

When is a Choice not a Choice? Pigeons Fail to Inhibit Incorrect
Responses on a Go/No-Go Midsession Reversal Task

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Author Note

This research was supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant and Discovery Accelerator Supplement to CB Sturdy and an NSERC Discovery Grant to ML Spetch. We thank Jason Long, Jeffrey Pisklak, Pauline Kwong, Joshua Yong, and Nuha Madi for assistance in running subjects, and Tad Plesowicz for animal care.

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Abstract

In a two-stimulus visual discrimination choice task with a reversal in reward contingencies midway through each session, pigeons produce a surprising number of both anticipatory errors (i.e., responding to the second-correct stimulus before the reversal) and perseverative errors (i.e., responding to the first-correct stimulus after the reversal). Here we used a go/no-go version of the task to examine the degree to which these errors can be attributed to failure to inhibit incorrect responses near the reversal. We presented pigeons with either a green or red stimulus (randomized across trials), with pecks to one reinforced with food, and pecks to the other stimulus leading to a 10-s time-out; the reward vs. time-out contingencies reversed after 40 trials. Pigeons rarely withheld responses when reward was provided for pecking, but produced many incorrect pecks near the reversal. Subsequent experiments examined these errors with longer sessions and multiple reversals, as well as on choice tasks. Our results suggest that pigeons' errors may be due to an inability to inhibit incorrect responses rather than a deliberate choice of the incorrect stimulus on simultaneous discrimination midsession reversal procedures. Results suggest that pigeons learned independent rules about the two stimuli, and that training with multiple reversals changed the rules that governed pigeons' responding.

Keywords: pigeons, interval timing, midsession reversal, go/no-go, choice

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Serial reversal learning has been investigated by those interested in behavioral flexibility, where the degree of perseveration on the prior contingency is indicative of the individual's flexibility (Shettleworth, 1998). More recently, reversal learning has been studied with a predictable, mid-session reversal in task contingencies, on which pigeons show a tendency to not only persevere after a change in reward, but also to predict the change. This effect was first demonstrated by Cook and Rosen (2010), who trained pigeons to match-to-sample with red and green alternatives in the first half of an experimental session and to choose the oddity-from-sample in the other half. With this consistent reversal in task contingencies, the researchers found that subjects showed a large number of errors after the reversal (i.e., pigeons continued to match-to-sample when doing so was no longer reinforced); further, they also noted that subjects likewise showed a large number of errors before the reversal (i.e., pigeons started non-matching before doing so was reinforced). These errors have since been termed *perseverative* and *anticipatory* errors (respectively), and when plotted probabilistically (averaged over sessions and birds) they suggest that pigeons gradually switch from one response to the other.

A flurry of recent research (Laude, Stagner, Rayburn-Reeves, & Zentall, 2014; McMillan, Kirk, & Roberts, 2014; McMillan & Roberts, 2012, 2014, 2015; Rayburn-Reeves, Laude, & Zentall, 2013; Rayburn-Reeves, Molet, & Zentall, 2011; Rayburn-Reeves, Stagner, Kirk, & Zentall, 2013; Rayburn-Reeves & Zentall, 2013; Stagner, Michler, Rayburn-Reeves, Laude, & Zentall, 2013) has examined this midsession reversal task using a simpler, simultaneous discrimination choice procedure. Generally, subjects are presented with two options, with responses to one reinforced for the first half of the session (Stimulus 1; S1) and to

the other reinforced for the latter half of the session (Stimulus 2; S2). The primary goal of these experiments has been to study the patterns of pigeons' errors with small changes to the procedure, and especially to understand why pigeons make such errors. It is important to note that maximal reinforcement could be obtained on this task by responding to S1 until the first trial on which doing so is not reinforced, and then switching to respond only to S2 for the remainder of the session. Researchers have questioned why pigeons appear to fail to use this 'reward-following' strategy, and also what strategy the pigeons use instead.

Cook and Rosen (2010) initially demonstrated that pigeons' errors in midsession reversal were likely due to interval timing; that is, pigeons timed from some point early in the session to the reversal, and compared subjective time to their reference memory for the typical reversal time. The researchers inserted extended temporal gaps 28 trials prior to the contingency reversal and found that pigeons showed more anticipatory errors after longer gaps (i.e., when subjective time was closer to the typical time of reversal). McMillan and Roberts (2012) extended this finding by training pigeons with 6-s intertrial intervals (ITIs) during baseline, and then doubling or halving the ITI duration on probe sessions. It was found that pigeons produced more anticipatory and perseverative errors (respectively), consistent with tracking interval time. These results suggest that pigeons track the temporal structure of the session on midsession reversal tasks, and have learned to reverse their behaviour based on this internal timer.

In relying on this interval timing strategy, pigeons' response behaviour on midsession reversal tasks shows remarkable insensitivity to actual trial-by-trial (local) reinforcement rates. For example, Cook and Rosen (2010) showed that pigeons' responding was highly similar to baseline when trials were nondifferentially reinforced on probe sessions (i.e., any response was reinforced); pigeons' reversal was almost entirely governed by internal control, rather than

attention to the outcome of individual trials. Likewise, when Rayburn-Reeves et al. (2011) trained pigeons with unpredictable reversal points (with the reversal occurring after Trials 10, 25, 40, 55, or 70 across sessions), pigeons produced many perseverative errors when the reversal was early and many anticipatory errors when the reversal was late. Pigeons neglect local reinforcement rates in midsession reversal, even when doing so imposes a heavy cost to obtaining food reward.

The typical midsession reversal procedure has a very simple structure, with the same stimulus always serving as the first-correct stimulus each session (e.g., red) and the second-correct stimulus (e.g., green) rewarded after a highly predictable number of trials (usually 40). Pigeons tend to respond as quickly as possible, and reach the reversal point at approximately the same time each session (e.g., four min) with very little within-subjects variability. It has been argued that pigeons learn the *temporal structure* of the session on these midsession reversal tasks (McMillan & Roberts, 2014). Perhaps the most interesting aspect of this behaviour is that typical interval timing theories (e.g., Scalar Expectancy Theory: e.g., Gibbon, 1977; Gibbon, Church, & Meck, 1984) commonly describe the internal clock as timing from the onset of a particular stimulus to the delivery of reinforcement, and most procedures used to study interval timing do so for individual trials. In midsession reversal procedures, animals appear to learn the interval duration to an unsignaled contingency reversal across many trials (and reinforcers). However, it is unclear how complex this temporal representation is, because only a single reversal is used on most midsession reversal procedures. Previous procedures have also almost exclusively used 80-trial sessions, with a few exceptions (96 or 144 trials with pigeons: Cook & Rosen; 5 trials with pigeons: Rayburn-Reeves & Zentall, 2013; 24 trials with humans: Rayburn-Reeves et al., 2011; 24 trials with rats: McMillan et al., 2014). No previous midsession reversal procedure has used

multiple reversals on each session such that, for example, S1 is correct for more than one block of trials per session; it is thus unclear whether pigeons can ‘map’ the temporal structure of a session with a more complex arrangement of contingencies than ‘S1, then S2’ (or ‘S1, then S2, then S3’, as demonstrated by McMillan & Roberts, 2015).

Rationale for the Present Research

Previous midsession reversal studies have carried the implicit assumption that pigeons make deliberate choice errors near reversals; that is, it has been assumed that pigeons rely on a particular strategy (or compromise between timing and local reinforcement strategies: McMillan et al., 2014; McMillan & Roberts, 2015) and that errors near reversals are caused by incorrect choices due to noise in deliberative systems. However, an unexplored possibility is that pigeons simultaneously track local reinforcement and interval time, and errors near reversals result from failures to inhibit incorrect responses based on time. Importantly, Bouton (1993, 2004) has argued that contextual modifications to inhibition are crucial for shifting behavior based on context (e.g., the temporal context of switching from responding to red to responding to green). In other words, the current time from the beginning of the session sets the occasion for the response-no reinforcer relationship, independently for each of the stimuli. A pigeon may be capable of using a reward-following strategy to drive its choice, but intrusion from a timing system leads the pigeon to fail to withhold responses to the currently-incorrect (but ‘proximally-correct’) option. It is also unclear whether pigeons observe simultaneously and choose between the two alternatives when they are presented, or rather serially encounter each spatially-distinct stimulus at random and either peck or inhibit a peck. Part of the difficulty in distinguishing between choice and inhibition failure in previous tasks is due to the non-independent nature of a

simultaneous discrimination: pecking red and not pecking green (or vice versa) are confounded together as a single choice response.

In the present research, we sought to disentangle choice and inhibition by presenting red and green alternatives across trials, using a go/no-go procedure. Pigeons were presented with either a red or green stimulus on each trial (varying randomly across trials between the left and right side of the screen, as in previous studies), with pecks to S1 reinforced in the first 40 trials and pecks to S2 reinforced in the following 40 trials. Because such a non-simultaneous discrimination no longer carries an inherent penalty for pecking the incorrect stimulus (i.e., pecking the incorrect stimulus does not cause a loss of scheduled food reward as it does in a choice procedure), we instituted a 10-s time-out for pecking a currently-nonreinforced stimulus. This go/no-go procedure allowed us to track how birds responded to each of S1 and S2 across the session, independent of responding to the other stimulus. We expected that if pigeons' reversal behaviour is driven by a failure to inhibit responding, then all of pigeons' perseverative errors would be to S1 and anticipatory errors to S2 (i.e., they would fail to withhold pecks when pecking was incorrect) rather than the inverse.

Midsession reversal tasks almost exclusively include only one reversal per session (though see McMillan & Roberts, 2014; Rayburn-Reeves et al., 2013). Though this is partially due to the novelty of the procedure, part of the issue with increasing the number of reversals is that increasing the number of trials to accommodate more reversals also increases the likelihood that satiety effects would confound the results. An interesting affordance of the go/no-go procedure is that it allows subjects only half as much total reinforcement per trial compared to the choice task, because half of trials are nonreinforced no matter the animal's behavior. After initial training with an 80-trial go/no-go task, we tested our subjects on 160-trial and 240-trial

tasks while maintaining a reversal every 40 trials (i.e., reward contingencies reversed three times and five times in the 160-trial and 240-trial test, respectively). We were interested in whether pigeons would successfully reverse their behaviour multiple times, and whether changing the temporal structure of the session would lead pigeons to adopt different strategies to change their responding across the session.

