Chickadees Discriminate Contingency Reversals Presented Consistently, but not Frequently

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Author Note

This research was supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant and Discovery Accelerator Supplement to CB Sturdy. We thank Joshua Yong and Erica Cheung for assistance in running subjects, and Tad Plesowicz for animal care.

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Abstract

Chickadees are high-metabolism, non-migratory birds, and thus an especially interesting model for studying how animals follow patterns of food availability over time. Here we studied whether black-capped chickadees (*Poecile atricapillus*) could learn to reverse their behavior and/or to anticipate changes in reinforcement when the reinforcer contingencies for each stimulus were not stably fixed in time. In Experiment 1, we examined the responses of chickadees on an auditory go/no-go task, with constant reversals in reinforcement contingencies every 120 trials across daily testing intervals. Chickadees did not produce above-chance discrimination; however, when trained with a procedure that only reversed after successful discrimination, chickadees were able to discriminate and reverse their behavior successfully. In Experiment 2, we examined the responses of chickadees when reversals were structured to occur at the same time once per day, and chickadees were again able to discriminate and reverse their behavior over time, though they showed no reliable evidence of reversal anticipation. The frequency of reversals throughout the day thus appears to be an important determinant for these animals' performance in reversal procedures.

Keywords: reversal learning, behavioral flexibility, interval timing, anticipation, chickadees

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Serial reversal learning, wherein task reward contingencies are continually reversed upon meeting performance criteria, has been extensively used to study behavioral flexibility and ‘learning sets’ (Shettleworth 2010, pp. 186-189). Animals perseverate on previously-successful responses after initial reversals, but over successive reversals they typically show accelerated response shifts; the degree to which response shifts accelerate relative to original learning is frequently used as a species- and task-agnostic means for studying flexibility or even general intelligence across species. Reversal tasks are also frequently used within-species, for instance in the literature on animal personality (i.e., individual differences that are stable across contexts): birds that are slow to explore novel environments more flexibly adapt to reversed rules in a category discrimination task than do fast-exploring birds (Guillette et al. 2011; Verbeek et al. 1994), even though fast-explorers tend to be faster learners (e.g., Boogert et al. 2006; Guillette et al. 2009). Flexibility is considered in behavioral ecology to be crucial for success in complex, dynamic environments (Bond et al, 2007; Lefebvre et al, 2004), and so there is extensive interest in using reversal performance as a correlate for this capacity in animals.

When reversals are presented at a predictable point within each session (rather than occurring between sessions), pigeons show both perseverative errors and surprising anticipatory errors (e.g., Cook and Rosen 2010; Rayburn-Reeves et al. 2011); that is, not only do they continue to respond to the previously-reinforced alternative (S1) when doing so fails to produce reward, but they also begin responding to the second-correct alternative (S2) before doing so is reinforced. This anticipatory and perseverative responding appears to be based on an interval time estimation of the reversal point relative to the beginning of the session (for full review, see Rayburn-Reeves and Cook 2016). Pigeons' errors in these within-session reversal tasks are largely controlled by elapsed time, rather than by trial or reinforcer number (Cook and Rosen 2010; McMillan and Roberts 2012); that is, pigeons determine that the reversal occurs roughly three minutes into the session (for example), and treat the task as a temporally-based biconditional discrimination.

Recently, researchers have argued that animals' errors on this mid-session reversal task are better characterized as failures of inhibition rather than of memory. McMillan and colleagues (2015) trained pigeons on a go/no-go task with a midsession reversal of task contingencies in which only one alternative was shown on any given trial, and found that subjects only made errors when a stimulus was unrewarded (i.e., they rarely failed to produce a response when responding was reinforced). Based on these results, it was suggested that when pigeons are presented with simultaneous choices on midsession reversal tasks, their errors are more likely to be a result of failures to inhibit the currently-incorrect response as the reversal nears than as deliberative choices of the incorrect response. These timing-based intrusion errors may also reflect the nature of how pigeons make choices: rather than weighing two alternatives simultaneously, pigeons may encounter and make a response decision to each stimulus serially. This is consistent with previous suggestions that the ecological rarity of simultaneous choices has led animals to treat choices as sequential decisions (Kacelnik et al. 2011). While reversal tasks are popular for studying behavioral flexibility, they are also useful for understanding more basic elements of choice and decision-making in animals.

Time-based reversal tasks bear striking resemblance to time-place learning tasks (Cook and Rosen 2010; McMillan and Roberts 2015; McMillan et al. 2015). Most pertinently, Wilkie and colleagues (1994) tested pigeons with four spatially-separated keys that each respectively produced reward for 15 min of a 60 min session. Pigeons in their experiment not only learned to successively move from one option to the next, but also sampled from alternatives that were not currently paying off but imminently would. The authors asserted that pigeons were tracking the interval time of food availability for each alternative. This comparison is important because, while timing a several-second interval between a light onset and delivery of food (as in prototypical interval timing experiments) is of dubious relevance to naturalistic foraging, time-place learning tasks likely better mimic how timing might be useful in the wild to track the relationships predicting when and where food is available. For example, in a time-place learning field study, Wilkie and colleagues (1996) studied the distribution of a number of scavenging birds across multiple spatial locations, and found that time of day (rather than number of people to scavenge from) was the best predictor of number of birds present at each site. This style of reversal, or more generally conditional discriminations with time as a contextual cue, thus can provide information about how animals integrate temporal information with other stimulus dimensions to make choices (McMillan and Roberts 2015; McMillan et al. under review).

