Anticipation of a Midsession Reversal in Humans

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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 anticipatory errors (i.e., responding to the second-correct stimulus before the reversal) based on failure to inhibit timing-based intrusion errors; limited prior research has suggested humans' performance is qualitatively different. Here we illustrate a partial replication of previous findings in humans, but suggest based on our results that humans process these tasks in a manner similar to pigeons. Humans made relatively few but consistent errors across both simultaneous- and successive-choice experiments. Anticipation errors were limited when the identity of the first-correct stimulus alternated between sessions, consistent with the behaviour of pigeons. Subsequent experiments found evidence for anticipation on a purely temporal simultaneous choice task, and fewer errors with symmetrical reinforcement and punishment of responses on a sequential choice task. Interval timing causes conflicts with decision-making processes on the midsession reversal task that are consistent, but differ in magnitude, across species.

Keywords: interval timing; midsession reversal; go/no-go; choice; comparative cognition

Anticipation of a Midsession Reversal in Humans

There has been considerable recent interest in using the midsession reversal procedure to study decision-making processes across species. In its simplest form, the midsession reversal procedure involves simultaneous choices between two alternatives (e.g., Rayburn-Reeves et al., 2011), one of which is correct for trials in the first half of a session (S1) and the other of which is correct for trials in the latter half of the session (S2). The primary finding of interest is that pigeons make errors both before and after the reversal (i.e., they *anticipate* the reversal by choosing S2 before doing so is reinforced, and *perseverate* after the reversal by continuing to choose S1 after doing so is no longer reinforced). Several studies have confirmed that interval timing tends to control pigeons' behaviour in this task (e.g., Cook and Rosen, 2010; McMillan and Roberts, 2012); pigeons learn to expect a reversal in reinforcement contingencies after a predictable amount of time since the start of the session (e.g., see Fig 1a). In testing humans on the midsession reversal procedure (Rayburn-Reeves et al., 2011), participants showed some anticipatory errors with fixed, but not with shifting, reversal points. Because these errors were relatively infrequent, subsequent papers have held the view that midsession reversal errors are particular to pigeons (e.g., see review by Rayburn-Reeves and Cook, 2016). However, the scarce and conflicting evidence from other species such as rats (McMillan et al., 2014; Rayburn-Reeves, Stagner, Kirk, & Zentall, 2013), coupled with demonstrations that pigeons show near-optimal performance under certain circumstances (McMillan et al., 2014, 2015; MacDonald and Roberts, 2018), suggest that this view should be more fully examined.

Though midsession reversal is often suggested as an extension of the serial reversal task, in reality it is closer in principle to procedures like the free-operant psychophysical procedure (FOPP; Stubbs, 1980), time-place learning tasks (e.g., Wilkie et al., 1994), or other temporallybased conditional discriminations. Pigeons have been shown to learn simple temporal ‘rules’: for example, that one particular stimulus (S1) is correct for approximately three minutes, and that the other stimulus (S2) is correct for the remainder of the session (see McMillan et al., 2015); this is conceptually similar to the temporal shifts in behavioural states associated with each stimulus in the learning-to-time model (LeT: Machado, 1997; Machado and Guilhardi, 2000). Importantly, if S1 varies from session to session (and even if the variation is a predictable alternation), pigeons’ behaviour is no longer controlled by time and instead they perform poorly (McMillan et al., 2016, 2017), which may have reflected the difficulty to apply simple ‘rules’ when the identity of S1 changed from session to session. Finally, in cases where the task was presented as a successive choice (go/no-go) rather than simultaneous choice task, it was revealed that pigeons’ incorrect choices were almost exclusively failures to inhibit pecking the incorrect stimulus rather than withholding responses to the currently-rewarded stimulus (see Figure 1b; McMillan et al., 2015). Findings such as these have allowed researchers to draw numerous conclusions about the nature of choice and control by time in pigeons (Rayburn-Reeves and Cook, 2016; McMillan et al., 2017; Smith et al., 2018). Given the wealth of recent pigeon research determining the factors underlying temporal and other decision-making processes in midsession reversal, we were interested in revisiting the midsession reversal procedure with human participants.