One problem with interpreting these results alone was that prior training with only one reversal may have biased pigeons toward a strategy that was less suited to a multiple-reversal task. To examine the effect of prior training, in Experiment 2 we started new birds on a 240-trial, five-reversal version of the task from the first session of training. In Experiment 3, we sought to control for the novel timeout procedure used in the first two experiments by training birds on a visual choice procedure, similar to that used previously (e.g., McMillan & Roberts, 2012) with the exception that incorrect choices were penalized with a 10-s timeout. Finally, in Experiment 4 we transferred all three groups of pigeons from the previous experiments to a novel 160-trial, three-reversal choice task. In this final experiment, we examined whether previous training with multiple reversals (for birds from Experiments 1 and 2) or with a choice task (for birds from Experiment 3) would lead to improved performance on a choice task with multiple reversals. A summary of the four current experimental designs is presented in Table 1.

Experiment 1

In Experiment 1, pigeons were trained on a procedure analogous to a typical midsession reversal task, except that they were only presented with one alternative on each trial. By providing reinforcement for responding to the currently-correct stimulus, and penalizing responses to the currently-incorrect stimulus with a timeout, we expected that pigeons' errors

would be informative as to whether they were reversing choices incorrectly, or conversely that they were failing to inhibit responses to the proximally-correct stimulus.

Method

Subjects. Five adult pigeons (*Columba livia*) were used. These subjects had previously been used in touchscreen and open-field experiments, but not in a midsession reversal experiment. Birds were maintained at approximately 85% of free-feeding weight throughout the experiment, with free access to water and grit. They were group-housed (8-10 per cage) in flight cages measuring 165 x 69 cm (floor) x 178 cm (height), under a 12-hr light-dark cycle with light onset at 7:00 a.m. Testing was performed between 8 a.m. and 4 p.m. for 6 days each week. This research was conducted with the approval of the University of Alberta Animal Care and Use Committee: Biosciences, meeting the standards of the Canadian Council on Animal Care.

Apparatus. Two custom-made, sound-attenuating operant chambers were used, one measuring 30 x 74 cm (floor) x 40 cm (height) and the other measuring 36 x 55 cm (floor) x 40 cm (height). The front wall of each chamber was open to a 22" Viewsonic VX2268wm FuHzion LCD computer monitor (resolution: 1680 x 1050 pixels; refresh rate: 120Hz), on which all stimuli were presented, with a Carroll Touch infrared touch frame (Elo Touch Systems, Inc., Menlo Park, CA) positioned between the monitor and the inside of the chamber used to record peck location. Grain reinforcement was delivered by electromechanical hoppers through two 6 x 6 cm openings in the front wall located near the floor, on either side of the monitor. Side of reinforcement was varied across trials, and feeding was monitored via an infrared beam at the opening to each hopper. Presentation of stimuli, reinforcement, and recording of responses were carried out by microcomputers, in an adjacent room, interfaced to the operant chambers.

Procedure. Pigeons were first autoshaped to peck blue, red, and green circle stimuli. On each trial, one of the cues (2.5 cm in diameter) was presented centrally on the monitor, or shifted 10 cm left or right of center, with cue color and location randomized across trials. Pecking the key, or failing to peck the key after 12 s, led to 2 s of food reward. Trials were separated by a 30-s intertrial interval (ITI).

After autoshaping, subjects were initially trained on 50 sessions of an 80-trial go/no-go midsession reversal discrimination task (*Baseline*), followed by 25 sessions of a 160-trial go/no-go task (*160-Trials test*), and finally 25 sessions of a 240-trial go/no-go task (*240-Trials test*).

Baseline. On each trial for 80 trials per session, pigeons were presented with a blue-filled circle (2.5 cm in diameter) in the center of a grey background on the touchscreen. A single peck on this stimulus began the trial, leading immediately to the presentation of either a green- or red-filled circle (2.5 cm in diameter) on either the left or right side of the screen (10 cm from center, with presentations of red vs. green and left vs. right randomized in blocks of four trials across the session). If the red or green stimulus was not pecked within 3 s of presentation, the stimulus was removed and was followed by a 3-s ITI, with the screen background still lit grey, followed by a new trial. Pecks from the first 1-s of stimulus presentation were disregarded in order to minimize incidental responding before the stimulus could reasonably be processed (e.g., wing touches); after removing these data, reaction times for both reinforced and non-reinforced ‘go’ responses averaged approximately 1250 ms. For three birds, a peck to the red circle was correct for the first 40 trials, and a peck to the green circle was correct for the latter 40 trials; these contingencies were reversed for the other two subjects. A single peck to the green or red circle led to the immediate removal of the stimulus: pecking the currently-correct stimulus was subsequently reinforced with 1-s access to food (measured from the time that the pigeon first tripped the

photobeam in the hopper); if the pigeon pecked the currently-incorrect stimulus, the screen was blackened for 10-s (timeout) before the next trial. Either result was followed by a 3-s ITI, with the screen background lit grey, subsequently followed by a new trial.

160-Trials Test. 160-Trials testing was identical to baseline, except that there were 160 trials per session, with contingency reversals after trials 40, 80, and 120. The first 80 trials were indistinguishable from baseline training, and the subsequent 80 trials were identical except that they were presented immediately following completion of the first 80 trials.

240-Trials Test. 240-Trials testing was identical to 160-Trials testing, except that there were 240 trials per session, with contingency reversals after Trials 40, 80, 120, 160, and 200. The first 160 trials were indistinguishable from 160-Trials, and the subsequent 80 trials were identical to baseline except that they were presented immediately following completion of the first 160 trials.

Analysis. Analyses used data from the last 25 sessions of the initial baseline condition, to remove early training effects. Trials on which S1 or S2 were presented were pooled and averaged across sessions. All 25 sessions of each phase of testing data were used, except where noted otherwise. The first 25 sessions of baseline training are provided in the Supplemental Materials as Figure A.

Results and Discussion

Figure 1a illustrates the birds' performance on the baseline condition of the go/no-go midsession reversal procedure. Contrary to the gradual, roughly symmetrical shift in choice normally shown in previous midsession reversal procedures, here the subjects performed at ceiling for responding to S1 for the first 40 trials, and showed a gradual decrease in responses to S1 after Trial 40; conversely, subjects showed a gradual increase in responses to S2 before Trial

40, with responses at ceiling for the last 40 trials. Essentially, birds rarely made errors by not responding when making a response was correct, and instead made most of their errors by responding when making a response was incorrect.

Pigeons' responding on each stimulus in this go/no-go version of the midsession reversal procedure may suggest that incorrect choices in other versions of the task arise from failures to inhibit incorrect responses. To illustrate this, Figure 1b shows the same data from Figure 1a plotted as a discrimination ratio (i.e., probability of making a response to S1, divided by the probability of making a response to either stimulus, averaged for each trial), and compared to choice of S1 from an analogous midsession reversal choice task (adapted from McMillan & Roberts, 2012). Though not exact, there is a striking similarity between the data observed in the present study compared to a choice version of the task, which serves as a simple proof-of-concept that pigeons' choices may be caused by failures of inhibition (i.e., the same underlying function may drive both patterns of results).

Figure 2a illustrates the responding of birds to S1 and S2 across 160-Trials testing. One of the most striking features of these data is the asymmetry in responses to S1 and S2 during the second half of the session. Where responses to S1 decreased dramatically while S1 was incorrect during the final 40 trials of the session, responses to S2 barely decreased during Trials 81-120 (i.e., when pecking S2 produced a timeout and no food). As a simple measure of the difference between errors to S1 and S2 during the last 80 trials of the session, we compared the average proportion of responses to S2 during Trials 101-120 ($M = 0.85$, $SEM = 0.10$) with those to S1 during Trials 141-160 ($M = 0.53$, $SEM = 0.13$). These blocks of trials were chosen because responding across birds reached asymptote in the latter half of each 40-trial reversal block, compared to gradual decreases in responding earlier in the block. A paired t-test confirmed that

birds responded significantly less to S1 than to S2 during the period of the last 80 trials per session in which each was nonrewarded [$t(4) = 4.59, p = .01, d = 1.75, 95\% \text{ CIs} = 0.57, 5.16$].

Figure 2b illustrates the responding of birds to S1 and S2 across 240-Trials testing. Errors to S1 and S2 during nonreinforced trials for each stimulus continued to be asymmetrical, though errors to S1 had increased and errors to S2 had decreased relative to 160-Trials testing. Similar to the previous analysis, we compared the birds' responding to S1 during each block of Trials 141-160 and Trials 221-240 with responses to S2 during each block of Trials 101-120 and Trials 181-200. We used a 2 x 2 [trial block (81-160, 161-240) x stimulus (S1, S2)] repeated-measures ANOVA to compare responding. There was a significant main effect of stimulus [$F(1,4) = 9.34, p = .038, \eta_p^2 = .70, 90\% \text{ CIs} = .01, .82$], but no significant interaction with [$F(1,4) = 2.43, p = .19, \eta_p^2 = .38, 90\% \text{ CIs} = <.01, .65$] nor main effect of trial block [$F(1,4) = 0.60, p = .48, \eta_p^2 = .13, 90\% \text{ CIs} = <.01, .48$]. Despite some reduction in the discrepancies noted in 160-Trials testing, birds on 240-Trials testing showed significantly less responding to S1 ($M = 0.55, SEM = 0.13$) than to S2 ($M = 0.77, SEM = 0.10$), during the latter 160 trials of the session, on trials in which either stimulus was not rewarded.