Design of the Present Research

Chickadees are high-metabolism animals that must eat throughout the daylight period (e.g., see Chaplin 1974). Previous operant experiments with chickadees have presented trials on a quasi-free operant schedule throughout day cycles, which can exceed 16 hours in outdoor-synchronized Northern locales such as Edmonton, Alberta, Canada. Chickadees are also non-migratory, and residency during seasonal change tends to be associated with flexible foraging behavior (e.g., see Sol et al. 2005). In contrast, high-elevation mountain chickadees (*Poecile gambeli*) fail on a reversal task that was passed by low-elevation subjects (Croston et al. 2017), which might indicate that harsh environments drive stronger memory but also less flexibility. This mix of nutritional requirements and foraging realities makes chickadees an interesting model for studying flexibility in the face of environmental contingencies that shift over time. We were initially interested in whether black-capped chickadees (*Poecile atricapillus*) could learn to anticipate reversals presented throughout the day, at regular intervals similar to those studied in discrete-session tasks in pigeons. We conceived of this procedure as a simple analog to the depletion and repletion schedules that food sources may undergo in the wild; this has previously been suggested as a possible context for reversal anticipation (McMillan and Roberts 2015; McMillan et al. 2015) and is ecologically similar to 'optimal sampling' foraging theories (e.g., Dow and Lea, 1987; Houston et al. 1982; Krebs et al. 1978).

In Experiment 1, we presented chickadees with a successive-choice, auditory go/no-go task in which reinforcer contingencies reversed every 120 trials; after every 240 trials, a five-min red cue demarcated the completion of one 'session'. These parameters were determined based on pilot studies that showed poor discrimination by chickadees with fewer trials per reversal and without discrete session markers. We expected either many anticipatory errors if chickadees tracked the temporal regularity of reversals as previously shown in other species, or near-optimal reversal of discrimination if having multiple reversals overshadowed use of interval time (as seen with pigeons in McMillan et al. 2015).

Previous studies using time-place learning tasks have often compared responding using circadian timers as well as interval or ordinal timers (for review, see Crystal 2009). In Experiment 2 we studied time-cued reversals in a within-day reversal task with chickadees. We sought to examine whether chickadees would anticipate a contingency reversal that occurred regularly at a particular time of day, rather than being based on trial number or criterion. While previous studies have examined the precision of circadian timers, these typically involve measuring responses that have no explicit cost (as opposed to the loss of food and/or timeouts that occur with anticipatory responding in the midsession reversal procedure), and thus we predicted this might be a useful procedure for studying timing across a day.

Experiment 1

Based on the failure by chickadees in a pilot experiment to discriminate between stimuli with contingency reversals every 40 trials (as typically used with pigeons; see McMillan et al. under review), we trained chickadees with two auditory stimuli with 240-trial continual ‘sessions’ (i.e., repeatedly cycling 120 trials with a 2 kHz tone as the S+ and 120 trials with a 4 kHz tone as the S+). In contrast with similar procedures using pigeons or rats, chickadees were able to initiate trials throughout the day cycle; rather than ending after one session, completing 240 trials led to a five-min cued delay followed by a new session. Because we continued to find poor discrimination and reversal in our subjects on this procedure, we subsequently trained these birds on a more standard criterion-based reversal wherein contingencies were not reversed for each chickadee until it had reached an 80% discrimination ratio; after successfully passing this procedure by completing four reversals, the chickadees were placed back on the mid-block reversal procedure (as described below).

Method

Subjects. Four female black-capped chickadees were used. These subjects had previously been used in song and call discrimination experiments, but not in a midsession reversal task or with the current experimental stimuli. Chickadees at least 1 year of age (determined by examining the color and shape of their outer tail retrices; Pyle, 1997) were captured in Edmonton (North Saskatchewan River Valley, 53.53°N, 113.53°W; Mill Creek Ravine, 53.52°N, 113.47°W), Alberta, Canada between January 2013 and February 2014.

Throughout the experiment, chickadees were individually housed in operant chambers (see Apparatus below), maintained on a light:dark schedule that mimicked the natural cycle for Edmonton, Alberta, Canada for the experimental period (October 2014 through February 2015). Chickadees had free access to water and grit, and were given one superworm (*Zophobas morio*) twice per day as nutritional supplementation; the remainder of their daily food allowance was only available as a reward for correct responding during the operant discrimination task (Mazuri Small Bird Maintenance Diet; Mazuri, St. Louis, MO, U.S.A.). This research was conducted with the approval of the University of Alberta Animal Care and Use Committee for Biosciences, meeting the standards of the Canadian Council on Animal Care.

Apparatus. During the experiment, chickadees were housed in modified Jupiter Parakeet cages (30 × 40 × 40 cm, Rolf C. Hagen, Inc., Montreal, QC, Canada) inside a ventilated, sound-attenuating chamber illuminated by a 9W bulb. Each cage contained three perches, a water bottle, a cuttlebone, and a grit cup. An opening (11 × 16 cm) on the side of the cage gave each chickadee access to a motor-driven feeder. Infrared cells in the feeder and perch nearest the feeder (‘request perch’) monitored the position of the subject. A personal computer connected to an Experiment Controller board (Payla and Walter, 2001) scheduled trials and recorded responses to stimuli. Stimuli were played from the personal computer hard drive, through an integrated amplifier, to a Fostex FE108Σ full-range speaker (Fostex Corp., Japan; frequency response range 80-18000 Hz) located beside the feeder. See Sturdy and Weisman (2006) for detailed description of the apparatus.