In the present studies we examined humans’ responses on simultaneous or successive (go/no-go) discriminations, with blocks of trials containing mid-block contingency reversals. Our procedure replicated the basic conditions of the task used with humans by Rayburn-Reeves et al., (2011), including instructions and procedural detail, with the exceptions that: we used 40-trial blocks as a compromise between 24-trial blocks previously used with humans (which we expected would be easy to count) and 80-trial sessions used with pigeons (which we expected might be intolerably boring for many humans); we used pigeon-like "button" choice stimuli rather than picking cards from a computerized deck; we included a "maze" task between blocks to accentuate the inter-block break. We also attempted to replicate recently-demonstrated findings with pigeons (McMillan et al., 2016) by including a condition in which the stimulus serving as S1 alternated across blocks (rather than being the same for every block).

1. Experiment 1

1.1. Methods

1.1.1. Participants

Participants with normal color vision (based on requirement posted in participant advertisement) were recruited from the University of Alberta Psychology Participant Pool (*N* = 135; 85 female; $M_{\text{age}} = 20.1$, *SD* = 2.3) for research credit in an introductory psychology course. Participants were recruited and instructed in groups of up to 15 but performed the task in individual test rooms; each was randomly assigned to one of four different test conditions. The study was approved by the University of Alberta Research Ethics Board (Protocol #058367).

1.1.2 Procedure

Participants played a computer-based task in which they were instructed to try to earn as many points as possible. On each trial for 40 trials per block, participants were presented with a blue-filled circle (2.5 cm in diameter) containing the word "PLAY", in the middle of a grey background on the monitor. A single click on the PLAY button led immediately to the presentation of the stimulus circle(s). In the simultaneous task, both a green-filled and a red-filled circle (2.5 cm in diameter) were presented the left or right sides of the screen (10 cm from center) and these stimuli stayed on until one of them was clicked. In the successive task, only one of these stimulus circles was presented on each trial, with the presented stimulus randomized. If the stimulus was not clicked within 2 s of presentation, it was removed and was followed by a 2-s intertrial interval (ITI), with the screen background still lit grey, followed by a new trial.

In both the simultaneous and successive procedures, the left and right location of the stimuli were randomized in blocks of four trials across the session. For half of the participants, a click to the red circle was correct for the first 20 trials in each block, and a click to the green circle was correct for the latter 20 trials; these contingencies were reversed for the other half of participants. A single click to the currently-correct stimulus led to the message "You have earned two points!"; if the participant clicked the currently-incorrect stimulus, the screen was blackened for 3-s (timeout) before the next trial. Either result was followed by a 2-s ITI, with the screen background lit grey, subsequently followed by a new trial. For half of participants (Group Fixed) the identity of the first- and second-correct colours was the same each block; for the other half (Group Alternating) the identities of each alternated each block.

Participants performed ten blocks of trials, with each block separated by a message to complete a "maze" from a stack of provided paper-and-pencil mazes (9 'intermediate' mazes: http://krazydad.com/mazes/sfiles/KD_Mazes_IM_v1.pdf). For half of the participants (Group Fixed) all trial blocks had the same S1+ (e.g., red was correct for the first 20 trials of each block); for the other half (Group Alternating), the S1+ for each trial block alternated.

1.1.3. Exclusion Criteria.

Results were excluded from participants who did not complete the entire task ($N = 3$). Results were also excluded if: choice of the correct stimulus averaged across the last five trial blocks was below 60%, indicating failure to discriminate (simultaneous task: Group Fixed $N = 3$, Group Alternating $N = 0$; successive task: Group Fixed $N = 7$; Group Alternating $N = 3$); or performance was above 99%, achievable only with explicit counting (simultaneous task: Group Fixed $N = 1$; Group Alternating $N = 5$; successive task: $N = 0$). Remaining participants were $N = 113$ (successive task: Group Fixed $N = 29$, Group Alternating $N = 27$; simultaneous task: Group Fixed $N = 27$, Group Alternating $N = 30$).

1.2 Results and Discussion

Figure 2 shows participants' performance in (A) the simultaneous choice task and in (B) the successive choice task. Analyses used data from the last 5 blocks o remove early training effects. Trials were pooled and averaged across sessions and participants; for participants in the successive task, trials were also pooled based on whether S1 or S2 was presented. In examining anticipation of and perseveration after the reversal, we examined two trial windows: the five trials prior to the first reversal feedback (i.e., Trials 17-21) and the five trials immediately after the trial in which feedback indicates the reversal has occurred (i.e., Trials 22-26).

