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## Dynamic Cue Use in Pigeon Mid-Session Reversal

Rebecca M. Rayburn-Reeves, Muhammad A. J. Qadri, Daniel I. Brooks, Ashlynn M. Keller, &

Robert G. Cook

Tufts University

All Correspondence To:  
Dr. Rebecca M. Rayburn-Reeves  
Present Address: Department of Psychology  
Tufts University  
490 Boston Ave.  
Medford, MA 02155  
Email: [beckyreeves02@gmail.com](mailto:beckyreeves02@gmail.com)  
Phone: (910) 352-0489

### Abstract

The systematic anticipation and preservation errors produced by pigeons around the reversal point in midsession reversal (MSR) learning experiments suggest that an internal time estimation cue, instead of a more efficient external cue provided by reinforcement, controls behavior over the course of a session. The current experiments examined the role and effectiveness of other external cues in the MSR task. In Experiment 1, providing differential outcomes based on response key location produced fewer errors prior to, but not after, the reversal as compared with a non-differential outcomes condition. Experiment 2a used alternating differentially colored ITIs (*cued sessions*) or dark ITIs (*un-cued sessions*) during each half of the session. The ITI cues improved switch efficiency both prior to and after the reversal. Experiment 2b introduced probe trials around the reversal, testing ITI color cues added to *un-cued sessions* or removed from *cued sessions*. Results showed control by the ITI cues when they were available and control by the time-based cue when they were unavailable. This suggests both cues were being simultaneously processed when available and that the cues could also independently provide sufficient information about future reinforcement. In Experiment 2c, ITI cues were inserted as probe trials in the opposite half of the session (*miscues*). The closer such miscue trials were to the reversal, the more the ITI cues exerted control over behavior. Together, these results indicate that as the utility of internal temporal cues is reduced, the use of external visual cues increases. These results have implications for the way in which cues dynamically shift in controlling behavior over time based on their relative rates of utility, and are discussed in light of an occasion setting perspective.

*Key Words:* internal, external, temporal, mid-session reversal, pigeons

Dynamic and complex environments often contain multiple cues that could provide relevant information about biologically significant outcomes. Depending on the particular situation, these cues can independently or jointly provide information about which behaviors might lead to profitable outcomes. When multiple cues are relevant, the extent to which a single cue comes to exert control over behavior depends on a number of factors, such as its saliency, relative utility, history, and redundancy with other available cues. Understanding how various cues come to control behavior at any moment and how this might change over time has been and continues to be an essential element to understanding adaptive behaviors across different species.

Recently, a novel reversal task has been developed that has provided new insight into the cues controlling the sequential and temporal organization of behavior (Rayburn-Reeves & Cook, 2016). In this mid-session reversal (MSR) task, a single discrimination reversal consistently occurs at the midpoint of each session. Thus, responses to one stimulus or contingency are reinforced for the first half of a session, whereas responses to a different stimulus or contingency are reinforced for the second half of the session (Cook & Rosen, 2010; Rayburn-Reeves, Molet, & Zentall, 2011). Pigeons trained in this task learn to accurately discriminate each of the competing task contingencies. Averaging their data over sessions reveals that pigeons gradually transition from performing the first discrimination to the second discrimination around the session midpoint. This *switching function* reflects how the predictable reversal at each session's midpoint allows the pigeons to learn to respond appropriately during both portions of a session.

The MSR task appears to have two distinct types of cues. The first type is consistent with the traditional meaning of *discriminative cues*. These are the visual stimuli available to the animal during a trial (e.g., red and green key lights) that directly receive choice behaviors and lead to rewarded outcomes as required by simple or conditional contingences. The second type of cue can

be thought of as the *switching cue*. This switching cue is a conditional, context-like cue that indicates which discriminative cue(s) the pigeon should differentially select over the course of the session. This switching cue in MSR could be based on estimating the elapsed time within the session (or a count of trials completed) as they can reliably predict when the reversal will occur and when to switch responding. Thus, much like a first-order occasion setter in an associative context (Arnold, Grahame, & Miller, 1991; Holland, 1992), this switching cue may help to modulate between different competing behaviors to the same discriminative stimuli, although in a temporal or sequential context.

The general finding in the MSR task, at least for pigeons, indicates that the passage of time is the most salient switching cue in controlling response shifts across the session (Cook & Rosen, 2010; McMillan & Roberts, 2012; Rayburn-Reeves et al., 2011). In order to use estimated time as a temporal switching cue, the pigeons must be able to track the time elapsed within the session. The use of elapsed time as a discriminative cue (i.e., interval timing) has been well documented in a number of non-human animal species in operant settings (Buhusi & Meck, 2005; Cheng & Miceli, 1996; Church, 2006; Higa & Staddon, 1997; Staddon & Higa, 1999). Compelling evidence for use of elapsed time as the switching cue for pigeons has come from direct manipulations of time within and across sessions. For example, Cook and Rosen (2010) found that inserting an empty temporal gap of different durations into the middle of the first half of a session resulted in systematic shifts in the onset of subsequent oddity-based behaviors. Additional support for the use of a timing cue in MSR has also been provided by post-acquisition manipulations of the inter-trial interval (McMillan & Roberts, 2012).

An additional alternative cue that is also consistently available in MSR tasks is recent reinforcement history. Given that the task has only one discriminative reversal with the

contingencies in a fixed order (e.g., S1+/S2- for the first half, S1-/S2+ for the second half), reinforcement from recent responses can provide sufficiently useful information. Humans, for example, seem to rely entirely on reinforcement cues, responding correctly on every trial except the first reversal trial; behavior indicative of a win-stay/lose-shift rule (Cook & Rosen, 2010; Levine, 1975; Rayburn-Reeves et al., 2011; Restle, 1962). The same appears to be true for rats (Rayburn-Reeves, Stagner, Kirk, & Zentall, 2013) and capuchin monkeys (Rayburn-Reeves, James, & Beran, in prep); when tested under comparable experimental conditions. Curiously, these reinforcement cues appear to be regularly overshadowed by the interval timing cue in pigeons, as well as sometimes in rats (McMillan, Kirk, & Roberts, 2014) and dogs (Laude, Pattison, Rayburn-Reeves, Michler, & Zentall, 2016). This difference suggests that the saliency of time as compared with the saliency of memory for recent response-reinforcement associations may differ importantly across species when organizing competing behaviors over the course of a session.

Whether a given cue exerts control over behavior is dependent on a number of factors beyond saliency, such as the complexity of the situation, the availability of other cues, and their relative utility (McMillan & Roberts, 2013). *Relative utility*, or the degree to which different cues reliably predict outcomes, lies at the heart of cue competition studies. Again primarily in associative settings, the competition among different cues has been extensively studied (Blaisdell, Denniston, & Miller, 1998; Rescorla & Wagner, 1972). As extended to MSR, when timing cues are made less reliable by varying the location of the reversal within a session, pigeons often continue to respond using time, although showing a clearly increased sensitivity to reinforcement (Rayburn-Reeves et al., 2011). Using spatial, as opposed to visual, discriminations (McMillan et al., 2014; McMillan & Roberts, 2012, 2015; Rayburn-Reeves, Laude, & Zentall, 2013) and shortening the inter-trial intervals (ITI; e.g., 1.5 s vs. 5 s; Laude, Stagner, Rayburn-Reeves, &

Zentall, 2014; Rayburn-Reeves et al., 2013) also seem to increase control by reinforcement outcomes resulting in greater accuracy by pigeons during MSR.

Despite the progress in examining the nature of the switching cue, a number of issues regarding how internal timing and different types of external cues interact to control responding in MSR remain to be clarified. For example, the majority of previous animal research on reversal learning has typically focused on assessing the contribution of a single relevant cue or dimension in the control of reversal behavior. Therefore, the interplay between different competing cues has not been extensively examined in this experimental setup. Further, the contribution of other external cues beyond reinforcement has not been examined. Thus, it is not known whether other types of external cues might be more effective than both timing and reinforcement contingencies in controlling switching behavior during MSR learning. Finally, one intriguing aspect about time as a switching cue in MSR is that its discriminative value appears to change over the course of a session. In an extensive review of the MSR paradigm, Rayburn-Reeves and Cook (2016) suggest that the reduced accuracy around the reversal location is produced by increased competition between the internal representations of the two response contingencies (see Figure 4, Rayburn-Reeves & Cook, 2016). This competition is produced by temporal similarity around the transition point where responses to S1 and S2 are rewarded across adjacent trials at the reversal location. This increased competition creates ambiguity as to which response will be rewarded and therefore, reduces the value of the temporal cue discriminating these trials. This in turn could allow other, potentially more useful, cues to gain discriminative control. How this more dynamic perception of time influences its modulatory function as an occasion setter or contextual cue and its interaction with other cue types has not been explored at all. In this vein, the degree of control by any cue

might be mediated in part by its relative utility and saliency in comparison to other cues present over the course of a session.