Stimuli. Stimuli were presented at approximately 75 dB as measured by a Brüel & Kjær Type 2239 (Brüel & Kjær Sound & Vibration Measurement A/S, Nærum, Denmark) decibel meter (‘A’ weighting, slow response) at the approximate height and position of a chickadee's head when on the request perch. The experimental stimuli were 2 kHz and 4 kHz pure sine wave tones, created as .WAV files using standard 16-bit, 44.1 kHz sampling rates with 5-ms ramped onset and offset in GoldWave (v. 6.10, GoldWave Inc., St. John’s, Canada).

Procedure. Trials were run continuously throughout each day’s light period. Onset of night cycle interrupted any part of a trial except stimulus presentation, and onset of light cycle began with the same trial that had been interrupted.

Pretraining. The purpose of pretraining was to ensure that chickadees responded equivalently to both experimental stimuli before discrimination training. A trial began when the chickadee landed and remained on the request perch for 900-1100 ms, which triggered either a 2 kHz or 4 kHz tone (pseudorandomly selected in blocks of four) to be played through the speaker for 1 s. If the chickadee left the request perch before a stimulus finished playing, the house light turned off for 15 s and the trial was recorded as ‘interrupted’. If the chickadee entered the feeder within 1 s after the entire stimulus played, the feeder raised for 1 s (allowing access to food), followed by a 15-s lit ITI. Leaving the request perch without entering the feeder after the entire stimulus played led to a 5-s lit ITI before the request perch would register another visit. If a chickadee did not leave the perch following presentation of the stimulus, another stimulus would not play until 60 s had passed or the chickadee left and returned to the perch, whichever occurred first. Interrupted trials, as well as trials on which birds remained on the perch, were not counted among responses for the purposes of calculating discrimination. Chickadees remained on pretraining until they completed six 90-trial blocks of at least 60% mean responding to both stimuli and at least four blocks with no more than 3% mean difference in responding between the two stimuli. After meeting these criteria, chickadees were given one day of free feed (a cup of Mazuri placed in the cage), and returned to pretraining until they again met each criterion at least once.

Mid-block Reversal. Mid-block reversal was identical to pretraining, except that only responses to one of the stimuli (2 kHz or 4 kHz tone) were reinforced at any given time; the two stimuli were again pseudorandomly selected in blocks of four. For two chickadees, responses to the 2 kHz tone were reinforced for the first 120 trials of a block (S1+), and responses to the 4 kHz tone were reinforced for the latter 120 trials of a block (S2+); these contingencies were reversed for the other two chickadees. Responses to either stimulus while it functioned as an S- resulted in a 15-s darkened ITI. After completion of each block of 240 trials, a red cue light adjacent to the feeder was lit for 5 min. During this interval, no responses were recorded and the chickadee was not able to trigger stimuli or obtain food. Chickadees were maintained on mid-block reversal for at least 65 trial blocks (15,600 trials) before moving on to the next phase.

Criterion Reversal. Criterion reversal was identical to the previous phase except that contingencies did not reverse based on number of trials. For two chickadees, responses only to the 2 kHz tone were reinforced, while only responses to 4 kHz tones were reinforced for the remaining two subjects. These contingencies reversed only after a subject met a criterion of at least two consecutive 90-trial blocks at 80% discrimination ratio, determined as the number of reinforced responses divided by the total number of responses. Contingencies reversed each time this criterion was met, but no more than twice per day, as reversals were initiated by experimenters following data inspection. After a total of four such reversals, chickadees were moved back to the mid-block reversal procedure for at least 20 trial blocks (4,800 trials) before exiting the experiment.

Analysis. Only the latter half of each subject's initial mid-block reversal data were analyzed, to remove early learning effects from the data. All data from criterion reversal and subsequent mid-block reversals were included.

Results and Discussion

Figure 1 illustrates average performance on mid-block reversal in chickadees in Experiment 1, with individual data presented in Supplementary Figure A. It is clear from these data that chickadees exhibited no meaningful discrimination between S1 and S2 in this reversal procedure, much less any differential responding indicative of reversal or anticipation.

Figure 2 illustrates each subject's criterion reversal performance. Chickadees learned to discriminate and reverse across blocks of trials, although performance varied considerably across subjects. Subjects took between 48 and 222 90-trial blocks to complete four reversals. Subject G-517 took the longest to learn the initial discrimination to criterion (130 blocks), with frequent responses to the S-. G-518 was the only subject to respond to the S+ less than 75% of the time overall, which contributed to noisy discrimination ratios, but nonetheless completed all four reversal criteria within 207 blocks, and also showed relatively few S- responses immediately after contingency reversals. O-132 was the only subject to respond more to the S- than to the S+ after the first reversal, but passed final criteria within 125 blocks. O-107 showed the best reversal performance of the present subjects, taking the fewest number of trials to learn the initial discrimination and showing little decrease in performance immediately after reversals, including the first reversal. It is possible that O-107 and G-518 showed some transfer of prior experience with reversals, even though the chickadees had not shown appreciable discrimination or reversal during midsession training. All four subjects took fewer trial blocks to reach criterion in blocks subsequent to the first two reversals. Though our data were not collected as to permit trial-by-trial analysis of improvement in reversal learning, chickadees were generally capable of discrimination and reversal of learned discriminations with this particular task configuration.