1.2.1 Simultaneous Choice Task

Responses to S1 decreased during the window of trials prior to the reversal, and Group Fixed chose S1 less often overall than did Group Alternating (i.e., Group Fixed appeared to anticipate the reversal more than did Group Alternating). A 5 x 2 mixed MANOVA [Trial (17-21) x Group (Fixed, Alternating)] showed main effects of both Trial [$F(4,52) = 4.60$, $p = .003$, $\eta^2_p = .26$] and Group [$F(1,55) = 5.20$, $p = .027$, $\eta^2_p = .09$], but no significant interaction between the effects [$F(4,52) = 1.95$, $p = .12$, $\eta^2_p = .13$].

Both groups were largely similar and stable in choosing S2 after the reversal, with little in the way of perseveration across trials or groups. A 5 x 2 mixed MANOVA [Trial (22-26) x Group (Fixed, Alternating)] showed no main effects of Trial [$F(4,52) = 2.36$, $p = .065$, $\eta^2_p = .15$]

or Group [$F(1,55) = 0.44$, $p = .51$, $\eta^2_p < .01$], and no significant interaction between the effects [$F(4,52) = 1.53$, $p = .21$, $\eta^2_p = .11$].

1.2.2. Successive Choice Task

Responses to S1 were uniformly high before the reversal in the Successive task. A 5 x 2 mixed MANOVA [Trial (17-21) x Group (Fixed, Alternating)] on S1 responses showed neither a main effect of Trial [$F(4,17) = 3.44$, $p = .34$, $\eta^2_p = .22$] nor Group [$F(1,20) = 1.80$, $p = .20$, $\eta^2_p = .08$], and no significant interaction between the effects [$F(4,17) = 1.60$, $p = .22$, $\eta^2_p = .27$].

Both groups showed declining choice of S1 across the trial window after the reversal. A 5 x 2 mixed MANOVA [Trial (22-26) x Group (Fixed, Alternating)] on S1 responses showed a main effect of Trial [$F(4,17) = 28.54$, $p < .001$, $\eta^2_p = .87$] but not Group [$F(1,20) = 0.03$, $p = .87$, $\eta^2_p = .001$], and no significant interaction between the effects [$F(4,17) = 0.10$, $p = .98$, $\eta^2_p = .02$].

The Fixed group showed more choice of S2 during the period just before the reversal than did the Alternating group. A 5 x 2 mixed MANOVA [Trial (17-21) x Group (Fixed, Alternating)] on S2 responses showed no main effect of Trial [$F(4,15) = 1.83$, $p = .18$, $\eta^2_p = .33$] but did find a main effect of Group [$F(1,18) = 6.24$, $p = .02$, $\eta^2_p = .26$], with no significant interaction between the effects [$F(4,15) = 2.29$, $p = .11$, $\eta^2_p = .38$].

Both groups were largely similar in choosing S2 after the reversal. A 5 x 2 mixed MANOVA [Trial (22-26) x Group (Fixed, Alternating)] on S2 responses showed a main effect of Trial [$F(4,16) = 4.78$, $p = .01$, $\eta^2_p = .54$] but no significant main effect of Group [$F(1,19) = 3.41$, $p = .08$, $\eta^2_p = .15$], and no significant interaction between the effects [$F(4,16) = 0.73$, $p = .58$, $\eta^2_p = .16$].

1.2.3. Summary

In general, humans on our tasks performed similarly to pigeons on midsession reversal tasks: anticipatory errors in the successive choice task were responses to S2 rather than withheld responses to S1, again consistent with the performance of pigeons (McMillan et al., 2015). These results are consistent with previous findings in humans (Rayburn-Reeves et al., 2011) and, in contrast to suggestions in the literature that pigeons respond uniquely on these tasks, they suggests that the difference between pigeons and humans is more quantitative than qualitative.

2. Experiment 2

Only one previous study (Rayburn-Reeves et al., 2011) has examined the performance of humans on the midsession reversal task, limiting the breadth of our understanding for the mechanisms in human discrimination (and potential differences compared to pigeons). For example, while pigeons have been shown to rely predominantly on time to predict the reversal (McMillan and Roberts, 2012), humans may instead use number. To examine this, we replicated the simultaneous-choice task from Experiment 1, but instead of basing the conditional discrimination on number of trials into the session, we set the reversal to occur after 90 s had elapsed in a particular block of trials. Because our human participants showed more variability in response times than is typical for pigeons, this procedural change makes use of number difficult and explicit counting would be less reliable.