The purpose of the current experiments was to investigate and further examine the relative contribution of timing to different types of external sources of information in the control of switching behavior in MSR. In particular, we wanted to explore how sources of external information besides reinforcement outcome influenced relative control by time within a session. Using a simultaneous spatial MSR discrimination and a within-subjects design, Experiment 1 first evaluated how adding differential spatial outcomes might improve switching accuracy. Experiment 2a evaluated whether the introduction of external colored ITI cues could improve switching accuracy. Experiment 2b evaluated how the selective addition and removal of these colored ITI cues influenced switching behavior across ongoing sessions. Finally, Experiment 2c evaluated how such ITI color cues and time, when placed in conflict, affected ongoing behavior across a session. The experiments reveal that providing external cues can improve the accuracy of switching behavior in pigeons. More importantly, the experiments reveal for the first time that there is an ongoing and dynamic competition between internal and external cues for control of the birds' MSR behavior across a session.

### **Experiment 1**

#### Contribution of Differential Outcomes to Mid-Session Reversal

Previous research has found that the addition of differential outcomes can improve the learning rate and accuracy of different discriminations. For example, conditional matching-to-sample discriminations are learned faster (Trapold, 1970) and better survive increased delays (Peterson, 1984) when differential outcomes are used as compared to non-differential outcomes. The purpose of Experiment 1 was to investigate whether differential outcomes might help to

promote increased switching accuracy in MSR. Specifically, we investigated whether the linking of the spatial location of reward to the side of the correct stimulus would increase attention to spatial information and reinforcement outcomes and reduce errors around the reversal location. The hypothesis was that providing a clear external cue (location) would promote better control by reinforcement-related cues than previously observed.

Pigeons were trained in two types of sessions using three different hoppers in the chamber. In both differential and non-differential outcome sessions, they performed a right vs. left spatial discrimination in an MSR task. On differential outcome sessions, the correct spatial response was paired with a hopper positioned on the same side of the chamber as the response (e.g., left response-left hopper, then right response-right hopper). In non-differential outcome sessions, all left and right correct responses were rewarded from a single, central hopper. The critical question was whether the addition of these external differential outcomes would improve switching performance by reducing anticipation and preservation errors. Such a result would suggest that reinforcement location may be a more salient cue than reinforcement outcome in controlling the pigeons' MSR performance.

## **Method**

### **Animals**

Four male White Carneaux pigeons (*Columbia livia*) were tested. All had experience in a non-related color discrimination task, but none had experienced in a simultaneous simple discrimination reversal task. Two subjects (#1G and #2M) had experience in a mid-session task using matching-to-sample and oddity-from-sample (though not in the experiments immediately prior to this one). Pigeons were maintained at 80-85% of their free-feeding weight and individually housed in wire mesh cages with free access to water and grit in a colony room

maintained on a 12:12 light/dark cycle. This protocol was approved by the Institutional Animal Care and Use Committee at Tufts University.

### **Apparatus and Stimuli**

Training and testing was conducted in a computer-controlled (Dell Optiplex 745), sound-attenuated operant chamber. Stimuli were presented on a color LCD monitor (NEC, Accusync LCD52VM) with a 1024 x 768 resolution visible behind a 32 x 24 cm infrared touchscreen (EloTouch; Harrisburg, PA) which comprised the front panel of the chamber and recorded pecks. A central house light located on the top panel of the chamber provided general illumination throughout the experiment, except during time-outs. A 5.0 × 5.5 cm central food hopper (Coulbourn Instruments) was located below the touchscreen and provided mixed-grain reinforcement after correct responses during non-differential outcome sessions. Two side hoppers (5.0 × 5.5 cm, Coulbourn Instruments) were located on the bottom-left and bottom-right side panels and provided reinforcement for correct responses on differential outcomes sessions. Discriminative stimuli consisted of green (RGB = 18, 194, 18) and red (RGB = 255, 19, 41) hues presented 2.5 × 2.5 cm in size.

### **Procedure**

*Pre-training.* All pigeons were shaped to peck at the two side key locations for both red and green color hues and to eat out of each of the three hopper locations prior to the start of training. This was achieved by trials in which a single stimulus would be randomly presented on the left or right side of the screen and pecking rewarded from one of three hoppers. For half of the subjects (#1G and #3L) the red stimuli were used only during non-differential outcome sessions and the green stimuli were used only during differential outcome sessions. This was reversed for the other two birds. The stimuli were always the same color within a session. On

differential outcome pre-training, a single peck to either stimulus resulted in a consistent stimulus/hopper location reinforcement period (e.g., left stimulus/left hopper). On non-differential outcome pre-training, left and right responses were rewarded from the central hopper. Pigeons were pre-trained for up to 20 sessions, at which point they were pecking all colors, response locations, and eating from all three hoppers.

***Differential/Non-Differential Reinforcement Training.*** At this point, MSR discrimination training began. Differential and non-differential outcome sessions alternated with one another. For both session types, pigeons started each trial by pecking at a centrally-located 2.5 cm circular white ready signal. This peck resulted in the ready signal being replaced by either two green stimuli or two red stimuli depending on the type of session. For the first half of each 80-trial session (trials 1-40), one side was designated correct, and for the second half (trials 41-80) of each session the other side was designated correct. For pigeons #1G and #2M, the left response key (S1) was correct during the first half, and the right response key (S2) was correct during the second half. The other subjects (#3L and #4B) received the complement of these assignments.

During differential outcome sessions, birds were rewarded with food from the same side as the correct response in the spatial discrimination. Thus, during the first half of differential outcome sessions, for pigeons #1G and #2M, a single peck to the correct left response stimulus resulted in both stimuli turning off and 2.0 s access to the left food hopper. A peck to the incorrect right response key turned off both stimuli and resulted in a 5.0 s dark time-out. These contingencies reversed starting on Trial 41 (S1-/S2+ and rewarded from the right hopper). During non-differential outcome sessions, choice contingencies were identical for each bird, except that all correct responses were rewarded from the single central hopper. All trials in a

session were separated by a 3.0 s lit ITI. Pigeons were trained with alternating sessions of differential outcome and non-differential outcomes for a total of 50 sessions.

### Results

Overall, the differential outcome manipulation improved switching accuracy in comparison to the non-differential outcome sessions. The results of the differential versus non-differential outcome training can be seen in Figure 1. Figure 1 depicts percentage choice of the first correct stimulus (S1) as a function of trial number for the two session types, averaged across subjects for the last 20 sessions of training (sessions 31-50). Optimal performance would consist of exclusive choice of S1 during the first half of the session, followed by exclusive choice of S2 on the second. As can be seen in the figure, the non-differential outcome sessions produced both anticipatory (before the reversal) and perseverative (after the reversal) errors around the reversal location as seen in previous experiments (e.g., Rayburn-Reeves et al., 2011) In comparison, the differential outcome sessions resulted in a large reduction in anticipatory errors and a slightly reduced number of perseverative errors. A paired samples *t*-test comparing percent correct on the two session types confirmed a significantly higher accuracy for the differential outcome session type ( $M = 95.4\%$ ,  $SEM = 0.95$ ) as compared with the non-differential outcome session type ( $M = 93.2\%$ ,  $SEM = 0.93$ );  $t(3) = 3.1$ ,  $p < 0.05$ .

To evaluate the number of anticipatory and perseverative errors, we analyzed accuracy on the five trials immediately preceding and following the reversal trial. On the trials immediately preceding the reversal, accuracy on the differential outcome sessions ( $M = 92.5\%$ ,  $SEM = 5.56$ ) was significantly higher than on the non-differential outcome sessions ( $M = 79.5\%$ ,  $SEM = 6.85$ ; paired-samples  $t(3) = 7.51$ ,  $p < 0.01$ ). Accuracy on Trials 42-46, however, was not significantly different across the differential ( $M = 83.0\%$ ,  $SEM = 3.87$ ) and non-differential ( $M = 75.5\%$ ,

$SEM = 4.35$ ) outcome sessions indicating no difference in perseverative errors ( $t(3) = 1.54, p = 0.22$ ).

