

Pigeons Perform Poorly on a Midsession Reversal

Task without Rigid Temporal Regularity

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Author Note

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

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1 Abstract

2 Animals make surprising anticipatory and perseverative errors when faced with a midsession
3 reversal of reinforcer contingencies on a choice task with highly predictable stimulus-time
4 relationships. In the current study, we asked whether pigeons could learn to anticipate changes in
5 reinforcement when the reinforcer contingencies for each stimulus were not fixed in time. We
6 compared the responses of pigeons on a simultaneous choice task when the initially correct
7 stimulus was randomized or alternated across sessions. Pigeons showed more errors overall
8 compared to the typical results of a standard midsession reversal procedure and they did not
9 show the typical anticipatory errors prior to the contingency reversal. Probe tests that
10 manipulated the spacing between trials also suggested that timing of the session exerted little
11 control of pigeons' behavior. The temporal structure of the experimental session thus appears to
12 be an important determinant for animals' use of time in midsession reversal procedures.

13 *Keywords:* reversal learning, interval timing, choice, pigeons

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16 Performance on the *midsession reversal* procedure has been extensively studied in the
17 last several years. Generally in this procedure, animals are presented with two options, one of
18 which is correct for the first half of the session (S1+) and the other of which is correct for the
19 second half of the session (S2+). Pigeons make surprising “anticipation” errors by switching
20 from responding on S1 to S2 before the reversal occurs. These errors appear largely controlled
21 by elapsed time; that is, pigeons determine that the reversal occurs roughly three minutes into the
22 session (for example), based on this interval estimation (Cook and Rosen 2010; McMillan and
23 Roberts 2012). Recently, McMillan and colleagues (2015) found that pigeons trained on a
24 simultaneous choice task with multiple reversals per session showed substantially fewer errors
25 than they had previously shown on such a task with only one reversal per session. One of the
26 main procedural differences of this multiple-reversal procedure compared to typical 80-trial,
27 single-reversal tasks is that interval time became a less reliable discriminative stimulus: having
28 multiple reversals likely made the temporal location of each reversal after the first more difficult
29 to determine.

30 Previous studies have used highly regimented sessions to study midsession reversal;
31 pigeons normally respond as quickly as possible, and ITIs are usually fixed, so session durations
32 are extremely stable within- and between-subjects. In the present set of experiments, we were
33 interested in whether pigeons would show anticipation of reversals that had less explicit temporal
34 structure than in previous work. We trained two sets of pigeons with a simultaneous choice
35 midsession reversal task with either an alternating or a randomized S1+. Additionally, in the
36 group with a randomized S1+ procedure, we used probe sessions (similar to those used by

37 McMillan and Roberts 2012) to examine whether the pigeons were sensitive to the time of the
38 session; these probe sessions either decreased or increased ITI duration (thus altering the
39 duration of the session, without altering trial number or other procedural components), or
40 provided nondifferential reinforcement for all responses (in order to demonstrate whether
41 pigeons changed their responding independent of trial-by-trial feedback). We sought in this
42 experiment to determine whether pigeons were sensitive to time with randomized or alternating
43 stimuli as the first S+, and whether any change in temporal control would translate into
44 impoverished choice performance.

45 **Method**

46 **Subjects & Apparatus**

47 Eight adult pigeons were used and two sound-attenuating operant chambers were used, as
48 described by McMillan and colleagues (2015).

49 **Procedure**

50 On each trial for 80 trials per session, pigeons were presented with a blue-filled circle in
51 the center of a grey background on the touchscreen. Pecking this stimulus began the trial, leading
52 immediately to the presentation of both a green- and red-filled circle, each on either the left or
53 right side of the screen (with presentations of left vs. right randomized in blocks of four trials
54 across the session). Pecks from the first 1-s of stimulus presentation were disregarded in order to
55 minimize incidental responding before the stimulus could reasonably be processed (e.g., wing
56 touches) and for consistency with prior experiments. Both stimuli were presented until the
57 pigeon made a choice response. Pecking the green or red circle led to the immediate removal of
58 both stimuli: pecking the currently-rewarded stimulus (determined by trial number and Group
59 assignment; see below) was subsequently reinforced with 1-s access to food (measured from the

60 time that the pigeon first tripped the photobeam in the hopper); if the pigeon pecked the stimulus
61 currently not rewarded, the screen was blackened for a 10-s timeout. Either result was followed
62 by a 3-s ITI, with the screen background lit grey, subsequently followed by a new trial.

63 Experiment trials continued until a response was made to one of the stimuli.

64 Pigeons were assigned to two groups: Group Alternating and Group Randomized. For
65 Group Alternating (four subjects), on odd-numbered sessions, a peck to the red circle was correct
66 for the first 40 trials, and a peck to the green circle was correct for the latter 40 trials; these
67 contingencies were reversed for even-numbered sessions. For Group Randomized, the identities
68 of S1+ and S2+ were pseudorandomly determined across sessions (distributed equally in blocks
69 of four). Group Randomized also had 50 sessions of Probe Testing after completing 50 sessions
70 of baseline.

71 During Probe Testing, all procedural details were identical to those during baseline,
72 except that every fourth session was replaced with one of three types of probe sessions
73 (determined pseudorandomly in blocks of three): 1-s ITI, 5-s ITI, and Nondifferential
74 Reinforcement. For each of the 1-s ITI and 5-s ITI probe sessions, the ITI between trials was
75 either decreased from 3-s to 1-s or increased to 5-s (respectively); this had the effect of
76 artificially increasing session duration without affecting the trial or reinforcer number prior to
77 reversal (see McMillan & Roberts, 2012). On Nondifferential Reinforcement probe sessions,
78 responses to either stimulus were always reinforced.