Data for follow-up mid-block reversals in the present subjects is shown in Supplementary Figure B. In brief, these data show little evidence for discrimination between S1 and S2 at any time during each trial block for any subject, including those that had previously been successfully trained with criterion reversal (e.g., O-107, which had previously reversed its behavior within 90 trials on criterion reversal). During criterion reversal, contingency reversals could not occur more than twice per day; the mid-block reversal procedure included many more reversals across the day, and under those conditions chickadees responded nondifferentially (consistent with pilot data). Lack of discrimination was endemic with mid-block reversals, even when chickadees were otherwise able to discriminate between stimuli and reverse their behavior on a similar task.

Experiment 2

Chickadees' failure to learn a mid-block reversal task is difficult to resolve against previous data. The main difference between our procedure with chickadees and that used previously with pigeons and rats is in the temporal structure of a session. Pigeons and rats in previous midsession reversal research have been limited to single daily sessions of between 20 and 240 trials each: session durations rarely exceed several minutes and are remarkably consistent within-subjects, making timing the typical duration between the onset of the session and the reversal straightforward. By contrast, chickadees' trial blocks were marked by inconsistent time between trials and only one cue to distinguish different 'sessions'. It was likely very difficult for chickadees to learn any particular timing rules, in contrast to the very specific rules that pigeons have been suggested to learn (e.g., "only respond to S2 after three min": McMillan et al. 2015).

In Experiment 2, we trained a new set of chickadees with a similar task to that presented in Experiment 1, except that reversals occurred at the same time each day (13:30), roughly representing the midpoint of the day for the time of year at the beginning of the study. This procedure establishes a degree of temporal regularity while providing longer training/discrimination schedules akin to criterion reversal. As chickadees in Experiment 1 were able to learn to reverse within a single day, we expected that the present subjects should be able to learn to discriminate and reverse on this task; further, we expected that they would come to anticipate the arrival of the change and to reverse their behavior before the contingency switch.

Method

Subjects and Apparatus. Seven male black-capped chickadee subjects were used in Experiment 2; these subjects had equivalent experience to those subjects used in Experiment 1. All aspects of husbandry and apparatus were identical to Experiment 1.

Procedure. Chickadees were pre-trained as described in Experiment 1. The reversal procedure was identical to pretraining, except that only responses to one of the stimuli (2 kHz or 4 kHz tone) were reinforced at any given time; the two stimuli were again pseudorandomly selected in blocks of four. For four chickadees, responses to the 2 kHz tone were reinforced from 09:00 to 13:30 (S1+), and responses to the 4 kHz tone were reinforced for the remainder of the day (S2+); these contingencies were reversed for the other three chickadees. Responses to either stimulus while it functioned as an S- resulted in a 15-s darkened ITI. During this interval, no responses were recorded and the chickadee was not able to trigger stimuli or obtain food. Chickadees were maintained on within-day reversal for 30 days. One chickadee was removed from the chamber early in reversal training due to low feeding and was excluded from further analyses.

Analysis. We used the last 15 days completed by each individual chickadee in analyses as a broad reflection of their asymptotic reversal performance.

Results and Discussion

Figure 3 illustrates discrimination ratios (DRs) by all six chickadees in first-portion (S1+, S2-) and last-portion (S1-, S2+) blocks of the day. Chickadees generally showed poorer discrimination during the morning block than after 13:30. Discrimination was significantly above chance after 13:30, $t(5) = 8.28$, $P < .001$, $d = 3.38$; contrarily, discrimination before 13:30 did not significantly exceed chance performance, $t(5) = 0.12$, $P = .12$, $d = 0.76$. These discrimination ratios also significantly differed from each other, $t(5) = 4.49$, $P = .006$, $d = 1.83$. As in Experiment 1, chickadees produced above-chance discrimination performance with reversals that occurred no more than once per day; however, this performance was asymmetrical on average, and only reliable during S2+. It is not clear whether this difference in performance was driven by a bias against S1 or impaired performance during the morning; it should be noted that the time duration of S2+ by the phase of the experiment analyzed here was longer than the S1+ phase (as light off times, but not light on times, were manipulated to keep pace with outside daylight hours, to a maximum sunset time of 19:48), which likely played a role. It may be that chickadees required greater than 4.5 hours' worth of trials to learn to consistently reverse their behavior on this tasks.

Figure 4 illustrates discrimination performance averaged across all six chickadees in the 20 trials before and after each reversal. Though discrimination was relatively poor across this period, there is an observable difference in 'go' responses to each stimulus across time: the negative correlation in responding to S1 relative to S2 over trials was significant, $r(41) = -0.32$, $P = .043$. The present data are too noisy to determine exactly whether the subjects anticipated the reversal, but there is no quantitative nor qualitative evidence that chickadees anticipated the contingency switch. This data does provide evidence that at least the chickadees were capable of adjusting their behavior to both stimuli on the scale of a few dozen trials, and not just over the course of the entire day.