### **Discussion**

Experiment 1 revealed that differential outcomes, as created by separating the location of reinforcement associated with spatial choices, improved switching accuracy relative to non-differential outcome sessions. This suggests that adding an external spatial cue as provided by food location can enhance switching behavior in MSR. What is not clear is how it does so. One possibility is that the nature of the switching cue changed from elapsed time, as used in the non-differential sessions, to food location. We think this unlikely as time continued to be a salient switching cue for the other half of the sessions. Rather we think it is more likely the information from the differential outcome cues added redundantly to the ongoing and continued use of a time-based cue across all the sessions. This redundant cue facilitation is responsible for the superior switching performance observed on the differential outcome sessions. That said, the additional control seemed to only selectively reduce the rate of anticipatory errors and not perseverative errors. Why would this manipulation help before, but not after, the reversal point?

One possible answer to this asymmetric benefit of differential outcomes requires a comparison of the two error types, anticipatory and perseverative. Anticipation errors are clearly the result of an interval timing process related to the time of reversal, but perseverative errors have multiple possible sources. One possible source is recently accumulated, within-session excitation or association with the previously correct stimulus, which has been suggested to be a fundamental source of perseverative errors in pigeons (Bouton, 2004; Cook & Rosen, 2010; McMillan, Sturdy, & Spetch, 2015). If the pigeons utilized spatial attention to successfully select S1 more during the first half of a differential outcomes session, they would also have increased

their excitatory association with the S1 stimulus. In this case, the benefit of spatial attention would reduce accuracy after the reversal, ultimately yielding performance that is no different than in non-differential outcomes sessions.

## **Experiment 2a**

### **Contribution of External ITI Cues to Mid-Session Reversal**

While the differential outcomes manipulation improved switching accuracy in Experiment 1, the increase in accuracy before the reversal raises the possibility that the cue the pigeons were using was their spatial location when the next trial began. This would account for increases in perseverative responding at the S1 location after the reversal, as incorrect responses would not activate the other hopper, indicating a need to change locations. Therefore, we hypothesized that introducing a stimulus prior to each trial across both halves of the session would decrease both anticipatory and perseverative errors. As a result, we changed our approach and the nature of the external cue that we tested. In Experiment 2a, we investigated whether adding a different type of salient, external cue prior to each trial might improve reversal accuracy on both sides of the reversal. This cue consisted of adding visual colors during the inter-trial interval (ITI) prior to the start of each trial that indicated both in which half of the session the pigeon was located (first or second) and which discriminative stimulus would be correct on the following trial (S1 or S2). Could the information provided by this ITI color cue result in the same or greater improvement in switching accuracy observed in Experiment 1?

## **Method**

### **Animals, Apparatus, and Stimuli**

The animals, apparatus, and choice stimuli were the same as in Experiment 1. Each subject continued to be trained on the same color and spatial assignments as during the non-

differential outcomes sessions in Experiment 1. Only the central hopper was used to reward correct responses during this and all subsequent experiments. The visual stimuli introduced during the ITIs consisted of blue (RGB = 0, 0, 255) and yellow (RGB = 255, 255, 0) colors that filled the entire  $32 \times 34$  cm front computer screen during the 3.0 s duration of the ITI.

### **Procedure**

The MSR procedure was similar to that in Experiment 1. Choices to the S1 stimulus during the first half of the 80-trial session resulted in 2.0 s of reinforcement, while choices to S2 during this half resulted in a 5.0 s dark time out. Either outcome was followed by a 3.0 s lit ITI. For the last half of the session, contingencies were reversed (S2+/S1-), with S1/S2 and left/right responses assigned as in Experiment 1.

Two session types were used: an *un-cued* session in which the entire front screen was completely dark during the ITI and a *cued* session in which the entire front screen was either blue or yellow during the ITI. Trials 1-40 were preceded by a blue ITI color cue and trials 41-80 were preceded by a yellow ITI color cue; therefore, the ITI color cue provided information about which stimulus would be reinforced on the following trial. This color sequence was the same for all birds. Pigeons were trained with alternating cued and un-cued ITI sessions for a total of 50 sessions (25 sessions for each Session Type).

### **Results**

Overall, the external ITI color cues improved accuracy as compared with the un-cued sessions in which these cues were absent. This improvement occurred both before and after the reversal. As with Experiment 1, we analyzed overall accuracy across the last 20 sessions (Sessions 31-50) for both session types, the five trials before (Trials 36-40) and five trials after (Trials 42-46) the reversal trial. Additionally, we analyzed the drop in S1 choice immediately

following the first reversal trial (Trials 40-41 for the cued session type and Trials 41-42 for the un-cued session type) to assess sensitivity to the reversal event.

Choice of the first correct stimulus (S1) as a function of trial number averaged across pigeons for sessions 31-50 can be seen in Figure 2. The cued and un-cued session types are separately plotted. As can be seen, accuracy on cued sessions was substantially greater than on un-cued sessions, as indicated by greater choice of S1 over the first half of the session and the greater choice of S2 in the last half. This difference in accuracy across the two session types emerged after Session 20 and was maintained throughout training. Overall accuracy for cued sessions averaged 95.44% ( $SEM = 1.15$ ), with un-cued sessions averaging 89.53% ( $SEM = 2.72$ ). A paired samples t-test comparing averages on the two session types across bird confirmed a significantly higher accuracy for the cued as compared with the un-cued sessions;  $t(3) = 6.12, p < 0.01$ .

We again analyzed the trials immediately preceding and following the reversal trial to assess differences in anticipatory and perseverative errors. We analyzed the percentage accuracy across the two session types as a measure of anticipatory errors across Trials 36-40. The percentage accuracy averaged on the cued session type ( $M = 92.50, SEM = 1.58$ ) was significantly higher than on the un-cued session type ( $M = 65.00, SEM = 2.24$ );  $t(3) = 3.28, p < 0.05$ . We also analyzed performance on the five trials immediately following the reversal trial (Trials 42-46) to measure perseverative errors. Similar to Experiment 1, we found no significant difference in accuracy for the cued ( $M = 87.00, SEM = 8.50$ ) and un-cued ( $M = 73.50, SEM = 3.30$ ) session types;  $t(3) = 2.26, p = 0.11$ .

Additionally, the two session types differ in when local information is available about whether a reversal has occurred. For the cued session type, this is the difference in choice of S1

between Trials 40 and 41, as the presence of the yellow cue *prior* to choice on Trial 41 is a clear external signal that the contingencies have reversed. In contrast, the best comparison for the un-cued session type would be between Trials 41 and 42, as the *outcome* of Trial 41 is the best external cue that the contingencies have reversed. For the cued session type, there was a significant drop in choice of S1 responses from Trial 40 ( $M = 90.00$ ,  $SEM = 4.08$ ) to 41 ( $M = 37.50$ ,  $SEM = 7.50$ ),  $t(3) = 5.09$ ,  $p < 0.05$ . This suggests the ITI cues were important in the control of choice behavior. As for the un-cued session type, the drop in S1 responding from Trial 41 ( $M = 52.75$ ,  $SEM = 13.15$ ) to Trial 42 ( $M = 47.50$ ,  $SEM = 8.54$ ) was not significant;  $t(3) = 1.00$ ,  $p = 0.39$ . This is consistent with prior findings that reinforcement outcome is not a strong reversal cue for pigeons. Finally, when analyzing the difference measure compared across session types, there was a significantly greater drop in choice of S1 for the cued ( $M = 57.50\%$ ) as compared with the un-cued ( $M = 5.25\%$ ) session type;  $t(3) = 4.26$ ,  $p < 0.05$ .

As a measure of time-based control over responding, we analyzed the average time to the reversal for each bird across the last 20 sessions of training for both the cued and un-cued session types. Overall, the average time from the start of Trial 1 to the reversal trial (Trial 40) was 5.95 minutes ( $SEM = 1.77$ ) for the cued and 5.90 minutes ( $SEM = 0.93$ ) for the un-cued sessions. One of the four birds showed consistently longer and more variable durations to the reversal point than the other three, reaching the reversal approximately 3.5 minutes later on both session types. Presumably as result, this bird was less accurate overall compared to the other birds.

### **Discussion**

The results of Experiment 2a indicate that pigeons can use an external visual cue during the ITI to significantly improve their switching accuracy. It appears that inserting a cue that provides contextual information just prior to the onset of a trial can serve as a reliable switching

cue for choice in MSR. Thus, two types of external cues, reinforcement location and ITI cue, can both serve to help pigeons process and possibly segment the conflicting portions of these sessions beyond their typical use of time. Although both cued and un-cued sessions allowed for use of the time and reinforcement cues, it is clear that the addition of the external ITI cues enhanced the pigeons' capacity to segment the session.