One difference between the simultaneous and successive conditions in Experiment 1 is the presentation of reinforcement and punishment: for participants in Group Simultaneous, every trial was met with either a reinforcement message or a timeout as appropriate; however, for Group Successive, reinforcement and timeout were only provided on trials for which the participants responded. No reinforcement or timeout was given when participants withheld responding, regardless of whether responding on that trial was 'correct'; the trial simply ended and was followed by the ITI. To control for the potential effect of this difference on choice behaviour, in Experiment 2 we replicated the procedure of Group Successive but added reinforcement and timeouts for correctly- and incorrectly-withheld responses (respectively).

2.1 Method

2.1.1. Participants

Participants with normal color vision were recruited from the University of Alberta Psychology Participant Pool ($N = 50$; 34 female; $M_{\text{age}} = 20.3$, $SD = 2.5$) for research credit in an introductory psychology course. The study was approved by the University of Alberta Research Ethics Board (Protocol #058367).

2.1.2. Procedure

All aspects of the experimental procedure were the same as in Experiment 1, except as follows. Only the Group Fixed condition was used. For Group Successive, reinforcement and timeout were provided for withholding a response to either the currently-incorrect or currently-correct stimulus during the session, respectively. For Group Simultaneous, correct contingencies were based on time rather than trial number; for half of participants, responses to the red circle were correct for the first 90 s from the start of each block, while responses to the green circle were correct for the remainder of the block, and these contingencies were reversed for the other half of participants.

2.1.3. Exclusions

Results were excluded from participants if choice of the correct stimulus averaged across the last five trial blocks was below 60%, indicating failure to discriminate (successive task: $N = 2$; simultaneous task: $N = 4$). Remaining participants were $N = 112$ (successive task: $N = 22$; simultaneous task: $N = 22$). No participants had >99% accuracy.

2.2. Results and Discussion

Figure 3 shows participants' performance in (A) the simultaneous choice task and in (B) the successive choice task. Analyses used data from the last 5 blocks to remove early training effects. Trials on which S1 or S2 were presented were pooled and averaged across sessions and participants. In examining anticipation of and perseveration after the reversal, we examined two trial windows in the successive choice task: the five trials prior to the first reversal feedback (i.e., Trials 17-21) and the five trials immediately after the trial in which feedback indicates the reversal has occurred (i.e., Trials 22-26). In the simultaneous choice task, a number of participants had at least one block with fewer than five trials before the reversal, so to exclude the fewest blocks possible we narrowed the window to the three trials prior to first reversal feedback and the three trials immediately after.

2.2.1. Simultaneous Choice Task

Responses to S1 dropped during the window of trials prior to the reversal, indicating that participants anticipated the reversal and selected S2 based on impending time to contingency change; a within-subjects MANOVA showed main effects of Trial [$F(2,20) = 3.80$, $p = .04$, $\eta^2_p = .28$]. Perseverative errors (choosing S1 after the reversal) were low and stable. A within-subjects MANOVA showed no main effect of Trial within the selected window [$F(2,20) < 0.01$, $p = 1.00$, $\eta^2_p = 0$].

2.2.2. Successive Choice Task

Responses to S1 were uniformly high before the reversal in the Successive task. A within-subjects MANOVA on S1 responses showed no main effect across Trials 17-21 [$F(4,17) = 2.54$, $p = .078$, $\eta^2_p = .37$] though participants did choose S1 significantly less than 100% of the time at Trials 21 [M = 0.85, SEM = 0.7, $t(21) = 2.17$, $p = .042$]. Choice of S1 declined immediately after the reversal, with few perseverative errors [$F(4,16) = 2.04$, $p = .14$, $\eta^2_p = .34$].

Though choices of S2 appeared to rise just before the reversal, this effect was limited. A within-subjects mixed MANOVA on S2 responses showed no main effect of Trial [$F(4,17) = 1.53$, $p = .25$, $\eta^2_p = .32$]; however, participants did choose S2 significantly more than 0% of the time at Trial 21 [M = .11, SEM = .046, $t(20) = 2.39$, $p = .027$] suggesting that anticipation was muted but still present. Choice of S2 was universally high after the reversal: a within-subjects MANOVA on S2 responses showed no effect of Trial [$F(2,16) = 1.00$, $p = .39$, $\eta^2_p = .11$].