Experiment 2

Experiment 1 showed that pigeons failed to inhibit incorrect responses in a go/no-go midsession reversal task, rather than failing to make responses when responding was correct. This may suggest that pigeons' errors on 'choice' versions of the midsession reversal task are not incorrect choices so much as failures to inhibit incorrect responses. Interestingly, when sessions were extended and multiple reversals used, pigeons showed asymmetric errors to the two stimuli; while subjects gradually inhibited responding to S1 when doing so was no longer reinforced, they initially failed to inhibit responding to S2 at any point after the first reversal, and even with

extended numbers of sessions and reversals did not inhibit responding to the same degree as to S1. This may suggest that pigeons learned separate ‘rules’ about the shifting contingencies for each stimulus. A remaining question is whether the pigeons’ responses were governed by their initial training with 80 trials (and only one reversal) per session. It is possible to solve a simple single-reversal-per-session task with two ‘rules’: 1.) begin the session by responding to S1, and cease responding when doing so is no longer reinforced; and 2.) respond to S2 after an elapsed interval of time (e.g., approximately five minutes). Use of the latter rule in particular may explain why pigeons showed little inhibition of S2 responses after the reversals at Trials 80 and 160. Importantly, use of these two rules (which conflict in the trials immediately preceding Trial 40) is consistent with anticipatory errors in both the current go/no-go results as well as in previous choice data. When faced with extended sessions and more reversals, pigeons may have only partially amended these rules post-hoc, and it is unclear whether the same responding would be obtained if the birds did not have extensive training with a ‘simple’ 80-trial, single-reversal procedure.

In Experiment 2, we trained birds with 50 sessions of 240 trials each (exactly identical to 240-Trials testing in Experiment 1, except without prior training on shorter midsession reversal tasks), in order to examine whether training with multiple reversals from the first session would influence pigeons’ inhibition of responding to S1 and S2.

Method

Subjects and apparatus. Five new pigeons were used in Experiment 2; these subjects had equivalent prior experience to those used in Experiment 1, and had not previously been used on a midsession reversal procedure. All aspects of animal husbandry and experimental apparatus were the same as in Experiment 1.

Procedure. After autoshaping, pigeons in this Experiment were initially trained on 50 sessions of a 240-trial go/no-go discrimination task, identical to the procedure used in the 240-Trials testing in Experiment 1 except for the number of sessions and the pigeons' prior training.

Analysis. Only the last 25 sessions of training were included in analyses, to remove early training effects from the data. The first 25 sessions of baseline training are provided in the Supplemental Materials as Figure B.

Results and Discussion

Figure 3 illustrates the responding of birds to S1 and S2 across each of 240 trials in Experiment 2. The data appear practically identical to that exhibited by birds in Experiment 1 on 240-Trials testing (Figure 2b). The same primary findings of Experiment 1 held here: 1.) asymmetric distribution of anticipatory and perseverative errors to S1 and S2, consistent with a failure to inhibit currently-incorrect responses; and 2.) more incorrect responses to S2 than to S1 during the latter two-thirds of the session.

We compared average responding to S1 during each block of Trials 141-160 and Trials 221-240 with responses to S2 during each block of Trials 101-120 and Trials 181-200, using a 2 x 2 [trial block (81-160, 161-240) x stimulus (S1, S2)] repeated-measures ANOVA. There was a significant main effect of stimulus [$F(1,4) = 21.25, p = .01, \eta_p^2 = .84, 90\% \text{ CIs} = .19, .90$], but no significant interaction with [$F(1,4) = 3.02, p = .16, \eta_p^2 = .43, 90\% \text{ CIs} = <.01, .68$] nor main effect of reversal [$F(1,4) = 0.12, p = .74, \eta_p^2 = .03, 90\% \text{ CIs} = <.01, .36$]. As previously observed in Experiment 1, birds showed significantly less responding to S1 ($M = 0.36, SEM = 0.11$) than to S2 ($M = 0.67, SEM = 0.11$) during the latter 160 trials of the session during the period in which either stimulus was not rewarded. Importantly, these birds showed identically asymmetrical patterns of responding to S1 and S2 as compared to birds in Experiment 1, despite

the differences in each group's previous training history (i.e., initial training with an 80-trial session for subjects in Experiment 1).

Experiment 3

Pigeons produced asymmetric patterns of errors to S1 and S2 on reversals subsequent to the first in Experiments 1 and 2. This may indicate that birds learned different 'rules' about response contingencies for the two stimuli, even in Experiment 2 where they were initially trained with multiple reversals. The primary difference in the experimental procedure of Experiments 1 and 2, when compared to prior midsession reversal experiments, was the presentation of stimuli independently across trials and recording responses vs. non-responses across trials (compared to more-typical choice procedures, where there is always a response and the measure of interest is which stimulus is chosen over trials). However, there are a number of distinctions between the procedures used in Experiments 1 and 2 compared to the rest of the midsession reversal literature. For example, many previous midsession reversal experiments have not used touchscreens as the operant apparatus, though touchscreens were used by Cook and Rosen (2010). In Experiments 1 and 2, we also included a blue stimulus as a ready cue before presentation of the stimuli, and this has likewise not been used in midsession reversal experiments other than by Cook and Rosen (2010).

A possibly more-significant change in the current procedure relative to previous choice procedures was the addition of timeouts for incorrect responses. In typical midsession reversal experiments, the penalty for making an incorrect peck (i.e., choosing the currently-nonrewarded stimulus) is the inability to obtain food on that trial; in Experiments 1 and 2 here, an incorrect peck (i.e., responding on the currently-nonrewarded stimulus) was penalized with a 10-s timeout. Our reasoning for including a timeout was that not penalizing pecking currently-nonrewarded

stimuli would make the obvious strategy for pigeons to peck either stimulus every time each was presented, or at least not to be judicious in inhibiting responses. This may have created a difference in punishing contingencies (i.e., a lengthy timeout rather than just a missed opportunity for food), and it also modified the timing of the session; where most 80-trial choice tasks take pigeons approximately five minutes to reach the reversal at Trial 40, each incorrect response in our procedure added 10 seconds to the time until the reversal. Importantly, this additional time was completely contingent upon how many errors pigeons made on individual sessions. Thus, the addition of the timeout may have decreased the accuracy of using interval time as a cue for the reversal, both in terms of the scalar variability of time being higher with longer absolute session lengths, and in terms of session durations being more variable. Given that interval time has been suggested as the primary cue that pigeons use in lieu of reward-following on midsession reversal tasks (Cook & Rosen, 2010; McMillan & Roberts, 2012, 2014), it is thus possible that our current results may be partially caused by the diminishing usefulness of time as a cue. This possibility was not necessarily predicted, as previous research has shown incredible robustness of pigeons' tendency to time the reversal on a visual discrimination, even when time was a highly unreliable cue (Rayburn-Reeves et al., 2011).

In Experiment 3, we replicated in a new, midsession reversal naïve set of subjects the procedure of previous choice-based midsession reversal tasks, except we used the apparatus, ready signal, and timeouts as presented in Experiments 1 and 2. Essentially, these subjects received the same procedure as the birds in Experiment 1, except that both red and green alternatives were presented on every trial.

Method

Subjects and apparatus. Five new pigeons were used in Experiment 3; these subjects had equivalent prior experience to those used in Experiment 1, and had not previously been used on a midsession reversal procedure. All aspects of animal husbandry and experimental apparatus were the same as in Experiment 1.

Procedure. Pigeons in Experiment 3 were trained on 50 sessions of an 80-trial midsession reversal choice task as described below.

On each trial for 80 trials per session, pigeons were presented with a blue-filled circle in the center of a grey background on the touchscreen. Pecking this stimulus began the trial, leading immediately to the presentation of both a green- and red-filled circle, each on either the left or right side of the screen (with presentations of left vs. right randomized in blocks of four trials across the session). Pecks from the first 1-s of stimulus presentation were disregarded in order to minimize incidental responding before the stimulus could reasonably be processed (e.g., wing touches). Both stimuli were presented until the pigeon made a choice response. For three birds, pecks to the red circle were reinforced for the first 40 trials, and pecks to the green circle were reinforced for the latter 40 trials; these contingencies were reversed for the other two subjects. Pecking the green or red circle led to the immediate removal of both stimuli: pecking the currently-‘correct’ stimulus was subsequently reinforced with 1-s access to food (measured from the time that the pigeon first tripped the photobeam in the hopper); if the pigeon pecked the stimulus currently not rewarded, the screen was blackened for a 10 s timeout. Either result was followed by a 3-s ITI, with the screen background lit grey, subsequently followed by a new trial. Unlike in Experiments 1 and 2, in this experiment trials continued until one of the stimuli was pecked.

Analysis. Only the last 25 sessions of training were included in analyses, to remove early training effects from the data. The first 25 sessions of baseline training are provided in the Supplemental Materials as Figure C.

Results and Discussion

Figure 4 demonstrates the average performance of birds on this visual choice midsession reversal task. Pigeons displayed somewhat better performance on this version of the task than previously observed (e.g., see Figure 1b), with both fewer anticipatory and perseverative errors than frequently observed. This may suggest that the addition of timeouts had punishing effects on errors over and above missing a reinforcer on a particular trial.

Birds still did not appear to be highly sensitive to local reinforcement rates, as observed in other similar midsession reversal tasks. Paired t-tests showed the birds' average change in choice of S1 from Trials 41-42 ($M = 0.19$, $SEM = 0.08$) was not significantly larger than either the change from Trials 36-41 [$M = 0.04$, $SEM = 0.01$; $t(4) = 1.73$, $p = .16$, $d = 1.18$, 95% CIs (-0.39, 2.48)] nor Trials 42-47 [$M = 0.06$, $SEM = 0.02$; $t(4) = 1.53$, $p = .20$, $d = 1.00$, 95% CIs (-0.48, 2.32)]. Although inspection of Figure 4, as well as these effect size estimates, illustrate that pigeons appeared to have at least some sensitivity to the reversal, this sensitivity varied appreciably across birds. Taken in the context of Experiments 1 and 2, these individual differences may have been the result of timeouts having different effects on inhibition for different birds.

Experiment 4

Experiment 3 demonstrated that, despite possibly showing better-than-typical performance for a visual discrimination, pigeons continued to make anticipatory and perseverative errors on a midsession reversal choice task with a timeout procedure implemented.

However, Experiments 1 and 2 also demonstrated that pigeons' patterns of errors on a go/no-go version of the task changed as they were trained with multiple reversals. With no previous research in multiple within-session contingency reversals between two stimuli, it is unknown whether training with multiple reversals would improve midsession reversal performance on a choice task. In Experiment 4, we used a 160-trial, three-reversal choice task to ask whether the pigeons used in Experiments 1 and 2 could transfer successfully to a midsession reversal choice task, and whether the pigeons used in Experiment 3 would transfer to a task with multiple reversals. This experiment serves to explore the effects of additional reversals (which alter the temporal structure of the session, but do not change the structure of the first 80 trials) on performance of birds with prior experience with multiple reversals or with midsession reversal choice tasks.