One possibility for the ITI cue's greater effectiveness in aiding MSR discrimination is its placement in the trial as compared to reinforcement outcome. When considering the placement of the ITI color cue and the reinforcement cue, it is important to note that the ITI cue immediately precedes the choice response on the subsequent trial, thereby providing information about which choice will be reinforced next (information for the immediate future). The reinforcement cue, however, occurs immediately after choice, providing information about what choice was correct on the previous trial (information about the immediate past). An important difference in the information provided by these two cues is that the delay between the ITI cue and the next available choice is smaller than the delay between the reinforcement cue and the next choice. This difference in temporal location between the switching cues and subsequent choice might be an important reason why accuracy is greater on the cued session type.

The present training involved redundant information provided by the timing and ITI color cues. The value of ITI cue is not necessarily dependent on the temporal cue. However, therefore, to understand whether the timing cue was necessary for the boost in performance during the ITI color cued sessions, or whether the information derived from the ITI color cue could be processed independently from the timing cue, we manipulated the occurrence and placement of the ITI color cues across sessions during Experiments 2b and 2c.

### **Experiment 2b**

### Addition and Removal of ITI Cues across Sessions

The purpose of Experiment 2b was to evaluate the contribution of time-based and visual context cues on performance. One major question stemming from Experiment 2a's results is whether the pigeons continued to attend to temporal estimations of the reversal location or not during the cued sessions. One possibility is that the ITI cues might replace the use of time in these sessions as the ITI signal is unambiguous. The second is that these external cues redundantly add to the continued encoding of time in both types of sessions. If time does continue to be encoded during the cued session type, then pigeons should be able to use either cue at any point within the session. To evaluate this we selectively added and removed the ITI cues during Experiment 2b.

We manipulated the occurrence of the ITI color cues within the two session types to evaluate the effect of their unexpected presence or absence on behavior within a session. We intermixed training sessions with probe sessions in which we either inserted ITI color cues during un-cued sessions or removed them during cued sessions around the reversal location. This manipulation provided an opportunity to see how the pigeons tracked the timing and visual cues simultaneously and the relative dominance of these cues at various points within the session. Our hypothesis was that these changes would cause pigeons to use the alternate informative cue during such tests, using time-based cues during un-cued probe trials within cued sessions and using ITI color cues during cued probe trials within un-cued sessions.

### **Method**

#### **Animals, Apparatus, & Stimuli**

The animals, apparatus, and stimuli were the same as was used in Experiments 1 and 2a.

#### **Procedure**

The same 80-trial MSR procedure was used as in Experiment 2a. Subjects were exposed to six different session types. In addition to the two session types (cued and un-cued) trained in Experiment 2a (now called cued and un-cued baseline session types), we created four different probe session types (proximal added, proximal removed, distal added, and distal removed). In the two *added* session types, we added ITI color cues in two 5-trial test blocks to otherwise ongoing un-cued sessions. The added ITI cues always matched the ITI cue appropriate to each session half during baseline, with blue ITI cues added prior to the reversal and yellow ITI cues added after the reversal. In the two *removed* session types, we removed the color cues in two 5-trial test blocks during otherwise cued sessions. When the ITI cues were removed, they were replaced with the dark ITI presented during un-cued sessions. All of these probe trials were non-differentially reinforced with all non-probe trials differentially reinforced as in baseline sessions.

The added and removed probe session types also differed in the location of the probe trials within the session. The *proximal* and *distal* locations were selected to evaluate whether the effect of the ITI cues differed based on their proximity to the reversal. Proximal probes occurred on Trials 36-40 and Trials 41-45 and distal probes occurred on Trials 31-35 and Trials 46-50. Each of the six session types were randomly presented once within 6-session blocks. A total of eight six-session blocks were conducted (48 total sessions).

## Results

Overall, adding ITI cues to otherwise un-cued sessions increased accuracy, while removing cues from cued sessions reduced accuracy. When ITI cues were unexpectedly removed, performance for those probe trials closely matched un-cued baseline accuracy levels. When the ITI cues were made unexpectedly available, performance increased for those trials to levels comparable to baseline cued sessions. Thus, regardless of whether pigeons *began* sessions

with the ITI cues or not, their presence or absence near the reversal caused the pigeons to show levels of accuracy comparable to the baseline sessions of that type.

Given that all six session types showed nearly identical accuracy during the non-manipulated blocks of trials (i.e., Trial blocks 1-30 & 51-80), we focused our analyses on the four critical trial blocks around the reversal. Figure 3 depicts the proportion of S1 choices averaged in 5-trial blocks across subjects for Trials 31-50. To provide the most direct comparison and illustration of the visual cue's effect, the results from cued and un-cued baseline session types are presented in continuous and dashed gray lines. The added (blue +) and removed (black ×) symbols depict the probe results across the proximal (36-40 & 41-45) and distal (31-35 & 46-50) trial blocks. Tests revealed that the non-manipulated portions of the probe session types did not significantly differ from their matching baseline conditions. As a result and because the effects of ITI cue addition and removal were short-lived, results from non-manipulated trial blocks during probe sessions were omitted from the figure, but they are reported in Table 1 along with the depicted data in Figure 3.

In order to evaluate whether the four session types (now cued and un-cued baseline, and added and removed probes) differed in accuracy across the four trial blocks, a  $4 \times 4$  [Session-Type (cued baseline, un-cued baseline, added, and removed)  $\times$  Trial Block (31-35, 36-40, 41-45, 46-50)] repeated measures (RM) ANOVA was evaluated. There was a significant Session Type  $\times$  Trial Block interaction,  $F(9, 27) = 11.31, p < 0.01$ , as well as significant main effects of Session Type,  $F(3, 9) = 18.12, p < 0.01$  and Trial Block,  $F(3, 9) = 14.46, p < 0.01$ .

As can be seen, the main source of the prior interaction is that the addition and removal of the cues caused each set of trials to behave like its comparable baseline session (for ITI cue addition, the cued baseline; for ITI cue removal, the un-cued baseline). To better focus in on the

effects of proximity to the reversal, we conducted pairwise comparisons of the baseline and respective probe conditions for each of the four trial blocks. The main comparisons were between the cued baseline and the added probe session types for the ITI present condition, and between the un-cued baseline and the removed probe session types for the ITI absent condition. Across all four trial blocks, there was no significant difference between accuracy on the cued baseline ( $M = 88.91$ ,  $SEM = 4.25$ ) and the added probe session type ( $M = 88.59$ ,  $SEM = 4.01$ ,  $p = 0.90$ ). There was also no significant difference between the un-cued baseline ( $M = 76.56$ ,  $SEM = 5.57$ ) and removed probe session type ( $M = 69.84$ ,  $SEM = 1.83$ ,  $p = 0.18$ ). Accuracy on the cued baseline was, however, significantly higher than for the un-cued ( $p < .05$ ) and removed ( $p < .01$ ) session types. Finally, accuracy on the added session type was significantly higher than for the removed session type ( $p < .01$ ) and approached a significantly higher accuracy as compared to the un-cued baseline session type ( $p = .070$ ).

### **Discussion**

In general, the results of Experiment 2b suggest that the external cue of ITI color and the internal, time-based cue operated simultaneously. When ITI cues were added to otherwise un-cued sessions, the number of errors decreased as would be expected from Experiment 2a's outcomes. More importantly, when ITI cues were removed in otherwise cued sessions, errors increased but to levels comparable to un-cued sessions. This suggests the pigeons were continuing to track time during the cued sessions and that the addition of these external cues did not eliminate the use of the timing cue.

The results of adding ITI color cues during un-cued sessions further suggest that pigeons were simultaneously processing both cues. The pigeons appeared to utilize the ITI cues as effectively as they did during baseline cued sessions, suggesting that the ITI cues did not have to

be present from the start of a session to be used effectively. Further, once these cues were no longer available, accuracy returned to levels closely approximating the un-cued baseline sessions, suggesting that pigeons were continuing to use time-based estimation cues throughout the session.

One exception to this simple conclusion is the performance after the reversal, during Trial block 41-45. Here accuracy for the proximal removed session type was poorer than one would expect from just time-based processing (i.e., baseline un-cued sessions). A similar effect happens with the proximal added sessions in this trial block, where accuracy with the added cues does not reach the same levels as accuracy in cued baseline sessions. The pigeons are detrimentally affected by unexpected cue manipulations in the period just after the reversal, although the reason for this effect is not clear, but appears to not be very long lasting.

