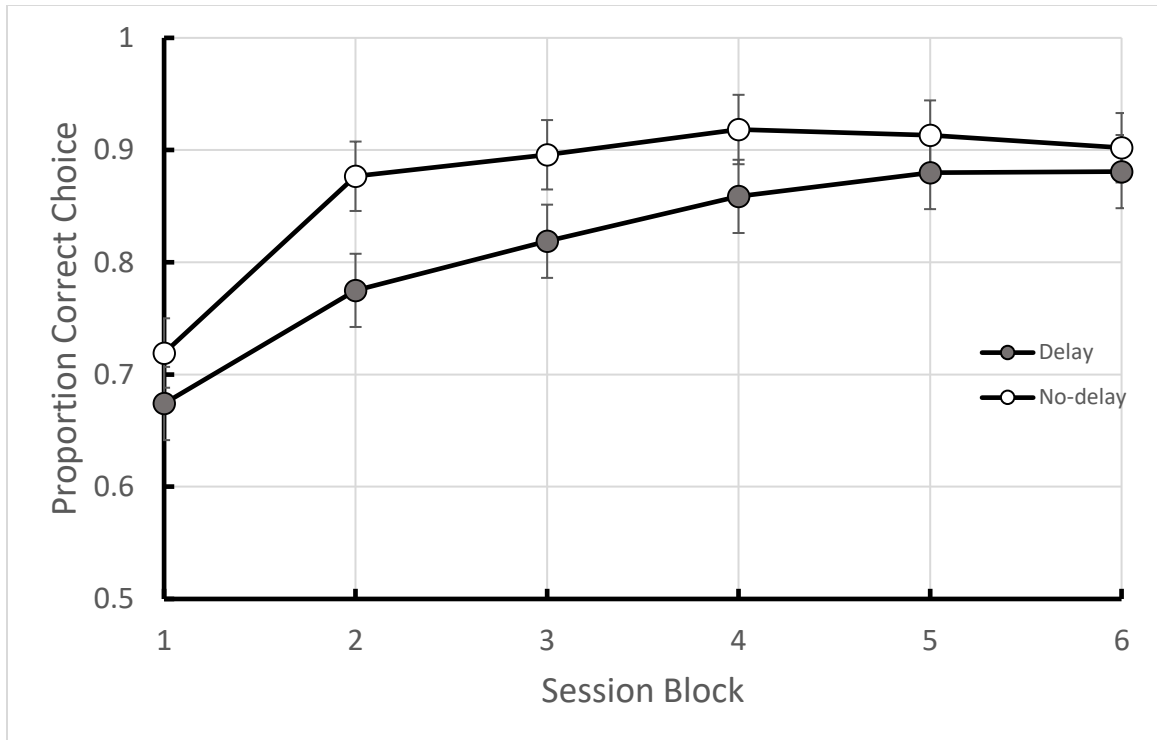


Figure 14. The first-half average proportion correct choice for the delay and no-delay groups across 10-session blocks (1: Sessions 1-10, 2: Sessions 11-20, 3: Sessions 21-30, 4: Sessions 31-40, 5: Sessions 41-50, 6: Sessions 51-60). Error bars = ± 1 SEM