Method

Subjects and apparatus. The same 15 pigeons used in Experiments 1-3 served as subjects for Experiment 4. All aspects of animal husbandry and experimental apparatus were the same as in Experiment 1.

Procedure. Pigeons were immediately transferred to the procedure described here on the session day following completion of their previous experiment. On each trial for 160 trials, pigeons were presented with a blue-filled circle in the center of a grey background on the touchscreen. Pecking this stimulus began the trial, leading immediately to the simultaneous presentation of a green- and red-filled circle on either the left or right side of the screen (with left vs. right randomized in blocks of four trials across the session). Both stimuli remained on the screen until the pigeon made a choice response. All other contingencies were identical to previous phases; pecks to one color were reinforced with access to food, pecks to the other

stimulus led to a 10-s timeout, and reinforcement vs. timeout contingencies reversed every 40 trials. The first-correct stimulus for each subject was also maintained from previous training.

Results and Discussion

Figure 5 illustrates the mean performance of each of the three groups of pigeons on this 160-trial, choice midsession reversal task. All three groups showed very little anticipation of any of the reversals, and rapidly reversed responding immediately after each contingency reversal. Interestingly, this pattern of responding was found even in birds from Experiment 3, though these subjects had previously shown relatively poor sensitivity to the reversal and many anticipatory errors when trained with only a single reversal per session. The illustrated data of subjects from Experiments 1 and 2 was indicative of their performance even on their first session, despite no previous training with a choice task; pigeons appeared to show excellent transfer from a go/no-go midsession reversal task to an otherwise-equivalent choice task.

Pigeons appeared to show few anticipatory errors before any of the reversals, regardless of group. We analyzed the anticipation of each reversal by measuring sensitivity as the drop in responding on the critical trials after the reversal (i.e., the change in responding from Trials 41-42, 81-82, and 121-122) compared with the change in responding in the five trials prior to each of the three reversals (i.e., anticipatory responding). A 2 x 3 x 3 (contrast [anticipatory, critical] x reversal [first, second, third] x group [Experiment 1, 2, 3]) mixed-effects ANOVA showed a significant main effect of reversal [$F(2,24) = 5.50, p = .01, \eta_p^2 = .31, 90\% \text{ CIs} = .05, .48$] and of contrast [$F(1,12) = 81.98, p < .001, \eta_p^2 = .87, 90\% \text{ CIs} = .69, .92$]; no interactions, nor the main effect of group, were significant ($F_s < 2.39, p_s > .079, \eta_p^2_s < .29$). Across the reversals, the mean change in responding immediately after the reversal ($M = .22, SEM = .02$) was greater than the mean change in the trials before the reversal ($M < 0.01, SEM < 0.01$), suggesting that pigeons

were sensitive to the change in contingencies relative to their anticipatory responding. The main effect of reversal was best described by a linear contrast [$F(1,12) = 11.58, p = .01, \eta_p^2 = .49$, 90% CIs = .11, .67], with pigeons showing a larger change in responding at earlier reversals than at later reversals; this decrease in sensitivity may have been caused by increased satiety past the 80 trials typically used in midsession reversal procedures. Most importantly, the lack of significant interactions suggest that the specific reversal point and the birds' prior experimental history did not affect pigeons' sensitivity to the reversals relative to anticipatory responding.

Pigeons also appeared to show relatively few perseverative errors after each reversal, with most change in responding occurring immediately after the reversal. We analyzed the perseveration after each reversal using a 2 x 3 x 3 (contrast [perseveratory, critical] x reversal [first, second, third] x group [Experiment 1, 2, 3]) mixed-effects ANOVA. There was a significant main effect of reversal [$F(2,24) = 5.79, p = .009, \eta_p^2 = .33$, 90% CIs = .06, .49] and of contrast [$F(1,12) = 39.02, p < .001, \eta_p^2 = .77$, 90% CIs = .47, .85]; no interactions, nor the main effect of group, were significant ($F_s < 3.01, p_s > .069, \eta_p^2_s < .28$). Across the reversals, the mean change in responding immediately after the reversal ($M = .22, SEM = .02$) was greater than the mean change in the trials following ($M = 0.06, SEM = 0.01$), suggesting that pigeons were sensitive to the change in contingencies relative to their perseverative responding. The main effect of reversal was best described by a linear contrast [$F(1,12) = 14.67, p = .002, \eta_p^2 = .55$, 90% CIs = .17, .71], with pigeons showing a larger change in responding at earlier reversals than at later reversals. Importantly, the lack of significant interactions suggest that the specific reversal point and the birds' prior experimental history did not affect pigeons' sensitivity to the reversals relative to perseveration.

Though the different experimental groups' data largely overlap across the 160-trial sessions, the primary difference among the three groups appeared after the second reversal, when S1 was rewarded for Trials 81-120. A 1 x 3 [experiment (1, 2, 3)] between-subjects ANOVA confirmed a significant difference between the three groups in choice of S1 during Trials 101-120 [$F(1,2) = 7.24, p = .009, \eta_p^2 = .55, 90\% \text{ CIs} = <.01, .87$]. Bonferroni-corrected post-hoc tests showed a significant difference between birds from Experiments 2 ($M = 0.92, SEM = 0.01$) and 3 [$M = 0.67, SEM = 0.06; t(8) = 4.18, p = .008, d = 2.95, \text{ CIs} = 0.82, 4.38$], but not for any other group comparisons ($ps > .128, ds < 1.33$). Birds that only had experience with multiple reversals showed significantly more choices of S1 during the second block in which responses to S1 were reinforced, compared to birds that had only previous experience with a single reversal. This was in spite of the birds from Experiment 3 being the only subjects with prior experience on a choice midsession reversal task.

Perhaps the most surprising aspect of these data is that the pigeons from Experiment 3, which had previously shown an appreciable number of anticipatory and perseverative errors, seemed to show greater sensitivity to the reversal in Experiment 4. This was true even at the first reversal, which was exactly the same as they had previously experienced (i.e., there was no procedural change to the first 80 trials relative to their previous experience). However, we noted a large change in the pattern of responding in these subjects through training on the present task; Figure 6 illustrates the choice of S1 in these birds on Trials 36-47 from Sessions 41-50 in Experiment 3, and from Sessions 1-10 and Sessions 16-25 in Experiment 4. Whereas initial training in Experiment 4 led to responding similar in slope to that in Experiment 3, pigeons demonstrated fewer anticipatory errors even early in Experiment 4. Extended training led to a

greater sensitivity to the reversal (i.e., the majority of pigeons' change in responding occurred immediately after the reversal).

Pigeons previously used in Experiment 3 appeared to increasingly use a win-stay, lose-shift strategy after training with multiple reversals, with most response switching from S1 to S2 occurring from Trials 41 to 42 rather than the trials before or after that point. As in previous analyses, we compared these birds' change in responding in the critical Trials 41-42 with their change in responding in the trials before and after that point. A 2 x 3 (contrast [anticipatory, critical] x timepoint [Sessions 41-50, 1-10, 16-25]) repeated-measures ANOVA showed a significant interaction [$F(1,5) = 8.58, p = .026, \eta_p^2 = .68, 90\% \text{ CIs} = .03, .78$], after correcting degrees of freedom for sphericity with Greenhouse-Geisser. A 2 x 3 (contrast [perseveratory, critical] x timepoint [Sessions 41-50, 1-10, 16-25]) repeated-measures ANOVA also showed a significant interaction [$F(1,5) = 8.53, p = .024, \eta_p^2 = .69, 90\% \text{ CIs} = .03, .78$], after correcting degrees of freedom for sphericity with Greenhouse-Geisser. As can be noted from visual inspection of Figure 6, sensitivity to the reversal after Trial 40 improved with increased training on multiple reversals.

General Discussion

In the present experiments we provide evidence that errors on the midsession reversal task are driven by pigeons' inability to inhibit incorrect responding based on interval time. Further, pigeons appeared to learn different, independent rules about the first- and second-correct stimuli in midsession reversal, even when trained with a 240-trial, five-reversal procedure. Pigeons appeared to show fewer errors on a visual choice task with timeouts than typically observed without timeouts, but were not pervasively more sensitive to the reversal of local reinforcement contingencies. Finally, pigeons transferred from a go/no-go task to a choice task

with multiple reversals, and even pigeons that had previously shown little sensitivity to a choice reversal task showed improved performance when multiple reversals were used. This also constitutes the first demonstration of near-optimal reversal performance in animals with a visual-discrimination midsession reversal procedure. Together, these results suggest that pigeons' behaviour was based on integration of two sources of information (local reinforcement and time) into rules that governed behaviour, and the amount of stimulus control by time varied based on the ease of using time as a predictive dimension.

One possible interpretation from our data is that choices on a simultaneous discrimination task may not be 'choices' in the lay sense of the word (i.e., a mental decision based on comparison of the merits of multiple options). Pigeons performing a go/no-go discrimination here showed anticipatory and perseverative errors only as incorrect responses (rather than incorrectly-withheld responses). This suggests that typical errors on a simultaneous discrimination may be due to a failure to inhibit time-based responding, rather than a deliberative choice of the incorrect versus the correct stimulus. That pigeons' errors on a midsession reversal task might be best explained as failures to inhibit incorrect responding might also be informative for why previous studies with rats (Rayburn-Reeves, Stagner, et al., 2013) and humans (Rayburn-Reeves et al., 2012) have failed to produce errors consistent with those of pigeons; these species might be better able than are pigeons to inhibit erroneous responding. Importantly, previous research examining humans on midsession reversal (Rayburn-Reeves, et al., 2012) did not report reaction times for trials. If humans are simply more successful at inhibiting incorrect responses than pigeons, it is possible that this sort of active inhibition of responding would produce longer reaction times. There is also no previous research on a go/no-go midsession reversal task in humans, which may be indicative of human error patterns.