3. General Discussion

Humans in Experiment 1 showed anticipatory errors on midsession reversal procedures that were qualitatively similar to those of pigeons; that is, they made timing-based anticipation errors prior to the reversal in fixed but not alternating S1+ conditions, and such anticipation errors were to S2 (rather than S1) in the successive choice condition. We replicated many aspects of the performance found in humans by Rayburn-Reeves and colleagues (2011), including generally high levels of accuracy, but consistency across people in the errors that did occur. Importantly, the typical midsession reversal effect was strongest in the fixed-order condition compared to the alternating condition, as seen in pigeons; as with pigeons, the fixed order condition may be more conducive to timing, by allowing use of a simple contextual ‘rule’ (such as “choose red for 90s”: McMillan et al., 2016) which is not available for the alternating condition. In Experiment 2, we showed anticipation in a simultaneous choice task with the reversal based purely on interval time rather than trial number. We also found that errors were limited when symmetrical presentation of reinforcement and punishment was provided in the successive procedure, though a few participants still demonstrated anticipatory errors.

In discussion with others, we have mused about the strange tendency of undergraduates to try to anticipate a midsession reversal (Robert G. Cook, pers. comm.); as with pigeons, the obvious and simple strategy to solve midsession reversal is to follow reward (i.e., respond only to S1 until the first nonreinforced response, and then respond only to S2). While a subset of humans appeared to use the optimal strategy, many of our participants anticipated the reversal. Other participants were removed from the current data after being identified as having counted trials despite instructions not to, or responding non-differentially (many of whom in the successive task appeared to simply click every stimulus presented). McMillan and colleagues (2014) previously suggested that optimal vs. timing-based performance is dependent on the particulars of the task in both pigeons and rats; when stimuli are presented such that the animal can orient during the ITI (e.g., with a spatial discrimination in an operant chamber) they tend to make fewer errors than when task parameters prevent this prospective orienting (e.g., in a T-maze where the ITI start box and choice point are spatially separated). Non-procedural differences in number of errors made across species have been explained as differences in inhibition or associational strength rather than ability, which is consistent with recent reviews suggesting that interval timing competes with other learning processes for control over behaviour (Matthews and Meck, 2016; McMillan et al., 2017). Humans' near-optimal performance on the midsession reversal task may simply reflect a better capacity to inhibit time-based responding, rather than ignoring time altogether. It is worth noting that while practically all pigeons studied show both anticipatory and perseverative errors, such errors were only apparent in some participants in the present studies. It may be that individual differences in inhibition are similar to the species-level differences in inhibition suggested by other authors.

It should be noted that an alternate explanation for errors on this task is similar to the “passport effect” (Call and Carpenter, 2001). Commonly discussed in the context of metacognition and information-seeking, this effect suggests responses that are unnecessary but nonetheless low-effort are made ‘just in case’, much like checking more than once to determine that one has their passport before leaving for the airport. This effect may be exacerbated in the successive task used in Experiment 1 and in the previous pigeon studies (ref), where there was little opportunity cost for an uninhibited response and overall reinforcement rates were lower (because only half of trials have an opportunity for reinforcement). This argument may be consistent with the low rate of anticipatory errors seen in Experiment 2.. It should be noted that even if errors can be explained based on ‘checking’ rather than failures of inhibition, this effect is still driven by a timing or similar mechanism, as these errors occur predominately only near the reversal (e.g., see McMillan et al., 2015) and did not occur with alternating S1s in the present results. Across species and procedures, errors in this task in close temporal proximity to the reversal might result from any combination of working memory load (Laude et al., 2014), failures of inhibition (McMillan et al., 2015), associative strength (Rayburn-Reeves and Cook, 2016), reward rate estimation (Smith et al., 2018), or checking the alternative option. We argue that inhibition failure most straightforwardly accounts for the majority of the data, but future work may disentangle the systems with which the interval timing process acts through and competes with (McMillan et al., 2017). One option will be to study the effects of differential reinforcement (such as monetary reimbursement for ‘correct’ responses or for avoiding incorrect responses) on humans’ tendency to anticipate the reversal.

Given the similar patterns of errors between pigeons and humans, yet the large quantitative differences, it is unclear why sensitivity to time is so different between pigeons and other species. The choice component of the task may be more difficult for pigeons to manage; for example, researchers have previously noted that remembering the previous trial's response and outcome to compare to the present choice may present undue working memory load for a pigeon (Laude et al., 2014); the same may be true for a T-maze midsession reversal task where rats also exhibit many timing-based errors (McMillan et al., 2014). Future studies in humans may be able to show more consistent patterns of errors by making the baseline choice more difficult, such as by using a more complex categorical or rule-based discrimination rather than the red vs. green choice used for pigeons. Limiting the ceiling performance illustrated by humans, and potentially showing pigeon-like errors across the interval in a larger percentage of participants, would allow for more intensive study of this phenomenon and of human decision-making in general.