One possibility is that the presence of the ITI cues at the start of a session does matter, but it is only evidenced when the discrimination is particularly ambiguous, such as right after the reversal. If ITI cues are present from the start of the session, this may result in biasing the birds to attend to visual information; therefore, removing the ITI cues when they have been recently available would cause a decrement in performance around the reversal when they exert the highest control over behavior. Likewise, when the ITI cues are suddenly introduced after the birds have been relying on timing, these ITI cues are not as effective as when they are available from the start of sessions. This extension, however, doesn't account for the apparently greater effect of removing the ITI cues than adding them back. One possible reason for the latter is that there were approximately twice as many perseverative errors compared to anticipatory errors on the un-cued trials relative to the cued trials. This might reflect the yellow ITI cue having become a more important general cue for the transition away from the first task's behavior. This bias

towards the ITI cue then resulted in time-based cues being less effective in aiding switching behavior during these trials.

### **Experiment 2c**

#### Testing Conflicting Timing and ITI cues

In Experiment 2c we further examined the interaction between the external ITI cues and time-based cues. Both of these cues seemed to act as possible occasion setters. That is, the presence of the blue ITI cue would indicate choice of the S1 stimulus while presence of the yellow cue would indicate choice of S2. Likewise, an “early” time cue would indicate choice of the S1 stimulus, while a “late” time cue would indicate choice of S2. From the results of Experiment 2a and 2b, it might appear that both cues made independent and redundant contributions to switching behavior. However, a portion of the results of Experiment 2b suggested more complicated possibilities.

One possibility we considered was that the relative strength of these different types of cues could vary within a session; in particular, the utility and value of the timing cue might change across a session. While this cue is highly salient to pigeons, it is clearly most effective at the endpoints of the session. As a session approaches the reversal, the time-based cue becomes less reliable due to the fact that time estimation (i.e., timing the exact trial in which the reversal will occur) is a noisy and imprecise process. This unreliability decreases the utility of the time as a switching cue near the reversal. It is at this point that the external visual cues may become more important, salient, and more heavily weighted in determining choice behavior.

Correspondingly at the beginning and end of a session, the external cues may be overshadowed and exert little control over responses because of the saliency of timing cues. This general idea we labeled the *relative utility hypothesis*.

Based on this hypothesis, we decided in Experiment 2c to include “miscue” trials throughout the session, in which correct response as cued by the time estimation process and the external visual cue were in conflict. For instance, we created miscue trials in which we purposely inserted ITI cues into the wrong portions of a session, thereby combining the ITI color associated with one temporal location (e.g., blue early) with a different temporal location (e.g., blue late). These miscue trials allow us to directly compare the relative use of the internal and external cues across a session and relative to the proximity of the reversal location. In a sense, these miscuing manipulations are akin to occasion setting transfer trials, where novel configurations of multiple cues can be presented to assess the relative control by each cue (Bonardi, 1998).

We tested miscue trials throughout a session for both cued and un-cued session types to assess the generalization of time cues when presented with conflicting ITI cues. This manipulation not only allowed us to assess whether a given cue is processed at particular points within the session (as in Experiment 2b), it also allowed us to assess the relative associative strength of these cues at various points within the session.

The major question was whether these miscues would produce behavior specific to the external cue depending on when in a session they were tested. If the effects of the miscues varied across time within a session, it would indicate a dynamic interaction in cue use, with the strength of a given cue being relative to, and depending on, the strength of information available from other cues at the time of choice. This effect would be consistent with the relative utility hypothesis and would be expected if the greatest ambiguity of the timing cue occurred in the middle of the session. On the other hand, if any miscuing effect was constant over a session, it would support a *time-independent hypothesis*, suggesting that the ITI cues were encoded as separate cues specific to a particular response and operating independently of time in a session.

In this vein, the task could be considered more a symbolic matching task, with the ITI cues serving as sample stimuli and the two discriminative stimuli serving as comparisons. Although time and ITI color provide consistent information with respect to the correct response, the highly reliable ITI cue might overshadow the timing cue and exert an independent influence on behavior. This doesn't suggest that time wouldn't compete with control by the ITI color, but that the value of the ITI color could be assessed independent of its location in time.

## **Method**

### **Animals, Apparatus, & Stimuli**

The animals, apparatus, and stimuli were the same as was used in previous experiments.

### **Procedure**

The cued and un-cued baseline session types from Experiment 2b continued to be tested. In addition, two miscue probe session types (cued and un-cued miscue) were presented across the testing phase. Within these, ten miscue probe trials were inserted over the course of a typical cued or un-cued session type. Beginning on Trial 6, these miscue trials were presented every eighth trial (i.e., trials 6, 14, 22, 30, 38, 42, 50, 58, 66, & 74). Trials 38 and 42 were exceptions to this pattern. This was done in order to present miscues both close to and symmetric across the reversal location. In both probe session types, yellow ITI color cues were presented on these probe trials during the first half of the session and blue ITI color cues were presented on probe trials during the second half, with the remainder of the session unchanged from the related baseline session. All probe trials were non-differentially reinforced with food for either response. We conducted 24 sessions (six sessions for each of the four session types) in randomized 4-session blocks.

## **Results**

We found a large differential effect of time on the impact of miscuing within a session. Further, we found that this effect was modulated by whether the ongoing trials were cued or not. Figure 4 presents the cued (top panel) and un-cued (bottom panel) baseline sessions compared with their respective miscue sessions. To better show and judge the impact of the miscue trials (green symbols), the results are shown for every trial within a session.

Looking across the two panels, the effect of miscuing had a greater impact on the birds' choice behavior when presented around the middle of the session than at either end. This effect was especially prominent during cued sessions, where miscuing greatly reduced accuracy in comparison to baseline trials during the middle of a session. In the cued sessions, the birds appeared to be attending more strongly to the ITI cues.

Without the miscue trials, the cued miscue session type and cued baseline session type were statistically equivalent. This is reflected in the fact that overall accuracy without miscue trials on cued-miscue sessions ( $M = 96.7\%$ ,  $SEM = 0.51$ ) averaged across bird was quite good and not significantly different from the cued baseline sessions ( $M = 97.0\%$ ,  $SEM = 1.15$ ) as indicated by a paired-samples  $t$ -test;  $t(3) = 2.25$ ,  $p = 0.11$ . As can be seen in the top panel, however, miscues during the ITI strongly influenced subsequent choice behavior on those trials. When compared with the same baseline trials, the miscues supported significantly worse accuracy,  $t(3) = 3.12$ ,  $p = .05$ . This was especially true between trials 20 to 42 where there were quite large effects of the miscues. Miscues before trial 20 and after trial 50 seemed to have far less or no impact as the birds appeared to respond in accordance with the time cue. The effects of the miscuing were relatively brief, as the birds quickly returned to near baseline levels of accuracy on the immediately following trials. Consistent with this, a Session Type (cued-miscue vs. cued baseline)  $\times$  Trial Block (across the 10 probe trials) RM ANOVA on accuracy revealed a

significant Session Type  $\times$  Trial Number interaction,  $F(9, 27) = 4.82, p < 0.01$ , as well as significant main effects of Session Type,  $F(1, 3) = 9.75, p = 0.05$  and Trial Block,  $F(9, 27) = 8.37, p < 0.01$ .

The same pattern is true for the un-cued miscue sessions, but the miscuing in this session type showed a slightly different pattern of results. When looking at the difference in accuracy between the un-cued baseline and un-cued miscue sessions,  $t(3) = 3.36, p < .05$ , the effect seemed confined to the test trials in the middle of a session, similar to the larger effect seen on cued session types. Unlike with the cued miscue session, however, there was a longer lasting effect of the ITI miscues on subsequent accuracy in following trials. That is, on the trials following a miscuing, there was consistently lower accuracy on the subsequent un-cued trials. Overall accuracy on the un-cued baseline sessions ( $M = 91.55, SEM = 1.49$ ) excluding the miscue trials was good and significantly better than on un-cued miscue sessions ( $M = 84.70, SEM = 3.05; t(3) = 3.31, p < .05$ ). This trend also became more pronounced as the session approached the reversal point and then less pronounced further through the session after the reversal point. A Session Type (un-cued miscue vs. un-cued baseline)  $\times$  Trial Block (across the 10 probe trials) RM ANOVA on accuracy revealed no significant Session Type  $\times$  Trial Number interaction,  $F(9, 27) = 1.53, p = 0.19$ , but significant main effects of Session Type,  $F(1, 3) = 11.29, p < 0.05$  and Trial Block,  $F(9, 27) = 19.01, p < 0.01$ .