It also remains to be determined exactly what led to the modestly improved performance of birds in Experiment 3 compared to typical visual-discrimination, midsession reversal choice procedures. Here we suggest that the inclusion of timeouts as penalty for incorrect responses (in addition to missing available reinforcement on choice trials) is the most likely possible cause of the improvement in performance. However, it is unclear whether the improvement in performance is caused directly by the punishing contingencies of the timeout or by the change in session time (and thus a decrease in accuracy of time as a cue) created by inclusion of the timeouts. It is also difficult to determine how punishing the timeouts used in the current procedure were, especially in light of the number of errors pigeons made with 160- or 240-trial sessions in Experiments 1 and 2. Increasing the duration of the timeouts in the present procedure may have increased their punishing value, but would also have decreased the usefulness of time as a cue (because of increased, and more variable, session times). While we considered utilizing differential reinforcement of other behavior (DRO) schedule instead of timeout penalties, pigeons can be difficult to train on DRO schedules because of classical conditioning effects (D. R. Williams & H. Williams, 1969; Schwartz & D. R. Williams, 1972). We were concerned that these effects might be particularly problematic because the midsession reversal procedure necessitates that both 'go' and 'no-go' responses are reinforced on the same stimulus. Future research should more closely examine the effects of timeouts on punishment value vs. change in interval time for modulating pigeon behavior on the midsession reversal task.

A lack of punishing value of timeouts cannot explain why pigeons produced an asymmetric number of errors to S1 and S2 after multiple reversals in Experiments 1 and 2. Data from these experiments suggest that pigeons may have learned independent 'rules' about S1 and S2. Pigeons produced more errors to S2 compared to S1 with multiple reversals, despite

equivalent overall rates of reinforcement and number or time of reinforced trials for S1 and S2. Also, though S1 and S2 were never rewarded at the same time, pigeons never seemed to learn to withhold pecks to one stimulus during the period in which they received reinforcement for pecking the other stimulus. Though we present S1 and S2 as part of the same task, pigeons may actually have learned the contingencies of each separately. In effect, pigeons may have treated presentations of S1 or S2 as two separate procedures, with independent rules governing when food is delivered for a response. For example, pigeons may have learned to attend to the local reinforcement rates of responding to S1, but primarily attended to the temporal contingencies of S2. An interesting question is whether pigeons learn S1 and S2 independently on simultaneous-discrimination tasks; that is, whether they use a strategy to search for the correct response, or rather encounter either stimulus at random and peck it (or withhold a peck and move to peck the other stimulus). In line with previous discussion, the latter behavior would not be consistent with the typical definition of a ‘choice’ between options.

These results also shed light on a previously-unconsidered reason for the dichotomy of results found when animals are presented with visual vs. spatial discriminations on midsession reversal tasks. It has previously been argued (Laude et al., 2014; McMillan et al., 2014) that a spatial discrimination allows animals to ‘cheat’ the working memory component of the task (i.e., by forming a response pattern of orienting during the ITI to the stimulus to next provide reinforcement), thus increasing the viability of a reward-following strategy when working memory is otherwise poor. However, another possibility is that orienting during the ITI prevents the animal from encountering the currently-incorrect stimulus, where on visual discrimination trials it may encounter either stimulus first if doing a serial search of the choices. Likewise, rats’ performance on a spatial discrimination on the radial maze (McMillan et al., 2014) may be

explained as an inability to inhibit timing-based errors when presented with both the left and right alleys at the same choice point (compared to when presented with spatially-distinct choices in the operant chamber: Rayburn-Reeves, Stagner, et al., 2013).

The most common explanation for pigeons' failure to use a reward-following strategy on the midsession reversal task is that their working memory is too impoverished to be useful or reliable (e.g., Rayburn-Reeves, Laude, & Zentall, 2013). Our current results are more compatible with an inhibition account than a working-memory account because pigeons' near-optimal reversal performance in Experiment 4 cannot be accounted for by improved working memory, especially in light of the improvement of responding by birds from Experiment 3. If pigeons' anticipatory errors in Experiment 3 were only due to poor working memory for the outcome of the previous trial, there should not have been improvement in Experiment 4 when the first 80 trials were identical to the procedure in Experiment 3 (i.e., working memory should have been equivalent in the two conditions). Instead, our results suggest that use of multiple reversals caused pigeons to inhibit anticipatory responses, or to no longer use a timing rule (and thus to no longer need to inhibit responses based on it).

A remaining question is why all three groups of subjects showed strong sensitivity to the reversals in Experiment 4, when subjects in Experiments 1 and 2 tended to respond during 'no-go' stimuli at rates well above zero with multiple reversals per session. While initial data on an 80-trial go/no-go procedure seemed to fit choice data with no modification (e.g., Figure 1b), data on 160-trial or 240-trial procedures would have predicted blunted preferences on a multiple-reversal choice task. Though this was partially consistent with pigeons' decreased performance during Trials 81-120 in Experiment 4, the general finding in Experiment 4 was that pigeons showed very few anticipatory errors and improved reversal performance with multiple reversals.

One possibility is that, as previously discussed, our timeout component was not sufficiently punishing as to decrease errors on a go/no-go task, relative to missed opportunity for food on a choice task, when multiple reversals were used. This does not explain why pigeons transferred from Experiment 3 improved in reversal performance on Experiment 4, however; nor does it explain why pigeons trained on an 80-trial go/no-go procedure produced more errors with 160 and 240 trials per session than with 80 trials.

Changing the structure of the session in Experiment 4 dramatically affected the pigeons' responding: pigeons with prior training with multiple reversals, but not choice tasks (i.e., pigeons from Experiments 1 and 2), showed rapid transfer to this task; pigeons with prior training on choice tasks, but not with multiple reversals (i.e., pigeons from Experiment 3), showed a rapid decrease in anticipatory errors and a slower-developing sensitivity to the reversal resulting in fewer perseverative errors. The change observed in pigeons' reversal performance from Experiment 3 to Experiment 4 is particularly striking in the first 80 trials, which were procedurally identical. Pigeons in previous studies (e.g., McMillan & Roberts, 2012) normally reach asymptotic midsession reversal performance in roughly 10-25 sessions; it is thus also unlikely that the improvement in Experiment 4 would be due to extended training alone. Therefore, the observed change in performance most likely was due to the change in the structure of the session: that is, the change in the global properties of the session (e.g., more trials per session, that S1 comes to produce reward after previously ceasing to be reinforced, and that S2 ceases to produce reward after previously being reinforced on the same session).

It has been argued that anticipatory errors on midsession reversal tasks are the result of the pigeon representing the temporal structure of the session (McMillan & Roberts, 2014), and we have argued here that that structure, in an 80-trial task with a single reversal, can be easily

represented by rules such as “S1 pays off until it ceases to produce reward, and S2 pays off after an elapsed period of time”. As stated, these rules cannot reliably predict reinforcement contingencies after Trial 80 on multiple-reversal procedures, and pigeons appeared to follow reward with multiple reversals while perseverating to the ‘no-go’ stimulus when it was presented. In a choice task, this behavioral strategy led pigeons to produce very few anticipatory errors, a sharp change in responding immediately after the reversal, and to persevere for a number of trials after the reversal (especially during Trials 81-120). Making the structure of the session more complex (by adding more reversals) led to a decrease, or even obliteration, of using the temporal structure of the session to predict reversals.

Additional reversals did not change the first 80 trials of the session between Experiments 3 and 4, but did modify the overall temporal structure of each session. That pigeons showed strong control by local reinforcement rates when the temporal structure was altered in this way suggests that pigeons’ rule-learning was tied to the complexity of timing reversals. For example, pigeons may have learned that S2 was rewarded after a particular elapsed time, but did not show control by this timing-based strategy in Experiment 4 when the rule would have been that S2 was rewarded after an elapsed time, but ceased to be rewarded after a second elapsed period, until after a third period. Modifying the temporal structure of the session radically altered pigeons’ response strategy use, and further research should examine other effects of session structure on midsession reversal performance, for example, by presenting midsession reversal procedures with S1 and S2 randomized for each session. By making the first-correct stimulus unpredictable until the first response, pigeons’ ability to form a simple temporal rule may be affected. This research would be illustrative of the complexity of representations of the interval time of sessions.

It has been argued previously that animals' decisions on simultaneous choice tasks may be based only on a sequential deliberative system rather than comparing between options (Kacelnik, Vasconcelos, & Monteiro, 2011), ostensibly because most choices animals make in the wild are encountered and processed serially (i.e., go/no-go) rather than as simultaneous encounters. Likewise, timing is important in a wide variety of foraging situations (Carr & Wilkie, 1997), such as sequential time-place learning (e.g., Crystal, 2009; Wilkie, 1995; Wilkie, Saksida, Sampson, & Lee, 1994). In effect, errors on the midsession reversal task may reveal choice and timing mechanisms that are relevant in nature, even if they lead animals to make surprising mistakes when faced with artificial problems.

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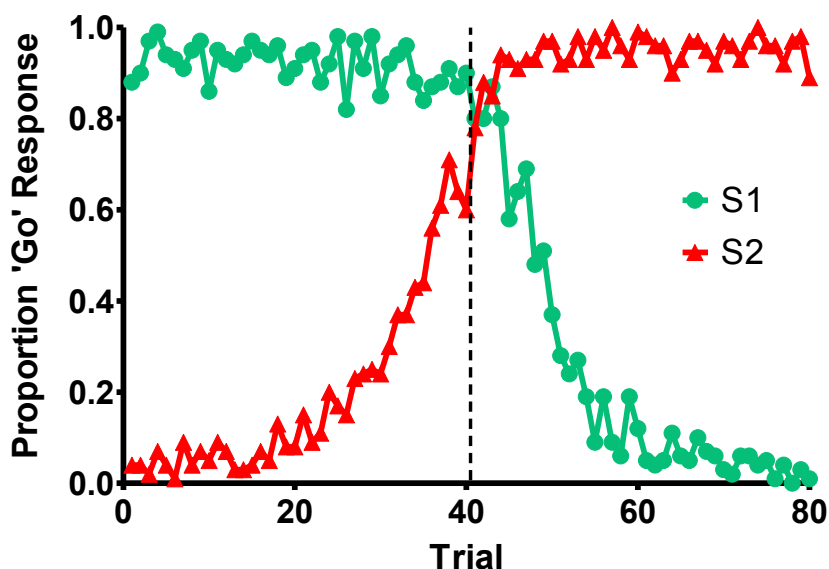
Williams, D. R., & Williams, H. (1969). Auto-maintenance in the pigeon: Sustained pecking despite contingent non-reinforcement. *Journal of the Experimental Analysis of Behavior*, 12, 511-520.