79 **Analysis**

80 Only the last 20 sessions of each subject's data were analyzed, to remove early learning
81 effects.

82 **Results**

83 Pigeons' average midsession reversal performance over the last 20 sessions is illustrated
84 in Figure 1. The difference in the present groups from previous data (see Figure 1c) with fixed
85 S1+s is obvious and striking. Further, there appeared to be little difference between alternating
86 and randomized S1 groups, even though the alternating group could have used the previous day's
87 contingencies to inform its choice each day. In the first trial of each session, the randomized and
88 alternating groups' responding were not significantly different from each other, $t(4) = 0.38$, $p =$
89 $.72$, $d = 0.28$. Pigeons started each session responding to both stimuli nondifferentially, with
90 monotonic increases in responding to S1+, relatively few anticipatory responses to S2
91 immediately prior to reversal, and slow behavior reversal during the S2+ phase. These effects
92 made a large impact on pigeons' access to food: where previous data with fixed S1+s has shown
93 average 80-trial accuracy above 90% (e.g., 93.5% in Experiment 3 of McMillan et al. 2015), here
94 pigeons had much lower overall performance with randomized (77%) and alternating (70%)
95 S1+s. Pigeons' patterns of responding suggest they did not respond predominantly on the basis
96 of time, and that their performance suffered as a result.

97 Pigeons' average midsession reversal performance on probe testing sessions is presented
98 in Figure 2. We predicted that stimulus control by session time would lead pigeons to produce
99 more anticipatory errors on 1-s ITI probes compared to 5-s ITI probes; in contrast, there was
100 little appreciable difference between these two session types. A 2×10 (Probe Type [1-s ITI, 5-s
101 ITI] \times Trial [37-46]) repeated-measures ANOVA found only a significant main effect of Trial
102 [$F(9, 27)$, $p = .007$, $\eta_p^2 = 0.53$]; neither the interaction with nor the main effect of Probe Type
103 were significant, $F_s < 5.07$, $p_s > .10$. While it is possible, noting the slight separation in data, that
104 5-s ITI probes led to slightly more anticipatory responding than did 1-s ITI probes, this was in

105 the opposite of the predicted direction for time-based responding, and generally manipulating the
106 session time did not strongly affect pigeons' reversal behavior in this task.

107 Figure 2c illustrates individual pigeons' average responding on Nondifferential probe
108 trials. Since there was no functional difference between S1 and S2 in these probes, the
109 assignment of S1 was designated as the stimulus that each pigeon responded to most in the first
110 half of the session. Pigeons appeared to reverse their initial preferences (either for red or for
111 green) between the two halves of the session, $t(3) = 6.80$, $p = .006$, $d = 3.06$, though it is unclear
112 on what they based initial preferences. This provides potential evidence that pigeons learn a
113 rough estimate of the duration of sessions and the general reversal of contingencies that occurred
114 after a predictable amount of time.

115 Discussion

116 Whereas previous research has found that animals reliably anticipate predictable
117 contingency reversals, in the present experiment pigeons showed no reliable anticipation
118 immediately before reversals. Pigeons also appeared to show little memory for the end of the
119 previous session (or little effect of memory on behavior); pigeons took up to 20 trials to learn the
120 identity of S1 on each session, even in cases where S1 was predictable as the S2 from the
121 preceding session (i.e., for Group Alternating). Pigeons' lack of timing-based errors on ITI probe
122 trials suggests that time failed to control behavior. The key feature differentiating the present
123 study from previous research was the absence of fixed time-contingency relationships (e.g., "red
124 is always correct for the first five minutes") allowing for easy prediction of which stimulus
125 provided reinforcement at which time. Simply changing the order of the reinforced stimuli across
126 sessions resulted in pigeons showing qualitatively different responding compared to midsession
127 reversal tasks using fixed S1+s and S2+s. This is consistent with recent work suggesting that

128 pigeons respond in midsession reversal tasks by binding time to item-specific rules (Daniel et al.
129 2015), and further that animals may *only* rely on time in midsession reversal tasks when it can be
130 tied to explicit temporal rules, such as “respond to red for the first five minutes” (see McMillan
131 et al. 2015).

132 The current results are partially consistent with previous suggestions that animals do not
133 learn general reversal learning sets (Mackintosh et al. 1968). Rather than learning a general rule
134 such as “reverse behavior after a set period of time”, animals in midsession reversal tasks may
135 predominately learn specific patterns of behavior, such as “respond to red until it is no longer
136 reinforced, and respond to green after three minutes”. However, nondifferential reinforcement
137 did lead to time-delayed choice preference reversals, suggesting that pigeons may have learned a
138 time-based general rule that nonetheless did not strongly control responding on typical sessions.
139 This is consistent with previous suggestions that interval timing is a preattentive process that
140 nevertheless does not automatically exert stimulus control (e.g., see McMillan and Roberts
141 2012), and that both time and local reinforcement exhibit stimulus control to different degrees
142 based on the particulars of midsession reversal procedures (e.g., see McMillan et al. 2014).
143 Timing is a versatile and ubiquitous tool for animals; however, time is not an innate sensory
144 property of objects (i.e., it is not sensed as energy emanating from the environment), and highly
145 predictable intervals are likely rare in nature. It is thus probable that, while timing is broadly
146 evolutionarily conserved and an extremely useful system to have, its ecological usage from one
147 situation to another may be ambiguous, and it likely competes with other systems for control
148 over behavior.

149

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166 **Ethical Standard**

167 This research was conducted with the approval of the University of Alberta Research Ethics
168 Office, meeting the standards of the Canadian Council on Animal Care.

169

170 **Conflict of Interest**

171 The authors declare they have no conflict of interest.