Finally, we compared accuracy between the two miscue session types using a Session Type (cued vs. un-cued)  $\times$  Probe Trial Number (using the matched set of 10 trials from each session type) RM ANOVA as with previous analyses. We found no significant Session Type  $\times$  Trial Number interaction or a significant main effect of Session Type (both  $F$ s  $< 1$ ); only a significant main effect of Trial Number,  $F(9, 27) = 15.99, p < 0.01$ . Due to the absence of a

significant interaction or main effect of session type, presented in Figure 5 are the combined effects of miscuing (collapsed across cued and un-cued miscue session types) across the ten probe trials within a session. The effect of a miscue is minimal on the first two probe trials, then increases steadily until Trial 42, at which point the effect rapidly decreases and remains minimal for the remainder of the session. Thus, besides the greater effect in the middle of a session already presented, there is also an asymmetry between the effects of miscuing before or after the reversal point. Together, these results indicate a strong modulation of the impact of the ITI cues depending upon their location and time within a session.

### **Discussion**

The results of Experiment 2c allowed a detailed analysis of the effect of the ITI cues within a session. It revealed that the effect of ITI miscuing was highly time dependent across a session. At the beginning or end of a session, miscuing had little effect, while in the middle it had a large effect on choice behavior. This outcome is consistent with the relative utility hypothesis, which suggests that the control by timing and ITI cues is dependent upon the relative utility and saliency of the two cues throughout the session. The timing cue appears to be more dominant at the session endpoints and the ITI cue more dominant in the middle of the session. The pigeons also appeared to be equally affected by miscue trials (i.e., drop to the same absolute level) regardless of whether the session type contained ITI cues during the non-probe trials within the session. The reintroduction of external cuing on non-probe trials increased accuracy much faster on cued sessions as compared to un-cued sessions, however. In the latter, the effects of miscues seemed to last for several trials in the absence of any external information to the contrary. The results of this experiment demonstrate that pigeons can process multiple switching cues simultaneously and that a shift in control from one cue to another is dependent upon the

relative utility and saliency of the cues at any given point in time. The fact that all session types looked so similar at the endpoints of the session strongly suggests that the temporal cue was overshadowing the external ITI cues at these points regardless of the nature of the cue involved and the external cues were more influential during the middle of a session.

### **General Discussion**

The purpose of the current experiments was to evaluate the relative strength of various cues on pigeon behavior in MSR. These experiments demonstrate that the addition of external cues improves choice accuracy by pigeons during MSR. Both manipulating the saliency of reinforcement cues (Experiment 1) and adding external ITI cues (Experiment 2) improved choice accuracy across a session. Most importantly, the relative control by these latter external cues was modulated by the time within the session (Experiment 2c). Timing cues were dominant at the beginning and end of a session, with external cues gaining discriminative control during the middle of a session. The latter finding is consistent with a relative utility hypothesis regarding how cues exert and compete for control across an extended session.

It is interesting that these external ITI cues control behavioral choice in mid-session reversal. Recent response-reinforcement contingencies are another available external cue, but previous research persistently shows that they exert little control over pigeons' choices (Rayburn-Reeves et al., 2011). Despite the highly informative nature of these cues, pigeons' within-session behavior appears to be less controlled by reinforcement-based external cues. Besides its greater visual salience, the external ITI cue may more readily capture discriminative control than reinforcement cues because it occurs closer in time to the upcoming trial. Specifically, to use the feedback from the outcome of the previous trial as a cue, pigeons would also have to remember the choice-reinforcement configuration across the 3.0 s ITI delay, akin to

a delayed, bi-conditional discrimination. In this case, the “sample” would consist of the compound of the response-outcome association from the previous trial, the 3.0 s ITI would be the delay, and the choice on the following trial would be a kind of comparison stimulus. In contrast, the ITI cue in the current set of experiments is akin to a delayed, symbolic matching task, where the ITI color is the sample and the correct comparison stimulus is dependent on the ITI color. By being closer in time to the future choice and by perhaps being a simpler or more salient signal, the ITI cues can function better than reinforcement outcomes for identifying different portions of a session.

An extension of this latter idea is the possibility that the ITI cue effectively serves as an occasion setter, modulating the hierarchical relationship between discriminative stimuli, time within the session, and reinforcement (Holland, 1989, 1991, 1992; Leising, Hall, Wolf, & Ruprecht, 2015). The external ITI cues may readily inform pigeons as to which half of the session is currently occurring in a way that reinforcement outcome of the previous choice cannot. Experiment 1 suggested that maybe reinforcement location could help divide the session, but this effect would need to be explored further. Given that the current set of experiments required learning a spatial discrimination as opposed to a visual one, the ITI cue might have better informed the animal as to which side would be reinforced on the following trial, allowing the animal to be positioned in front of the correct key during the ITI and further helping to bridge the gap between trials. It would be interesting to know whether the ITI cue would function similarly when it informed the animal of which color to choose on the following trial, independent of spatial location.

Based on the data from the current experiments, we can begin to illuminate and better theorize how behavioral choice is controlled by multiple sources of information across time and

how the dominance of a cue depends on its relative utility to other sources of information available at the time of choice. The saliency of time (the difference in temporal representations of the two response contingencies) is likely highest at the two end points, as it seems to exceed or overshadow the external ITI cues. As a session's midpoint approaches, however, the difference between the two response contingencies in time is increasingly similar, thereby resulting in greater competition between these two responses. It is this decline in predictive value by the timing cue, as evidenced by increases in accuracy on cued compared with un-cued sessions, which is assumed to be tied to the increase in control by the ITI cue. At this point, the ITI cue comes to dominate control of responses and continues to do so until the difference in time between the two competing responses increases to a level sufficient to regain discriminative control by time. This is why miscuing is so much more impactful in the middle of the session.

The results from the current set of experiments continue to illustrate how strong timing cues are for pigeons compared with other internal and external cues. Why this is the case in mid-session reversal for this species remains a mystery. The ITI cues introduced here were effective, but the timing cues still exerted control over responding, especially at the endpoints of the sessions. This was true even though the ITI cues were completely and equally informative across the entire session. Why would the cues switch back and forth in controlling responses across the session? One possibility is that the order with which different cues are trained makes a difference. In the current study, the pigeons were trained on a differential and non-differential outcomes task prior to the ITI cue training (Experiment 1). Thus, the timing cue became more dominant overall due to its initial and greater exposure compared to the external ITI cue (i.e., perhaps a form of blocking). Additionally, the simultaneous training of the un-cued and cued session types in Experiments 2a-2c could have inflated control by the timing cue as well. The

timing cue was always available and relevant in every session regardless of type, whereas the ITI cue was only relevant during half of the sessions. It would be interesting to see whether initially training the ITI cue prior to and independent of the timing cue would result in an increase in use of this external cue as compared with the current results. In this way, pigeons could be trained initially on the cued session type and then exposed to the un-cued session type, or given initial sessions without a simple reversal in which the blue and yellow ITI cues occurred randomly across trials within the session (similar to matching-to-sample tasks). Such manipulations would provide further evidence of the development and strength of the timing cue relative to other cues present in a mid-session reversal context.

The current experiments provide good evidence that as an extended temporal landscape changes, discriminative behavior appears to be controlled by different sources of information. No other paradigm to our knowledge allows for the assessment of dynamic cue use as a function of time within a single session where the value of a single, dominant cue might be constantly changing. By perhaps mimicking some of the properties of time within a “day”, such reversal tasks allow us to explore how time serves to organize different types of behavior by predicting the appropriate discriminative response. This kind of task can be used to assess relative changes in cue use by other non-human animals and their employment of the relative utility hypothesis.