General Discussion

In the present experiments, chickadees showed poor flexibility of behavior with rapid reversals, and no anticipation of a reversal regardless of condition. Chickadees did not learn to alter their behavior at all with multiple short-term reversals per day, even though both chickadees and pigeons have otherwise been shown to produce good discrimination performance on similar go/no-go reversal tasks (see Experiment 2 and criterion reversal in Experiment 1, and McMillan et al. 2015, respectively). This finding follows logically from previous results suggesting that whatever rules are learned about S1 and S2 are independent and rudimentary (McMillan et al. 2015); whatever processes underlie reversal of behavior do not appear to be flexible enough to combine temporal reward information that conflicts across sessions (McMillan et al. 2016), or in the present case over long or unpredictable periods of time.

As an exploratory study, Experiment 1 features several limitations that future studies may be designed to address. One problem for interpreting the current results is that trial blocks were frequently broken by long ‘breaks’ where either the chickadee did not land on the request perch or (perhaps more problematically) were interrupted by the duration of the night cycle. Chickadee performance did not improve when blocks containing extremely long ITIs were removed from the data; nonetheless, the presence of these blocks may have prompted chickadees to avoid using time to guide behavior. We expected that difficulties with using interval time do not stem only from the durations used (rats have been shown to time intervals in excess of 20 hours: Crystal 2006), but rather from the lack of cyclic regularity from one interval to the next. However, Experiment 2 demonstrated that even circadian regularity of the reversal was not able to produce anticipation in chickadees. As well, we have gathered data on pigeon choice (McMillan et al. under review) and go/no go performance with randomized S1+s across sessions; qualitative similarities of the current data with pigeon performance data illustrate that regular ITIs are not sufficient for producing accurate discrimination and reversal in this task.

Another limitation of the current results was first noted by McMillan and colleagues (2015) in that the use of timeouts for incorrect responses has indeterminate punishing value. While timeouts were introduced in order to account for the lack of penalty for an incorrect choice (relative to concurrent choice procedures, where an incorrect choice is penalized by missing a chance at food), the failure by subjects to inhibit currently-incorrect responses may at least partially reflect a lack of punishment by timeouts. Additionally, where previous studies with chickadees have tended toward longer, 30-s timeouts, here we used 15-s timeouts in order to decrease the interval effects of timeouts as well as to maintain similarity with pigeon studies. However, all four chickadees in Experiment 1 were able to learn a criterion-reversal discrimination with identical reinforcement and timeout properties, and we have previously shown evidence of good discrimination by pigeons on a similar procedure (McMillan et al. 2015). Future studies may directly disentangle the punishing value of timeouts of different durations and qualities, but we argue on the broad basis of our results that our current data reflect poor discrimination based on the temporal properties of sessions.

The present work represents only a first step in studying the implementation of large-scale daily foraging models with reversal, and leaves a number of open questions for obtaining better performance from animals. For example, unlike standard time-place learning tests, our chambers only have one location at which chickadees could obtain food; better performance might be obtained if chickadees could make explicit time-place relationships for S1 and S2, for example if the task were presented as a simultaneous spatial discrimination. We used arbitrary tones rather than more naturalistic stimuli commonly used with this species (e.g., conspecific calls and songs); though this was in keeping with pigeon stimulus presentations (which are simple visual stimuli), it is possible that naturalistic stimuli would be better attended to by chickadees. Finally, our within-day reversal in Experiment 2 was time-locked to 13:30 despite shifts in lights-off times; our intention here was to maintain the interval from lights-on to a specific duration, though this may have hampered use of circadian timing. Future studies may easily modify the current procedure to study circadian timing in a different manner than other common tasks (i.e., providing large 'meals' at a particular time of day and monitoring feeder visits), which would be fruitful in studying both behavioral flexibility and circadian timing.

Conventional wisdom in midsession reversal studies suggests that animals are hamstrung by their tendency to time the reversal of their behavior: that their timing-based anticipatory and perseverative errors represent suboptimal performance compared to a local reinforcement approach of responding based on the previous trial's outcome. Importantly, it has been noted that pigeons appear to maintain both time and local reinforcement information (e.g., McMillan and Roberts 2012; Rayburn-Reeves et al. 2011) and patterns of errors are representative of how they strike a compromise between the two systems (e.g., McMillan and Roberts 2015). However, in the present and other recent studies it has been shown that animals perform poorly when they are unable to use timing to guide their decisions, even though one might have expected performance to improve when only local reinforcement rates could be used. Though timing-based errors have previously been blamed on failures to inhibit intrusions from the timing system (McMillan et al. 2015), the present results and other recent data (McMillan et al., under review) demonstrate that animals make far more errors if they cannot make precise use of time to predict within-session reversals. For example, successive go/no-go performance in two separate experiments with pigeons is illustrated in Figure 5; the only difference between the studies was that McMillan and colleagues (2015) trained pigeons with the same first-correct stimulus every session, while results presented in a recent review (McMillan et al., under review) were obtained from pigeons trained with S1s that alternated each session. Pigeons with alternating S1s showed much poorer discrimination than those with fixed S1s, and only one of four birds showed any differential performance between stimuli across the session. The use of time to track contingencies in regular reversals seems to be critically tied to forming straightforward temporal 'rules', which appears impossible with reversals that shift in time or order (McMillan et al., 2016).