Table 1

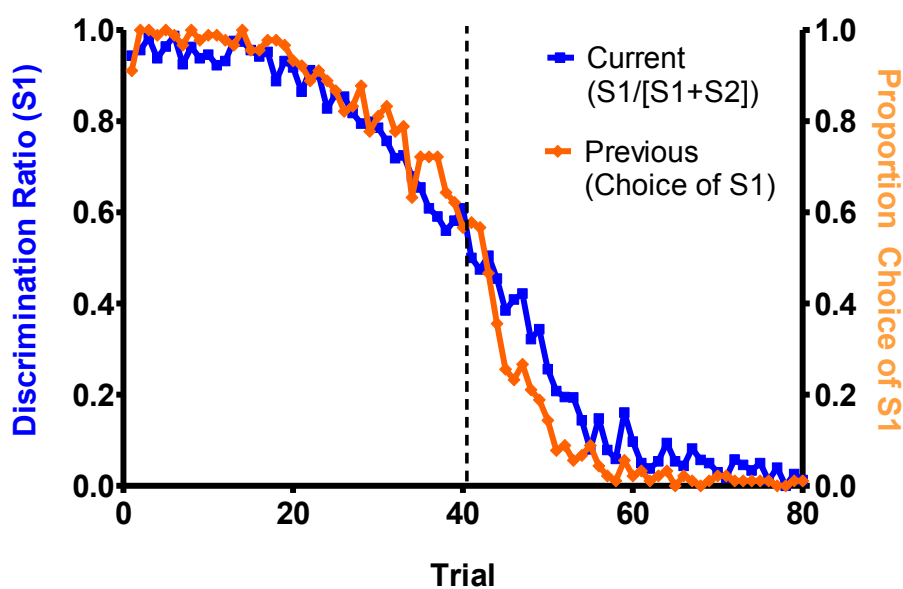
Summary of Experiment Designs

Experiment	Procedure	Reversals	Subject History
1	Go/No-Go	1, 3, and 5	Reversal-naïve
2	Go/No-Go	5	Reversal-naïve
3	Simultaneous Choice	1	Reversal-naïve
4	Simultaneous Choice	3	Used in Experiments 1, 2, or 3

Note. Subjects in Experiment 1 were trained with one reversal per session, followed by 3 reversals per session, and finally 5 reversals per session.

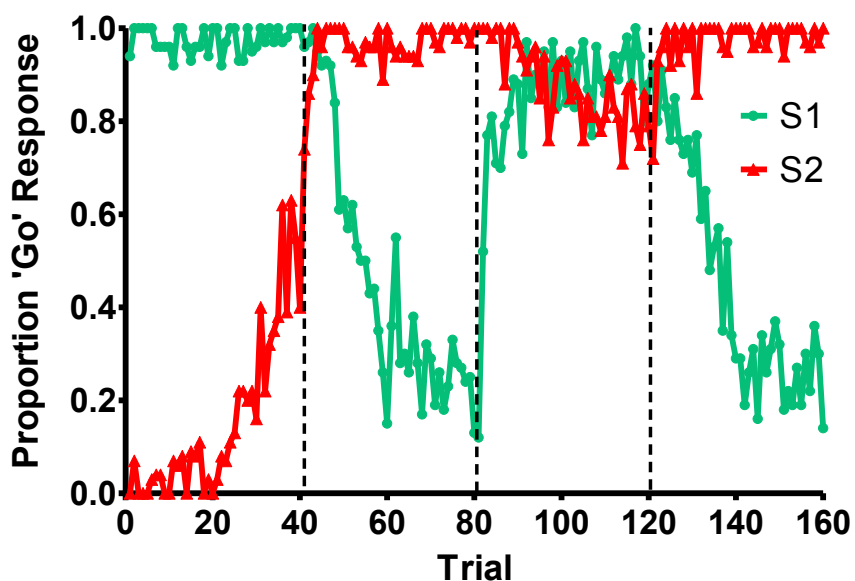


a.

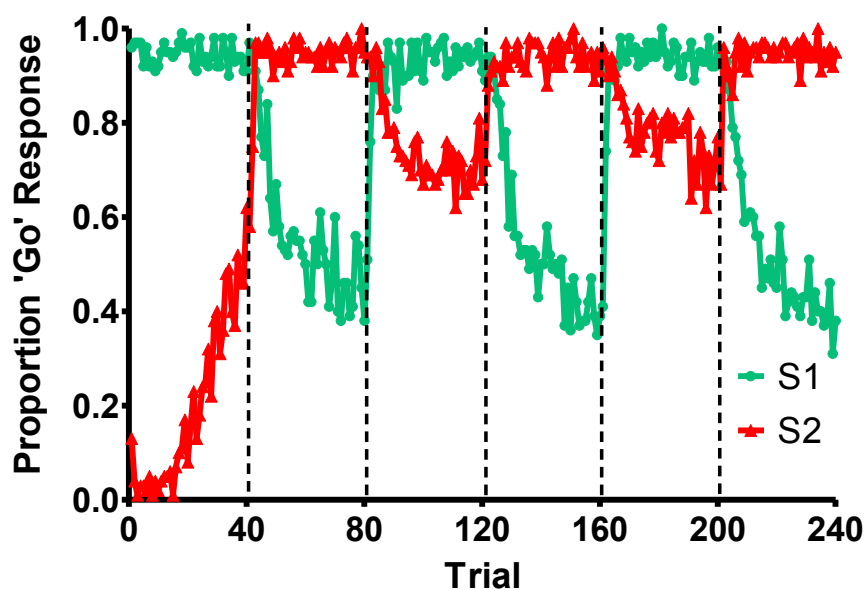


b.

Figure 1. Experiment 1: (A) Comparison of 'go' responses to S1 and S2, averaged across the last 25 sessions of training, at 80 trials per session; (B) The data from Figure 1a, plotted in blue as a discrimination ratio of 'go' responses to S1 divided by 'go' responses to S1 and S2. Previous data (McMillan & Roberts, 2012) on a midsession reversal choice task are included in orange for visual comparison. Vertical hatched lines indicate contingency reversals after Trial 40.



a.



b.

Figure 2. Experiment 1: Comparison of 'go' responses to S1 and S2, averaged 25 sessions of testing, at (A) 160 trials per session; and (B) 240 trials per session. Vertical dashed lines indicate contingency reversals (every 40 trials).

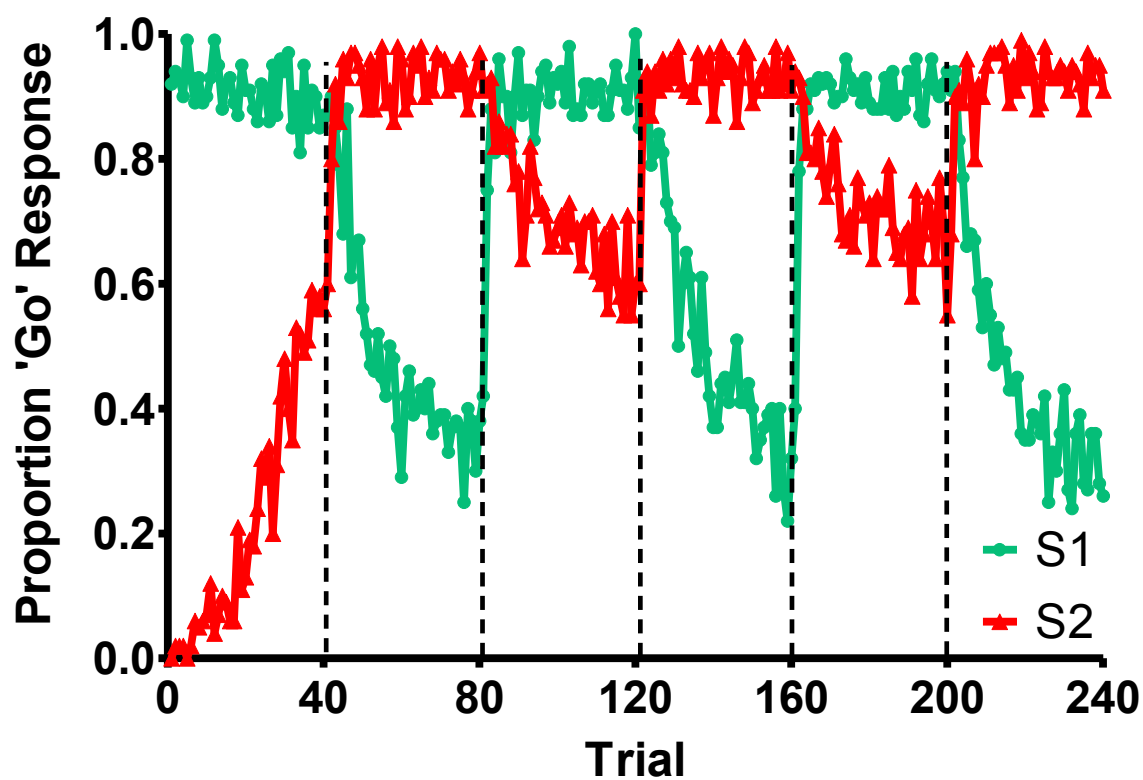


Figure 3. Experiment 2: Comparison of responding to S1 and S2, averaged across the last 25 sessions of training, at 240 trials per session. Vertical hatched lines indicate contingency reversals (every 40 trials).