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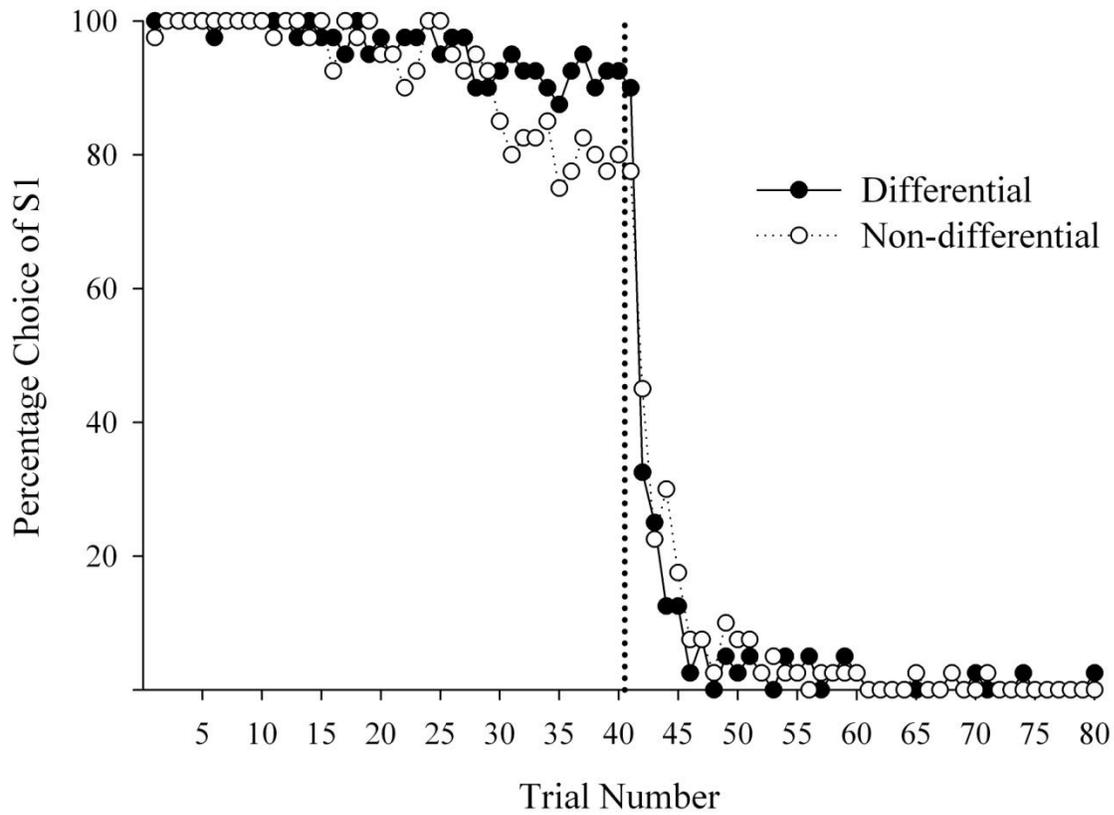
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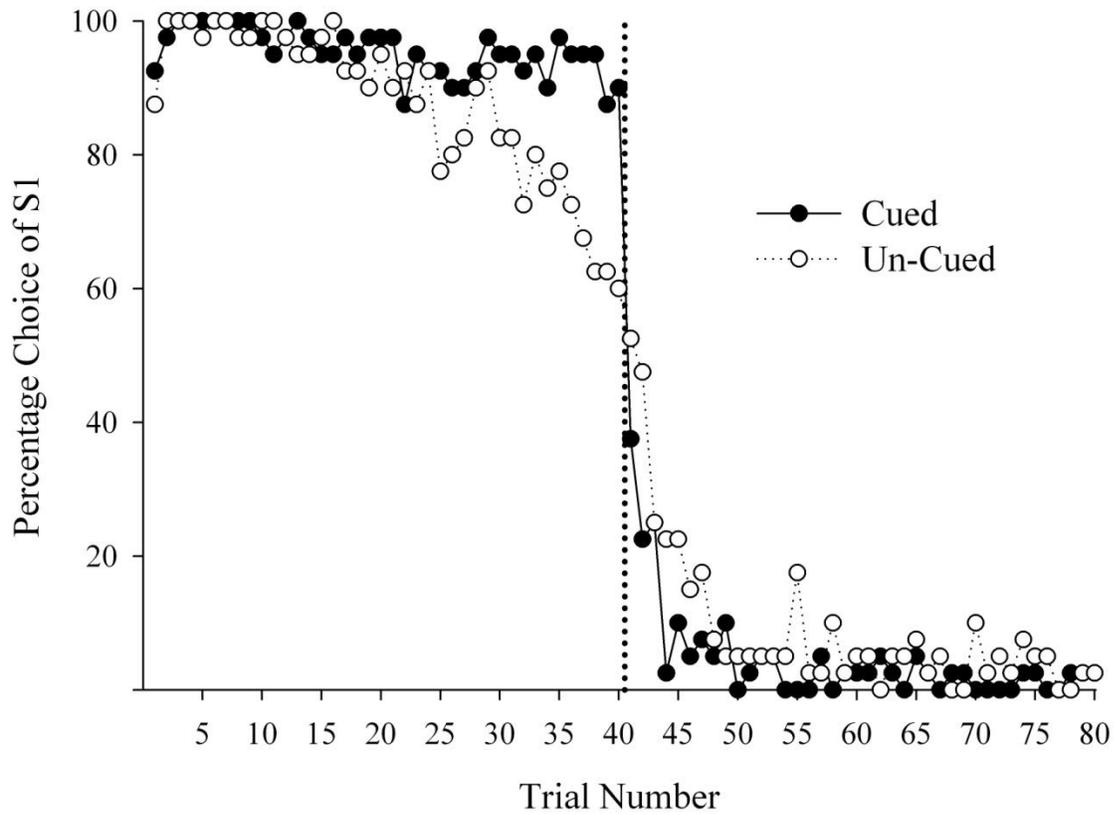
Table 1

Percentage Choice of S1 as a function of trial block for the four probe session types in Experiment 2b.

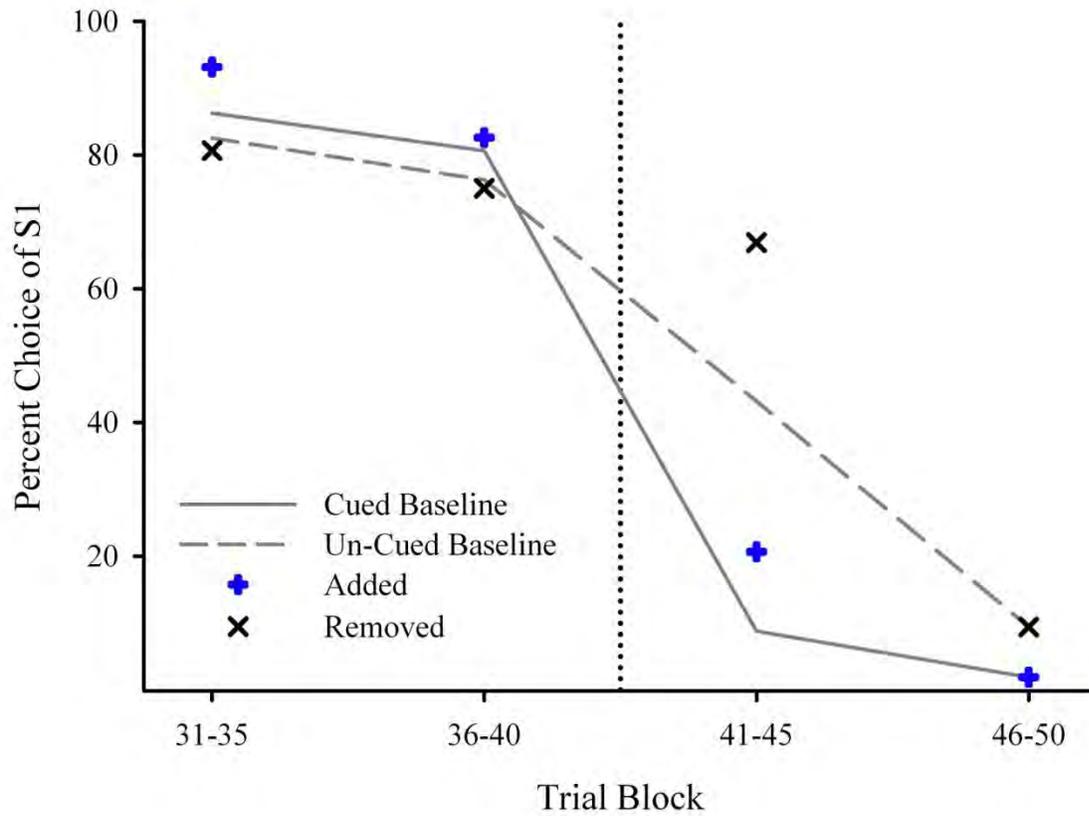
		<b>Trial Block</b>			
		31-35	36-40	41-45	46-50
<b>Probe Session Type</b>	Proximal Added	76.1	82.6	20.7	12.9
	Proximal Removed	89.4	75.0	66.9	13.8
	Distal Added	93.1	73.1	40.0	1.88
	Distal Removed	80.6	86.3	18.8	9.4



*Figure 1.* Experiment 1. Percentage choice of S1 responses as a function of trial number averaged across subjects. Closed circles depict the Differential reinforcement condition while open circles depict the Non-differential reinforcement condition. Reversal location is indicated by the dotted line.