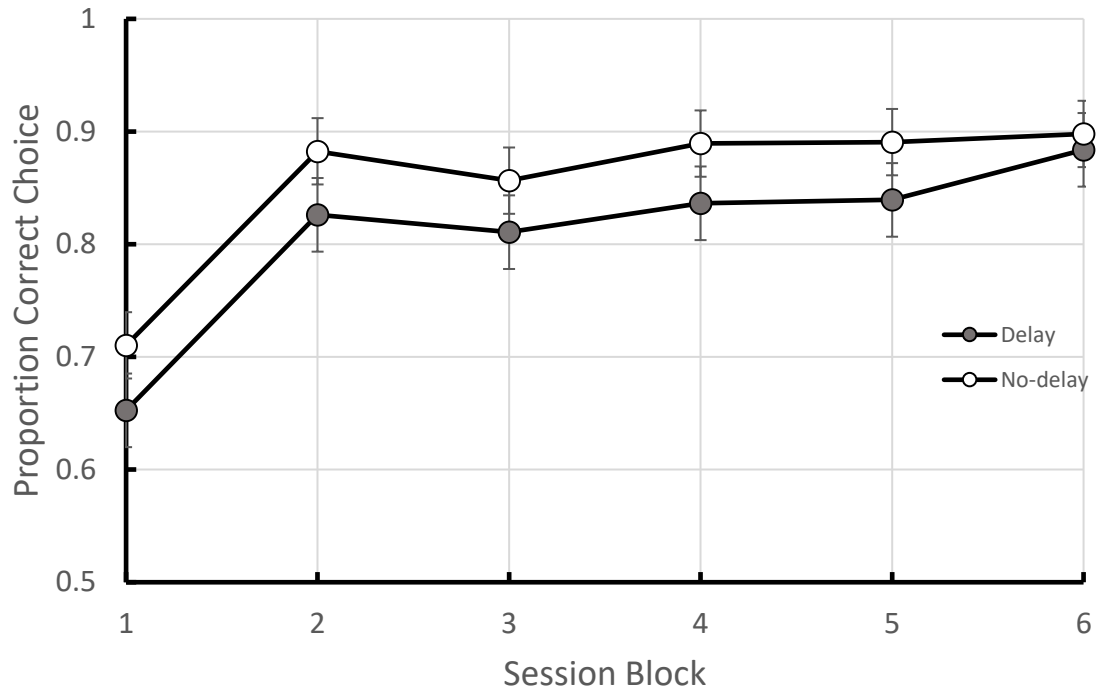


Figure 15. The second-half average proportion correct choice for the delay and no-delay groups across 10-session blocks (1: Sessions 1-10, 2: Sessions 11-20, 3: Sessions 21-30, 4: Sessions 31-40, 5: Sessions 41-50, 6: Sessions 51-60). Error bars = ± 1 SEM

CHAPTER 4. DISCUSSION

While some significant differences (Sessions 11-20) and nearly significant differences (Sessions 21-30 and Sessions 31-40) were observed in overall accuracy between the delay group and the no-delay group, there was ultimately no significant difference between groups after completion of a sufficient number of sessions to establish response stability. The differences that did occur can be attributed to slower learning by pigeons in the delay group. There were also significant or nearly significant differences on four of the six ten-session blocks (Sessions 1-10, 21-30, 41-50 and 51-60) when comparing pre-reversal errors versus post-reversal errors, regardless of group type, with fewer pre-reversal errors. This means that overall, pigeons in both groups were responding more accurately immediately preceding the reversal, but continuing to respond to S1 immediately following the reversal when it was no longer providing reinforcement. Importantly, there was no difference in accuracy close to the reversal between the two groups across any of the ten-session blocks. This implies there was no effect of the inserted delay on the assumed impulsivity that pigeons exhibit on this task. These results are inconsistent with a number of tasks, including the ephemeral choice task (Zentall, Case & Berry, 2016) and the gambling-like task (Zentall, Andrews & Case, 2017), that have been shown to increase optimal choice behavior in pigeons when introducing a short delay between the choice response and reinforcement.

There are differences between the midsession reversal task and the two previously mentioned studies that may account for the inconsistent outcomes

when implementing a short choice-reinforcement delay. For example, the inherent timing nature of the midsession reversal task is unique as compared to the ephemeral choice task and gambling-like task. In these “non-timing” tasks, the optimal choice remains fixed across the duration of the session and therefore the entire experiment. The optimal choice for midsession reversal, however, changes as a function of trial number and therefore when failing to use the optimal win-stay/lose-shift strategy by utilizing reinforcement feedback, pigeons resort to timing the occurrence of the reversal.

In both the ephemeral choice task and the gambling-like task, each trial has the potential to receive reinforcement for either choice, but for the midsession reversal each trial has an absolute correct response resulting in reinforcement. In the ephemeral choice task, subjects receive reinforcement on every trial, but if responding optimally, can obtain two reinforcements for each trial. For each trial in the gambling-like task, choosing optimally provides reinforcement 100% of the time, while choosing suboptimally still provides reinforcement 50% of the time (Zentall, Andrews & Case, 2017). In the mid-session reversal, however, in each trial, one stimulus provides reinforcement while the other does not, so a clear discrimination must occur to obtain reinforcement. The possibility of receiving reinforcement with choice of either stimulus, like in the ephemeral choice task and gambling-like task, may inherently encourage impulsive choice. With this assumption, the midsession reversal may not encourage impulsive choice and would explain why a delay does not improve accuracy under these circumstances.