Our results starkly demonstrate that chickadees cannot learn a simple reversal that occurs at frequent intervals, even in cases where the same birds demonstrate good discrimination and reversal on criterion-based tasks with the same stimuli. Chickadees showed a limited ability to discriminate and reverse behavior with within-day contingency changes, suggesting that this procedure might be useful for studying full-day foraging behavior. However, the general difficulty exhibited by chickadees for learning these superficially simple reversal procedures suggests possible species- or task-specific constraints for behavioral flexibility. This is consistent with other recent data suggesting that black-capped chickadees also struggle with shifting foraging strategies, illustrating inattention to the renewal/depletion schedules of foraging locations over time (Course et al. 2016). It is not clear whether difficulties with training chickadees to "follow reward" is best explained by cognitive deficit, evolutionary foraging history, lack of naturalistic transfer, or alternative explanations. However, this work is important for understanding how animals integrate temporal and reward-based information in order to survive the constant shifting of contingencies in ecologically relevant situations.

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Ethical Standard

This research was conducted with the approval of the University of Alberta Research Ethics Office, meeting the standards of the Canadian Council on Animal Care. Chickadees were captured under permits granted by the Canadian Wildlife Service, Alberta Environment and Parks, and City of Edmonton Partners in Parks.

Conflict of Interest

The authors declare they have no conflict of interest.

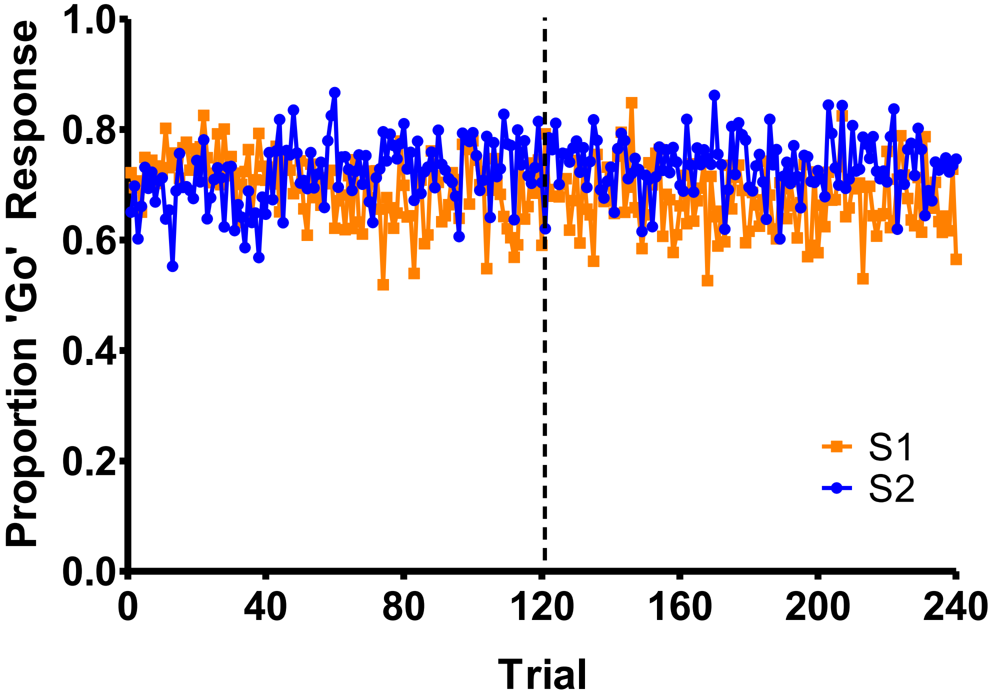

Figure 1. Go/no-go discrimination performance on a midsession reversal procedure in black-capped chickadees, averaged across four subjects. Vertical hatched line indicates contingency reversal after Trial 120.