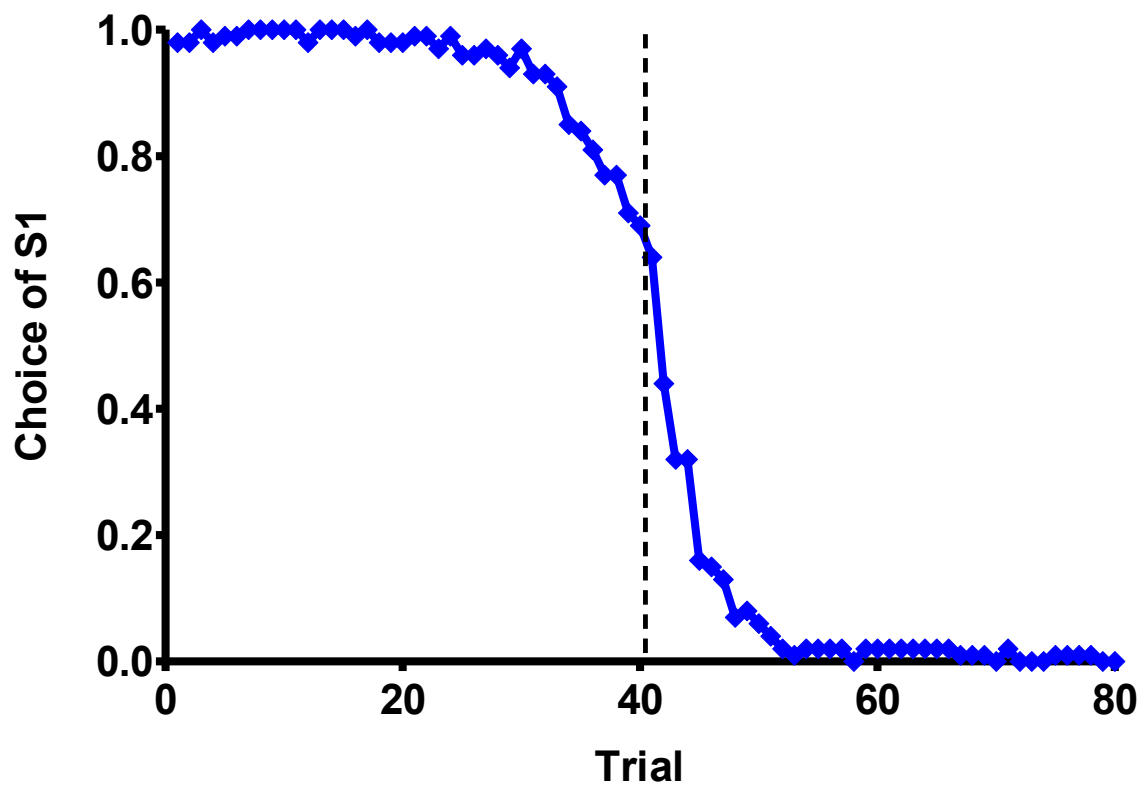


Figure 4. Experiment 3: Choice of S1, averaged across the last 25 sessions of training, at 80 trials per session. Vertical hatched line indicates contingency reversal (after Trial 40). Note that choice of S2 are the reciprocal of S1, and not included here as they are redundant.

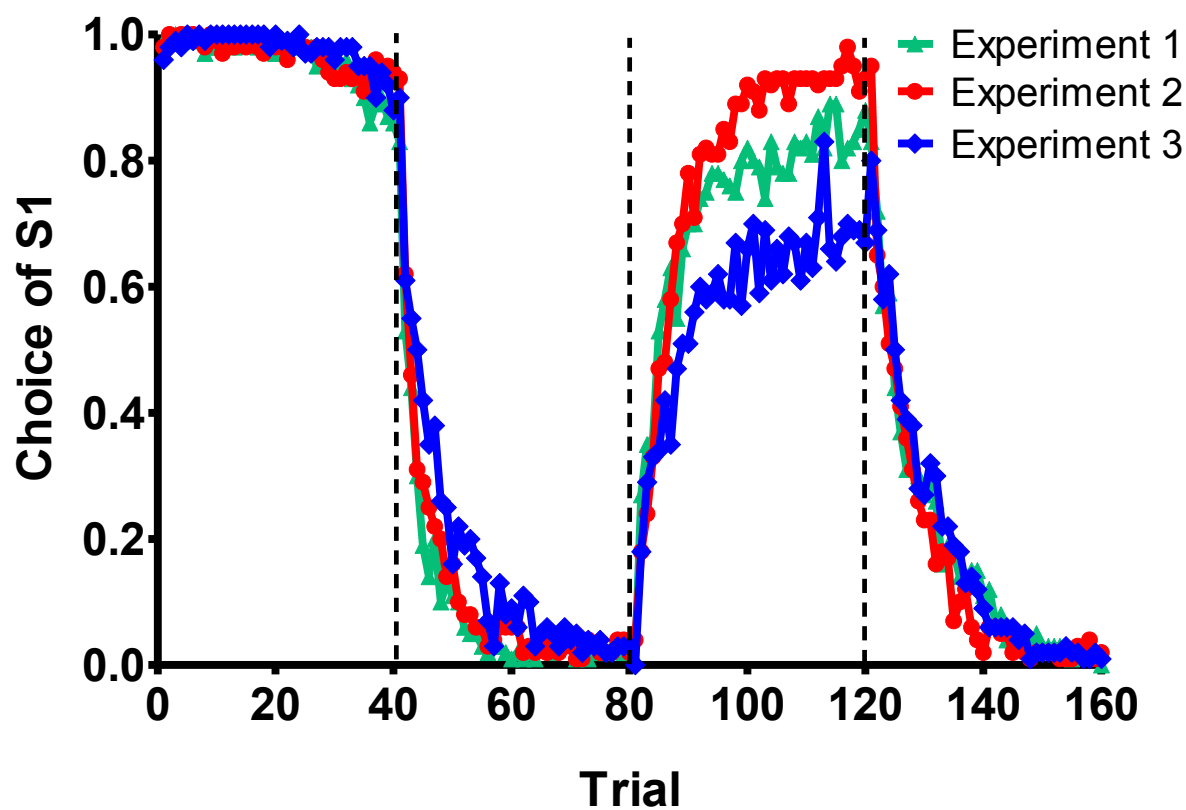


Figure 5. Experiment 4: Comparison of subjects from Experiments 1-3 on choice of S1 in Experiment 4, averaged across 25 sessions with 160 trials per session. Vertical hatched lines indicate contingency reversals (every 40 trials).