*Figure 2.* Experiment 2a. Percent choice of S1 responses as a function of trial number averaged across birds and Sessions 31-50. Closed circles indicate the Cued ITI sessions while open circles indicate the Un-Cued ITI sessions. Reversal location is indicated by the dotted line.



*Figure 3.* Experiment 2b. Percent choice of S1 responses as a function of Trial-Block for Trials 31-50 averaged across bird and 36 sessions. Added probes are indicated by blue plus (+) signs and removed probes are indicated by a black letter “x”. Proximal probes are presented for Trial blocks 36-40 and 41-45 and distal probes presented for Trial blocks 31-35 and 46-50. Reversal is indicated by the dotted line.

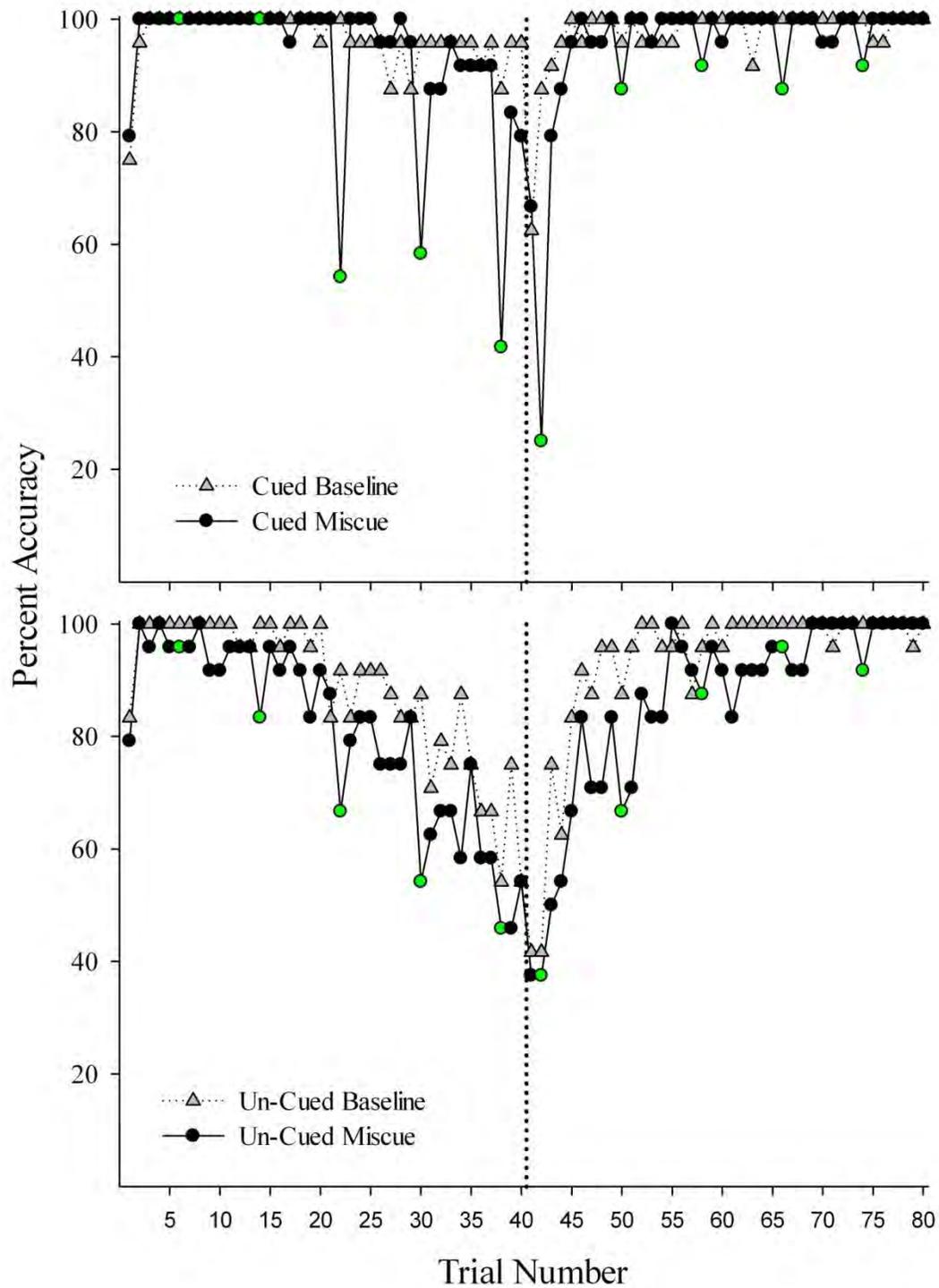
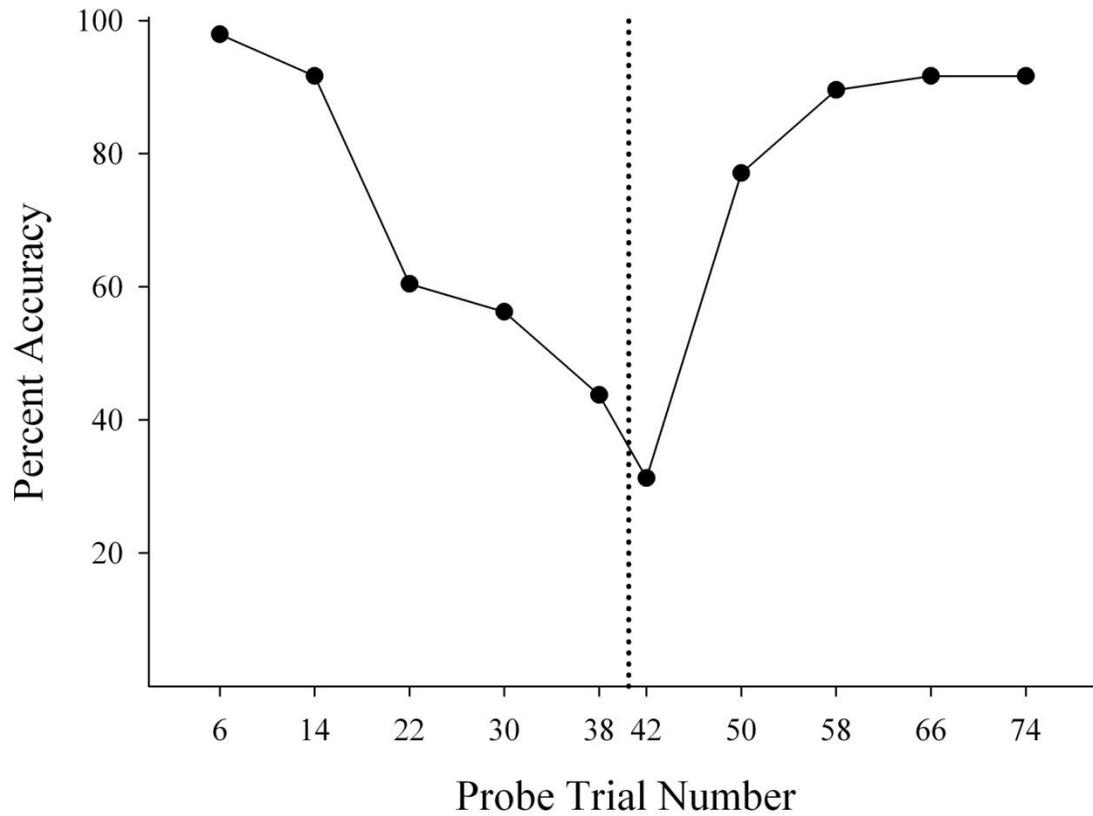


Figure 4. Experiment 2c. Percent accuracy for Cued (top panel) and Un-Cued (bottom panel) sessions based on trial number. Gray triangles indicate baseline session types while black circles indicate miscue session types. Within miscue sessions, green circles indicate miscue probe trials. Reversal is indicated by the dotted line.



*Figure 5.* Experiment 2c. Percent accuracy as a function of probe trial number collapsed across both miscue probe session types. Reversal is indicated by the dotted line.