Studying the midsession reversal procedure may have concrete implications for human neuroscience research. Interestingly, midsession-like reversal has been used in human fMRI experiments as a measure of flexibility (e.g., Cools et al., 2002) in place of the more standardized serial reversal procedure, likely owing to the constraints of limited resources and participant attrition rates in applying serial reversal in the magnet. However, because the animal literature with midsession reversal is so new, the behavioural component of the task is still not well-understood. We are only just starting to understand the ways in which time is used in the task, so activation noted in participants may reflect any combination of temporal, inhibitory, reward, working memory, or other processes, and therefore the procedure is not as straightforward as researchers may have assumed. Conversely, however, use of functional brain analyses with the midsession reversal procedure might also be able to better disentangle the roles of attention, inhibition, and timing in this task in humans and other species.

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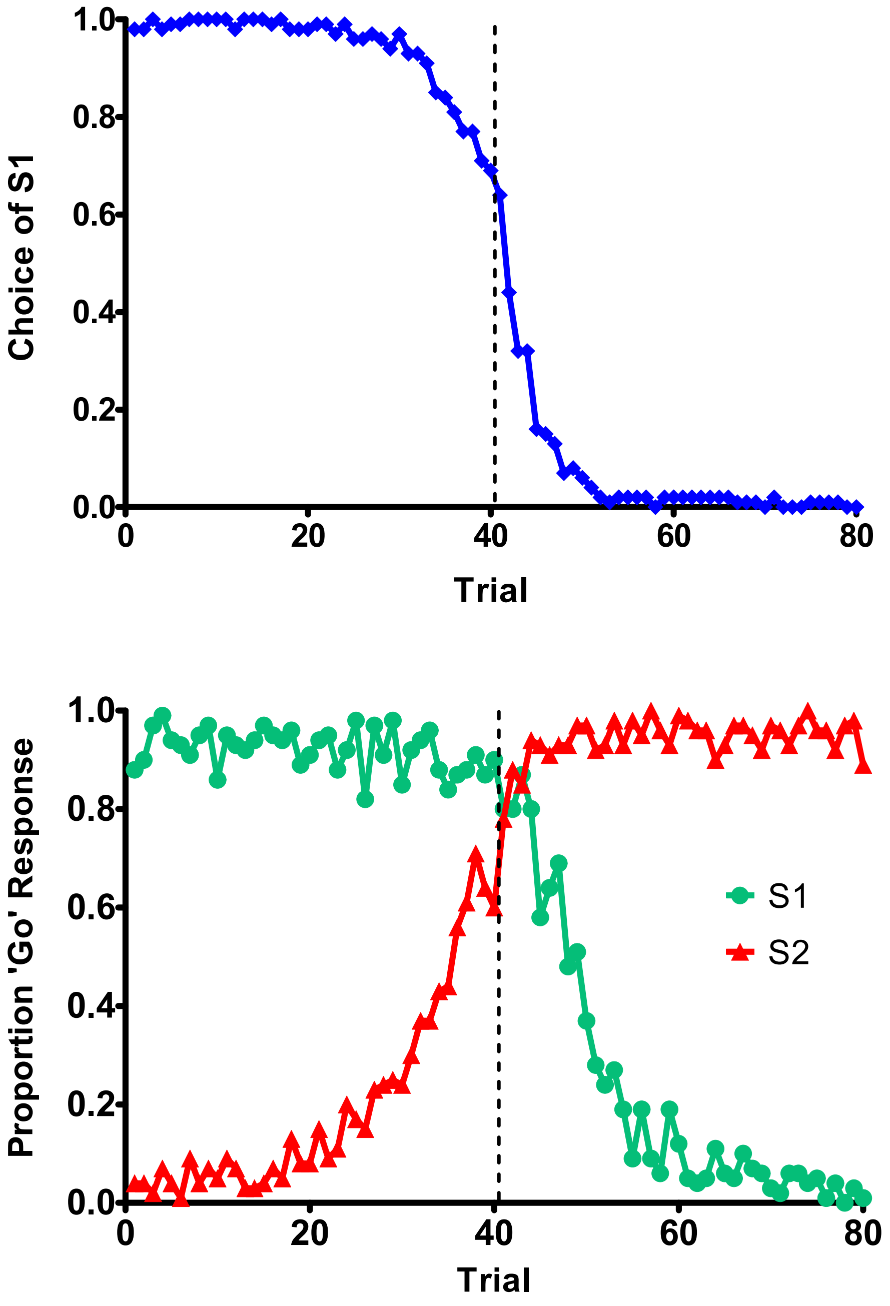