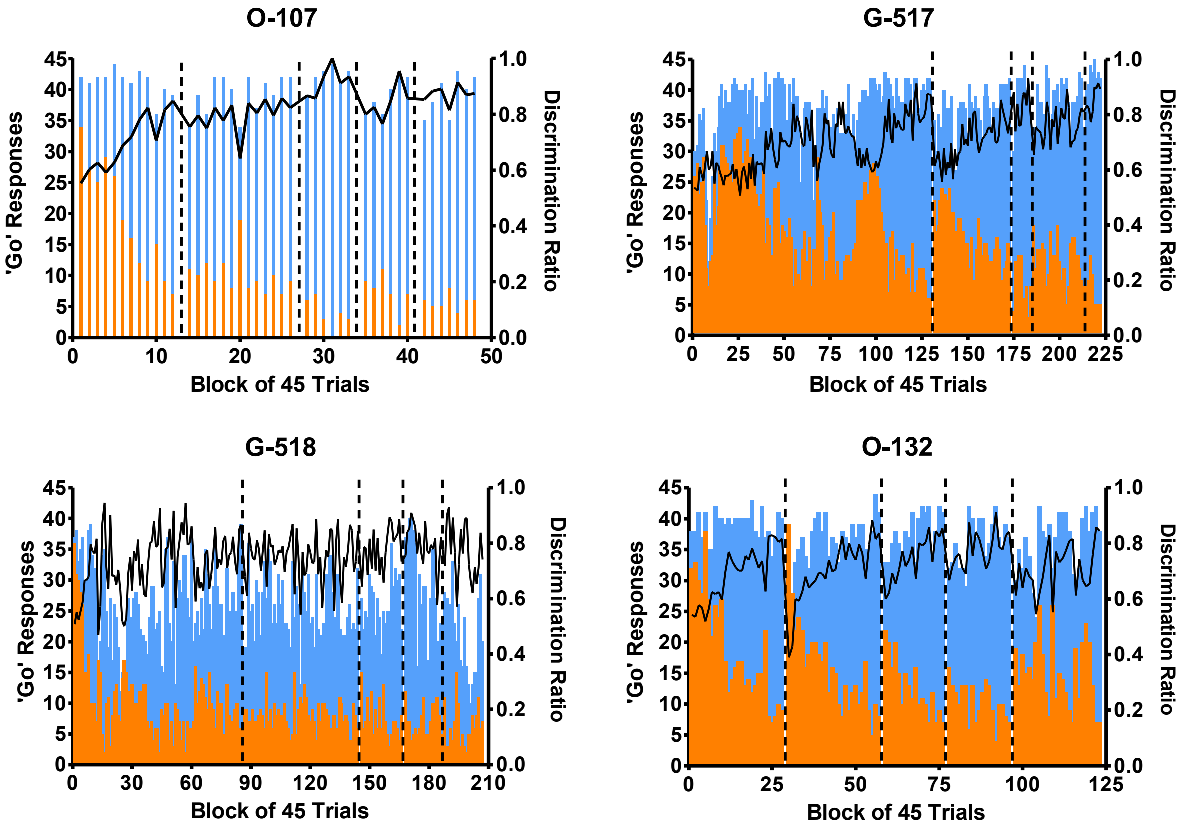

Figure 2. Go/no-go discrimination performance on a criterion reversal procedure in each of four black-capped chickadees. Blue bars indicate reinforced ‘go’ responses while orange bars indicate nonreinforced ‘go’ responses (left y-axes); black line graph illustrates discrimination ratio (i.e., reinforced ‘go’ responses divided by total ‘go’ responses; right y-axes). Vertical hatched lines indicate contingency reversals.

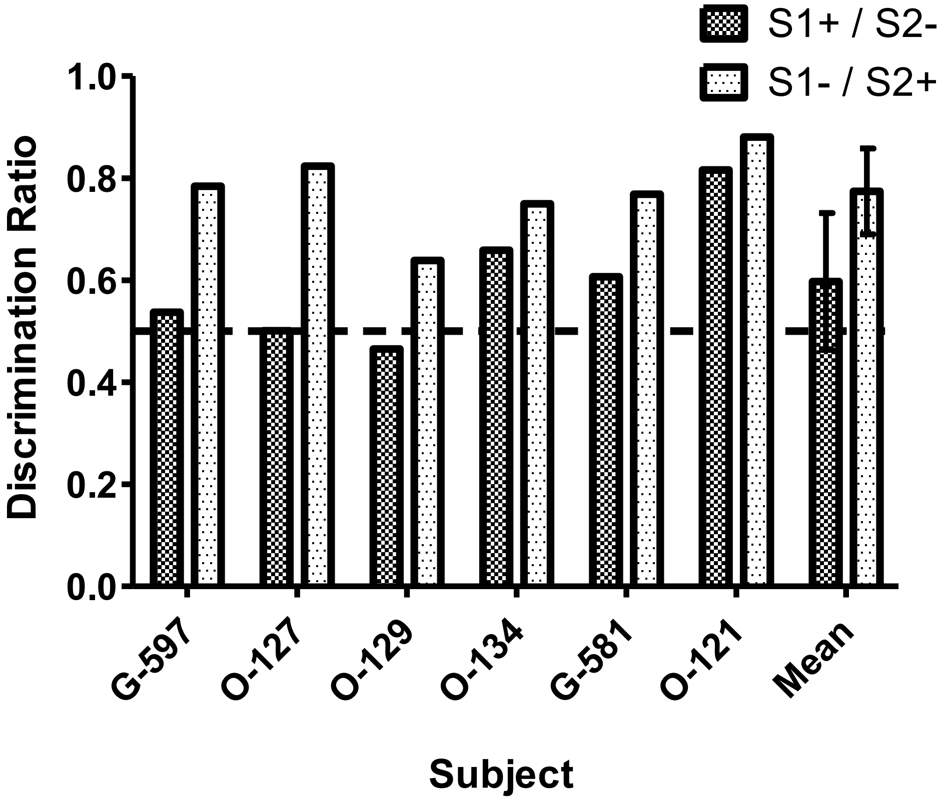

Figure 3. Go/no-go discrimination performance on a within-day reversal procedure in each of six black-capped chickadees, for each daily time period (i.e., before and after 13:30). Discrimination ratios are calculated as total 'go' responses to the rewarded stimulus divided by all 'go' responses. Mean is averaged between-subjects; error bars are 95% CIs calculated between-subjects. Horizontal hatched line indicates chance performance.