This further suggests that a pigeon's inability to adopt the optimal win-stay/lose-shift strategy is controlled by something other than impulsivity.

Mid-session reversal tasks have been utilized to assess cognitive flexibility in a variety of species, with the assumption that adopting a win-stay/lose-shift strategy implies higher cognitive flexibility. As mentioned previously, both humans and rats employ this strategy when given a reversal task (Rayburn-Reeves, Molet & Zentall, 2011; Smith et al. 2017). Pigeons, however, have difficulty adopting this optimal strategy, but some research has shown that the dimension of the discrimination can affect task accuracy.

McMillan and Roberts (2012) conducted a three-phase experiment using both visual and spatial discriminations as well as varying ITI durations. Phase 1 was a traditional midsession reversal task with the reversal occurring at the midpoint of the session. It included a visual/spatial discrimination with red always presented on the left and green always presented on the right. In this way, pigeons were able to use both spatial location and key color to determine stimulus choice on each trial. Phase 2 used strictly visual discriminations with red and green being presented randomly on the left and right-side keys. After initial training (20 sessions), probe sessions were introduced every 4th session. The probe trials either reduced the ITI by half (3s) or doubled it (12s). This phase examined the effect of a one-dimension (color) stimulus discrimination as well as the effect of ITI duration on anticipatory and perseverative errors. The final phase essentially combined Phase 1 and Phase 2 by presenting the combination visual/spatial discrimination as in Phase 1 with the probe sessions of Phase 2. This allowed for

the comparison of visual-only discrimination with the combined visual/spatial discrimination. In all three phases there was an initial 20 sessions of training without probe sessions.

The results showed that pigeons use win-stay/lose-shift strategies as well as interval timing depending on the discriminative stimulus dimension. In both Phases 1 and 3, with visual/spatial stimuli, subjects were sensitive to the feedback from local reinforcement and exhibited few anticipatory errors, even with varying ITI duration in Phase 3. Conversely, in Phase 2, pigeons were less sensitive to the reversal resulting in more anticipatory and perseverative errors with most perseverative errors occurring with the shortest ITI (3s) and most anticipatory errors with the longest ITI (12s). This indicates that pigeons reverted to relying on timing cues when visual discrimination alone was used, as compared to visual/spatial combination discriminations. Importantly, when the change in responding to S1 from Trials 41 to 42 (the reversal point) are compared across all three phases for the initial training sessions (Sessions 1-20) there was a significant difference between Phase 1 and 2 and between Phase 2 and 3. However, there was no significant difference between Phase 1 and 3. This further supports the conclusion that stimulus dimension could affect the cues that the pigeons used to determine when to switch to S2, primarily feedback from the results of the prior trial in the case of the visual/spatial discrimination, but importantly, time from the start of the session in the case of the visual discrimination alone.

In a follow-up study, McMillan, Kirk and Roberts (2014) trained pigeons on a visual/spatial combination discrimination and then transferred the birds to a

discrimination in which red and green were presented randomly across sides. However, to see if previous experience on the combination stimuli would help when transferred, half of the pigeons had a visual-only discrimination and the other half a spatial-only discrimination (i.e. one side was correct for the first half regardless of stimulus color). While all of the birds performed optimally on the combination discrimination, when the birds were transferred, only the spatial group continued to perform optimally. Additionally, a spatial-only group was included that did not complete prior training with the visual/spatial combination stimuli discrimination. This group performed similarly to the spatial group transferred from the combination training implying that the previous experience with the task did not affect accuracy. These results are inconsistent with Rayburn-Reeves et al. (2013) in which only the group with a shortened ITI improved accuracy for a spatial discrimination.

As a comparison, rats perform optimally in a midsession reversal task with spatial discrimination (Rayburn-Reeves et al, 2013; Smith et al, 2016; Rayburn-Reeves et al, 2018; Santos & Sanabria, 2019), but little research has been conducted to assess a rat's ability on a non-spatial discrimination of this task.