Figure 1. (A; upper panel) Choice of the first-correct stimulus (S1) by pigeons in a simultaneous-choice midsession reversal procedure, and (B; lower panel) comparison of ‘go’ responses to S1 and S2 in a successive-choice midsession reversal procedure. Data averaged across the last 25 sessions of training, at 80 trials per session. Vertical hatched lines indicate contingency reversal (after Trial 40). Data previously presented in McMillan et al. (2015, Experiment 1).

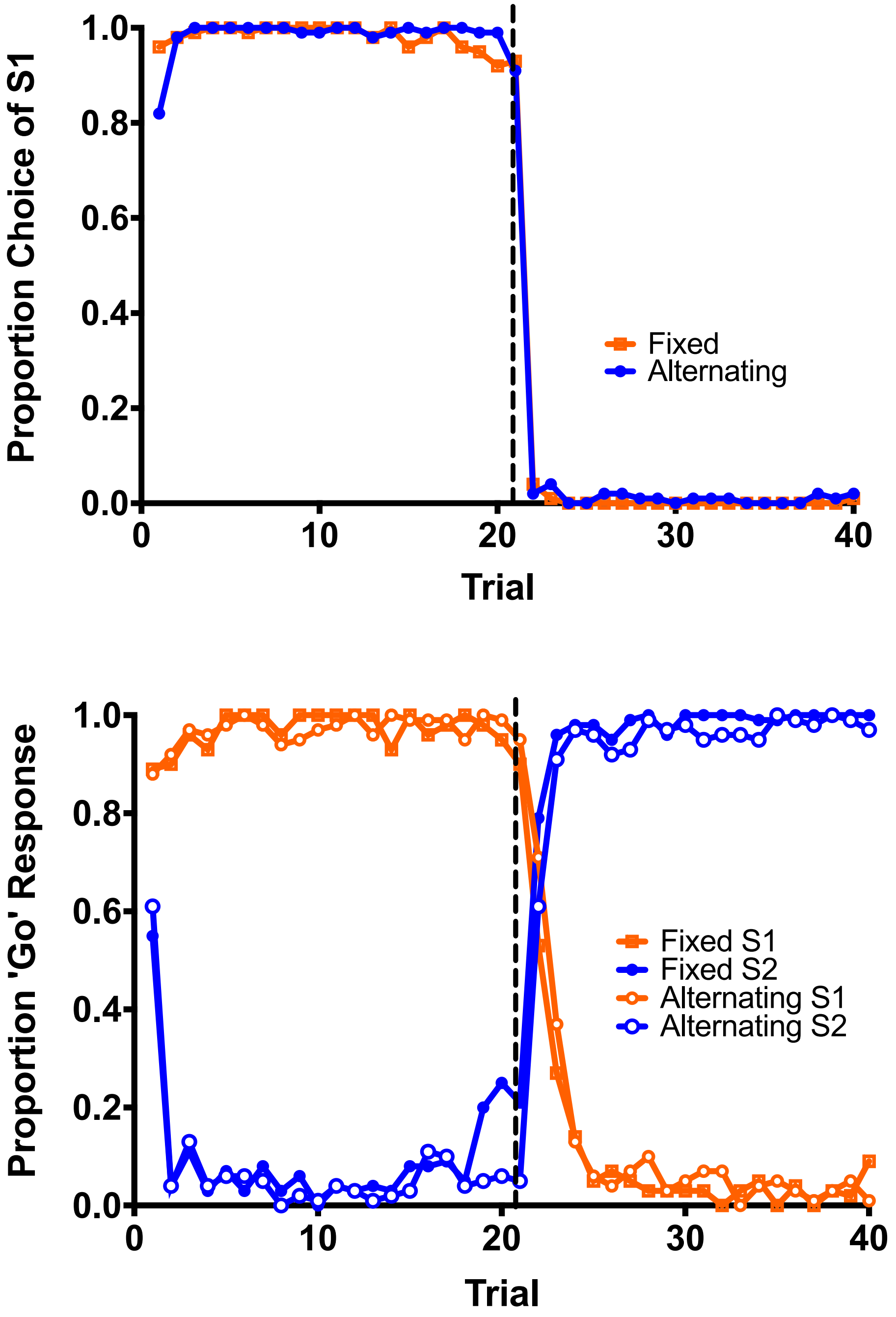

Figure 2. Experiment 1: Participant responses, across fixed and alternating conditions, illustrated as (A; upper panel) choice of S1 in the simultaneous choice group and (B; lower panel) comparison of ‘go’ responses to S1 and S2 in the successive choice group. Responses in each condition averaged across the last 5 blocks of training, at 40 trials per block. Vertical hatched lines indicate contingency reversal (after Trial 20).