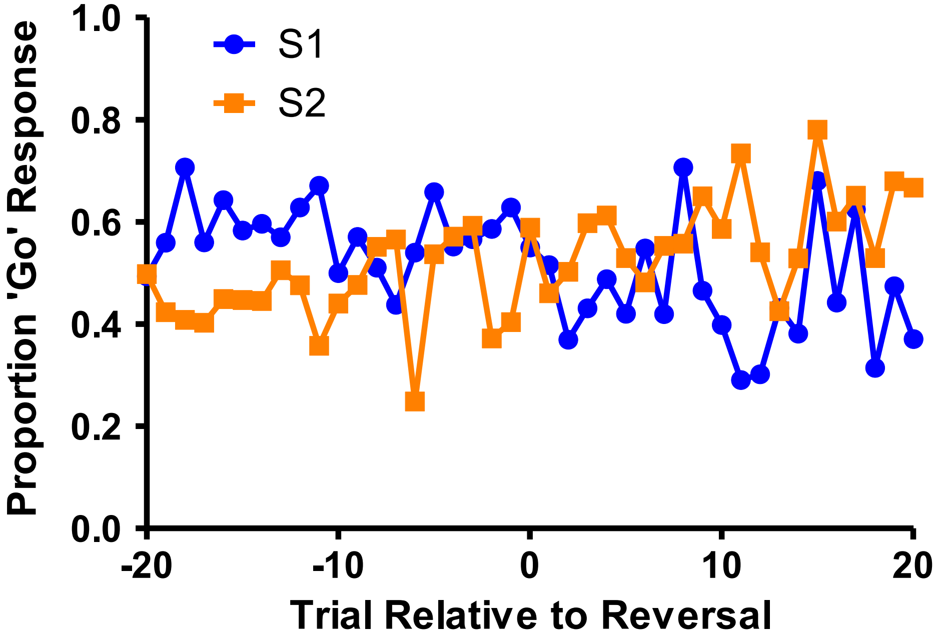

Figure 4. Discrimination performance on the last 20 trials previous to, and 20 trials immediately following, a within-day reversal averaged across six black-capped chickadees. Performance is calculated as proportion of 'go' responses over total number of trials with each stimulus at each trial location relative to reversal.

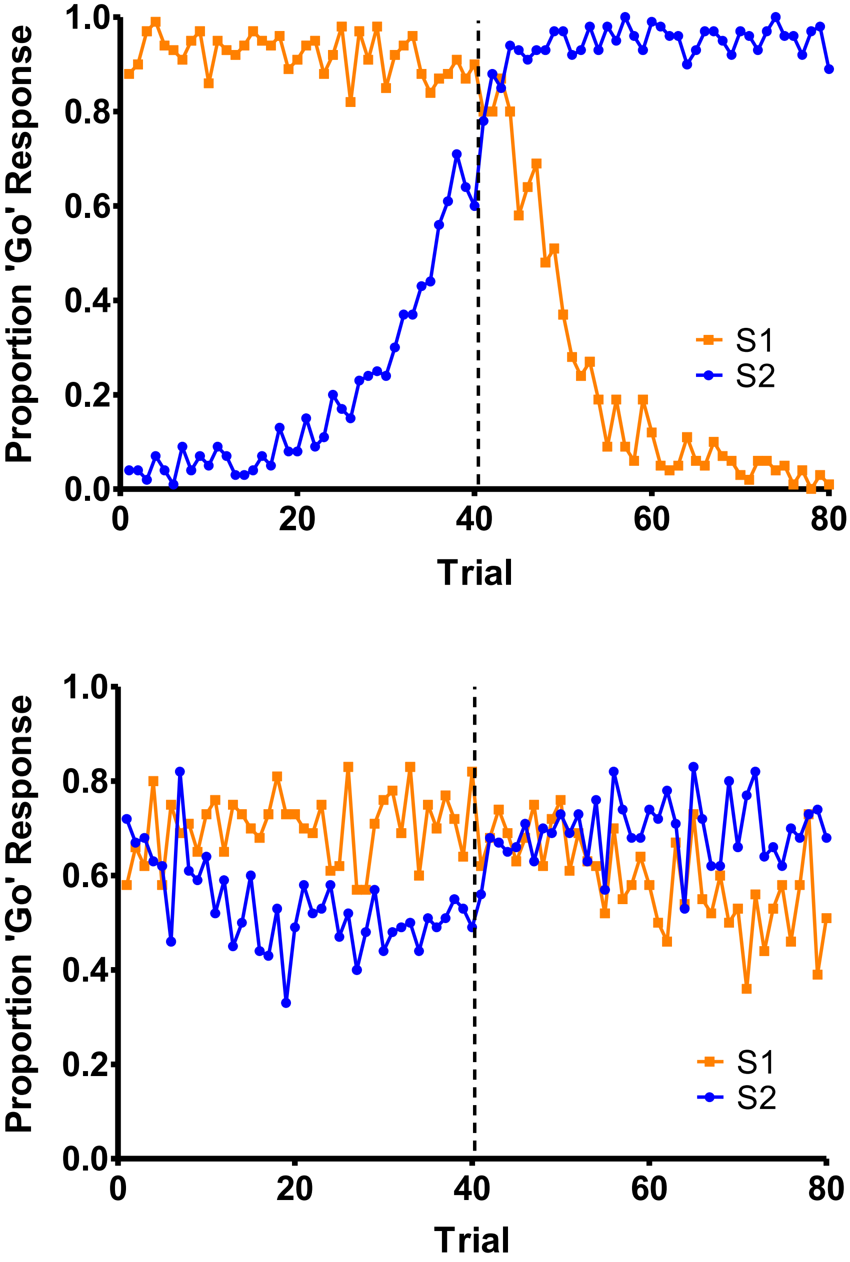

Figure 5. Experiment 1: Comparison of 'go' responses to S1 and S2, averaged across the last 25 sessions of training, at 80 trials per session, in (A; upper panel) pigeons trained with fixed S1 and S2 contingencies across sessions (data from McMillan et al., 2015); and (B; lower panel) alternating S1 and S2 identities across sessions (data from McMillan et al., under review). Vertical hatched lines indicate contingency reversals after Trial 40. Averaged data used with permission.