As noted earlier (McMillan & Roberts, 2012), a spatial discrimination allows for spatial orientation to the stimulus location prior to viewing the stimuli which could facilitate memory for the preceding stimulus choice. McMillan, Kirk and Roberts (2014) tested rats on a midsession reversal task in a T-maze in which the rats were brought back to a start chamber before each new trial so they could not easily orient to the correct location between trials. They found that anticipatory and

perseverative errors for rats in the T-maze were similar to pigeons tested on a visual discrimination. It may be that the number of errors produced by pigeons in a visual midsession reversal task is directly related to the way the stimuli are presented. Furthermore, this study implies that pigeons do not necessarily perform worse on this task as compared to rats, but instead are presented with a stimulus discrimination differing from that of rats. In order to more accurately compare pigeons to other species, namely rats, it is imperative to develop a task with a comparable stimuli discrimination.

For example, providing rats with a discrimination in which a light is illuminated over one lever, but not the other would be an analogous task to a visual discrimination with pigeons. In this task, for one group the lever with the light would be correct for the first half of the session, while the lever press without the light would be correct for the second half. These conditions would be reversed for a second group. The light would appear randomly across the left and right levers throughout the duration of the session. In this way, rats are still required to use their visual system, like pigeons, but are not hindered by their relatively poor vision.

4.1 Limitations

Although the typical control group in a midsession reversal experiment involves a 5-s ITI with no delay, the 10-s ITI no-delay group from the present experiment looked quite similar to the 5-s ITI no-delay group from Rayburn-Reeves et al. (2013). Importantly, the data from all three conditions looked quite similar, in spite of the fact that the duration of the session for the 5-s no-delay condition was

considerably shorter than the session duration for both of the groups in the present experiment, and with the shorter session duration for the 5-s no-delay condition (only about half as long), the time of the reversal should have been somewhat easier to time. For this reason, comparison of the 5-s no-delay condition with the conditions in the present experiment may not be appropriate.

Additionally, in both the ephemeral choice task (Zentall, Case & Berry, 2016) and the gambling-like task (Zentall, Andrews & Case, 2017) the choice-reinforcement delay was 20 s, whereas it was only 5 s in the present midsession reversal study. It may be that the 5s delay was not sufficient to eliminate impulsive responding, however increasing the delay to 20s would have extended each session by about thirty minutes and made the reversal even more difficult to time.

4.2 Conclusions

Inserting a delay between choice and reinforcement was not effective in reducing perseverative and anticipatory errors in pigeons performing the mid-session reversal task. A 5-s delay modestly slowed down learning during earlier session blocks as compared to the no-delay group, but the two groups performed similarly upon the completion of 60 sessions. These results imply that instead of impulsivity controlling choice, other factors, such as stimulus dimension, and memory for the preceding stimulus chosen and its outcome do appear to be important. Ultimately, further research should be conducted to properly evaluate the ability of pigeons in this task and what its implications are for the behavioral flexibility of this species.

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EDUCATION

BA Psychology and BS Biology
University Honors and Departmental Honors
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PROFESSIONAL EXPERIENCE

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Lab Manager Comparative Cognition Laboratory
University of Kentucky, Lexington, KY

2018-present

Teaching Assistant
Lab instructor for Evolutionary Psychology and Cognitive Processes
Online Instructor for Introduction to Psychology
University of Kentucky, Lexington, KY

2016-2018

Lab Manager for the Department of Biochemistry and Molecular Biophysics
Kansas State University, Manhattan, KS

GRANTS & AWARDS

2013

CSURF Travel Grant
UNCW Undergraduate Research Scholar
Henry Alexander Martindale Honrs Award
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RESEARCH PUBLICATIONS

- Goeckl, M.E., Basgall, E.M., Lewis, I.C., Goetting, S.C., Yan, Y., Halloran, M., and Finnigan, G.C. (2019) Modulating CRISPR gene drive activity through nucleocytoplasmic localization of Cas9 in *S. cerevisiae*. *Fungal Biol Biotechnol.* 6:2.
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