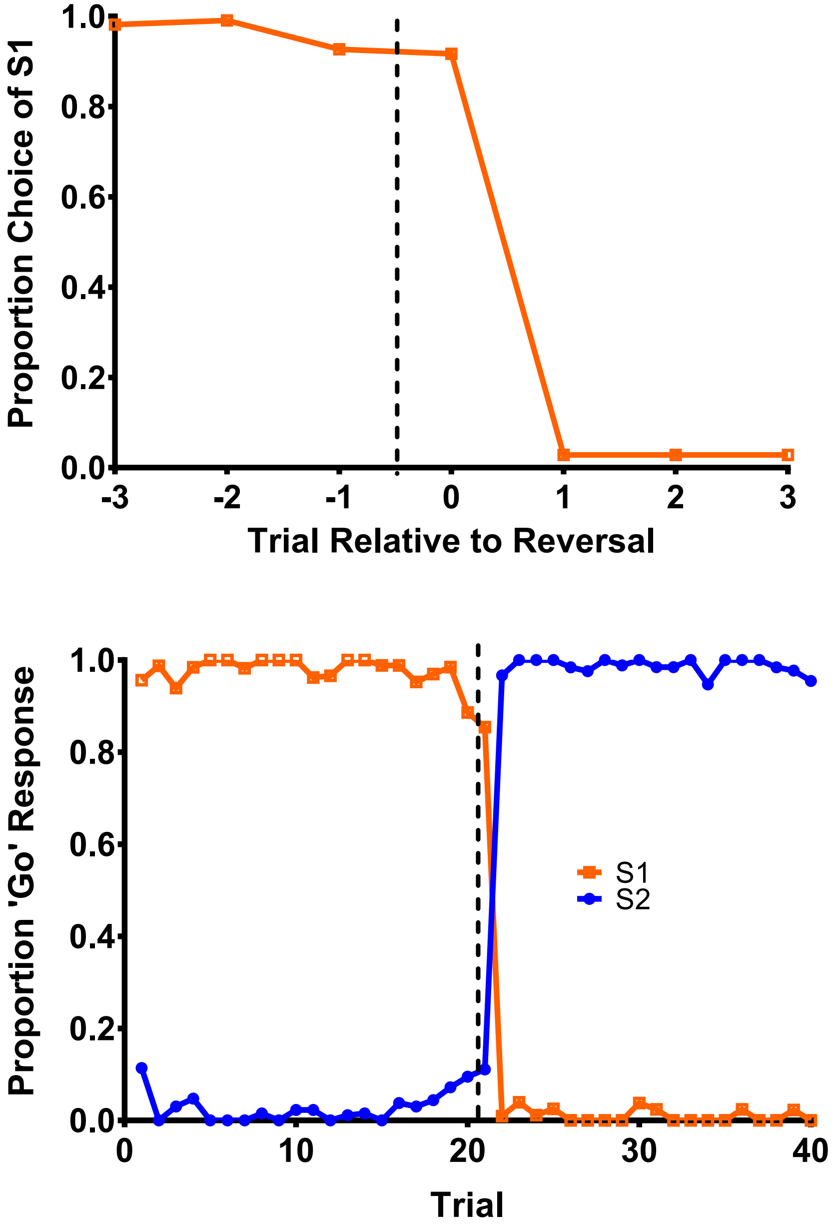

Figure 3. Experiment 2: Participant responses illustrated as (A; upper panel) choice of S1 in the simultaneous choice group on each trial relative to the reversal at 90 s (i.e., Trial 0 is the first trial with reversed reinforcement contingencies) and (B; lower panel) comparison of ‘go’ responses to S1 and S2 in the successive choice group. Responses in each condition averaged across the last 5 blocks of training, at 40 trials per block. Vertical hatched lines indicate contingency reversal.