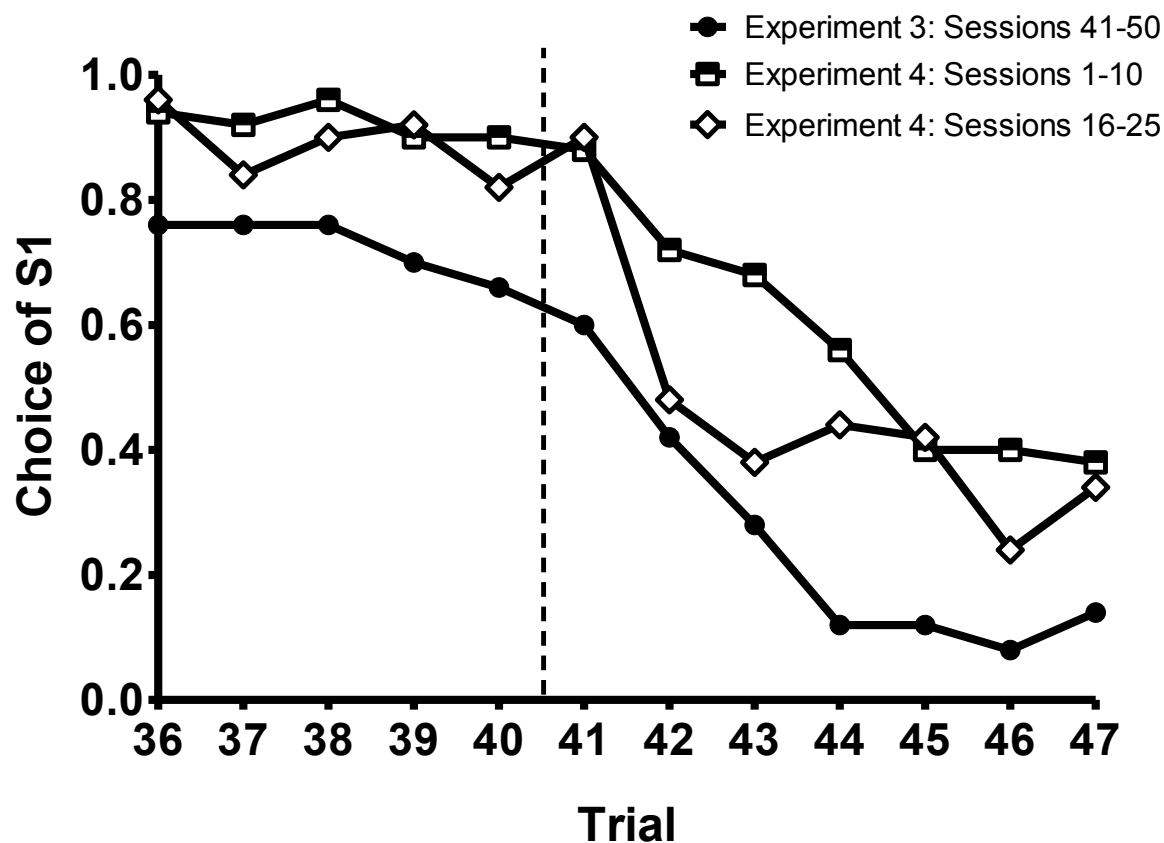
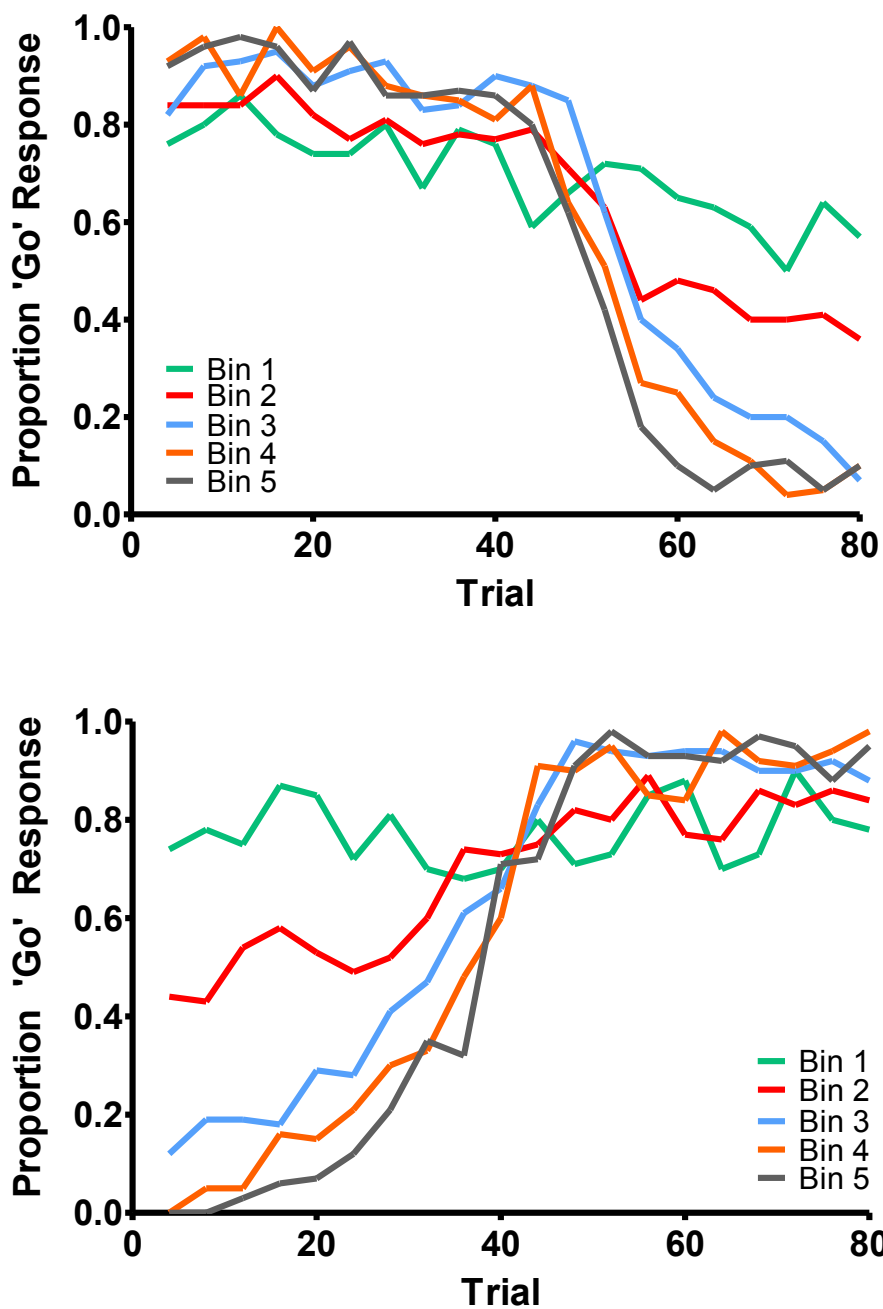
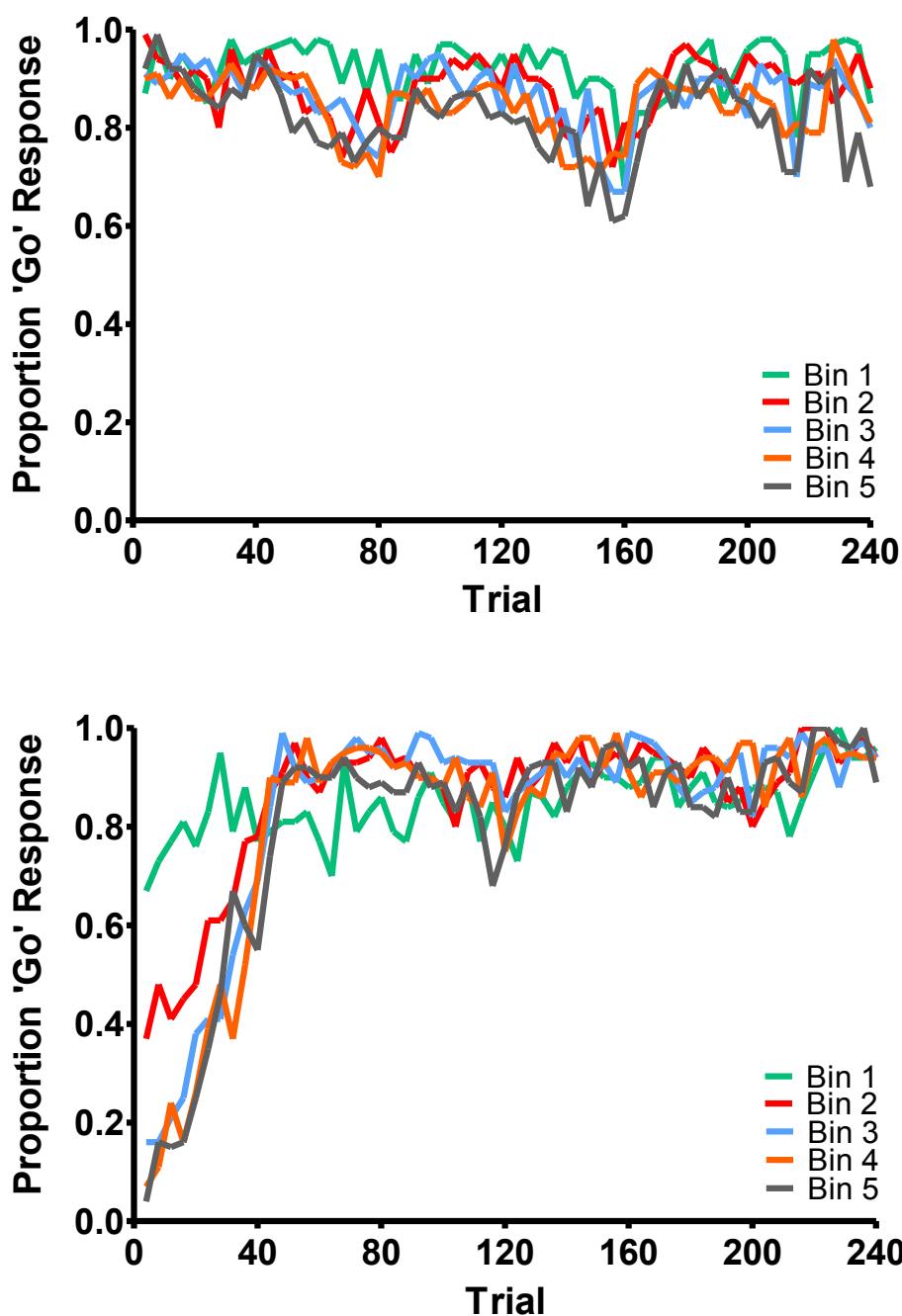


Figure 6. Comparison of subjects from Experiment 3 on choice of S1, averaged across the last 10 sessions of Experiment 3, the first 10 sessions of Experiment 4, and the last 10 sessions of Experiment 4. Vertical hatched line indicates contingency reversal after Trial 40.

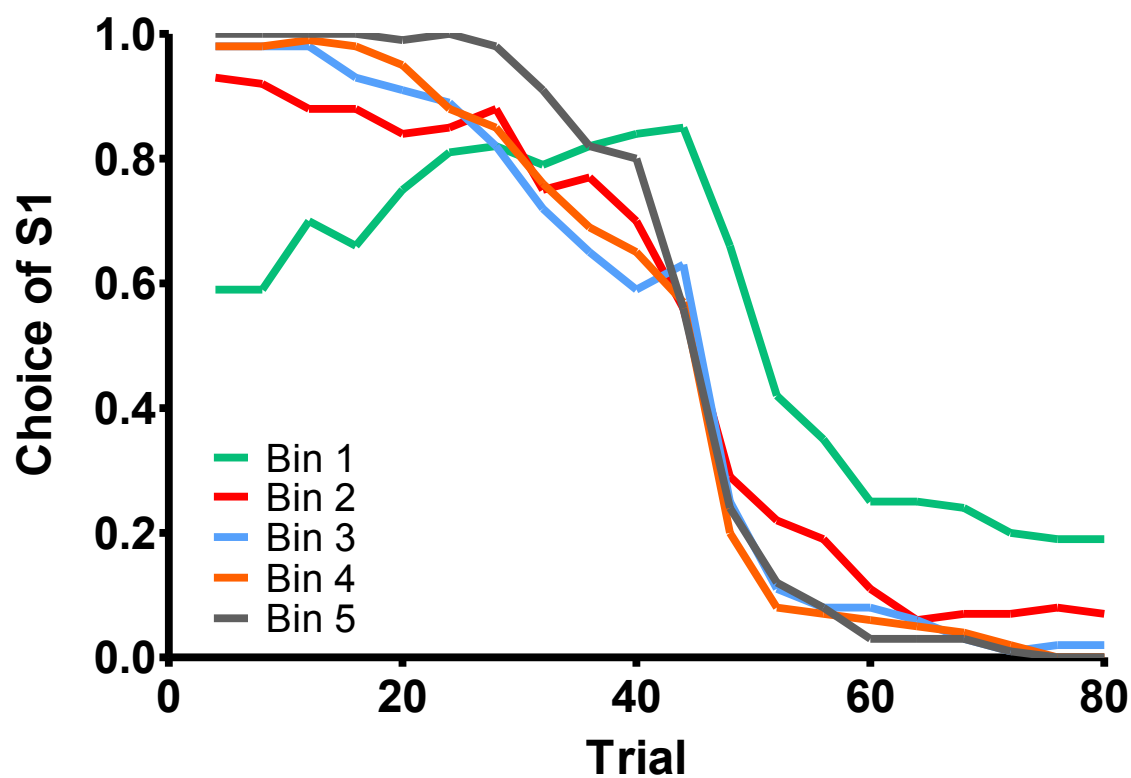
Supplemental Materials



Supplemental Figure A. Experiment 1: Acquisition data comparing 'go' responses, averaged in bins of five sessions (e.g., Bin 1 contains Sessions 1-5) and plotted in bins of 4 trials for (Upper Panel) responses to S1 and (Lower Panel) responses to S2.



Supplemental Figure B. Experiment 2: Acquisition data comparing 'go' responses, averaged in bins of five sessions (e.g., Bin 1 contains Sessions 1-5) and plotted in bins of 4 trials for (Upper Panel) responses to S1 and (Lower Panel) responses to S2.



Supplemental Figure C. Experiment 3: Acquisition data comparing choice of S1, averaged in bins of five sessions (e.g., Bin 1 contains Sessions 1-5) and plotted in bins of 4 trials.