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38	Abstract	<p>Response-sequence learning is often studied by manipulating consequences for sequence completion. Results of research evaluating how changes in discriminative stimuli disrupt the accuracy of response sequences suggest that transitions to reversed but highly predictive discriminative stimuli are more disruptive than the removal of discriminative stimuli. Two experiments assessed effects of changing discriminative stimuli on response-sequence accuracy while reinforcement remained contingent on a left-peck, right-peck response sequence. Initially, pigeons were trained on the response sequence in which the S+ key was illuminated red and the S- key was illuminated white. For all conditions of both experiments, the “accurate” response sequence that led to food was the same, but the way the accurate sequence was signaled sometimes differed. In Experiment 1, after training, discriminative stimuli were either removed (by lighting both keys white) or reversed. Accuracy was lower when discriminative stimuli were reversed than when they were removed. Experiment 2 showed that after training with discriminative stimuli, a history of reinforcement without discriminative stimuli was sufficient for the response sequence to emerge at high levels of accuracy when the discriminative stimuli were reversed. Results suggest a parsimonious explanation for why highly predictive discriminative stimuli sometimes fail to control behavior based on behavioral history.</p>
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39	Keywords separated by ' - '	Feature-positive effect - S-R compatibility - Motor skill learning - Stimulus control - Behavior chain - Pigeons
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40	Foot note information	Portions of these data were presented at the Southeastern Association for Behavior Analysis annual meeting in Columbia, SC in 2012.

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ORIGINAL ARTICLE

**Q1 4 Behavioral History and Pigeons' "Guiding Cues" Performance**

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**Abstract** Response-sequence learning is often studied by manipulating consequences for sequence completion. Results of research evaluating how changes in discriminative stimuli disrupt the accuracy of response sequences suggest that transitions to reversed but highly predictive discriminative stimuli are more disruptive than the removal of discriminative stimuli. Two experiments assessed effects of changing discriminative stimuli on response-sequence accuracy while reinforcement remained contingent on a left-peck, right-peck response sequence. Initially, pigeons were trained on the response sequence in which the S+ key was illuminated red and the S- key was illuminated white. For all conditions of both experiments, the "accurate" response sequence that led to food was the same, but the way the accurate sequence was signaled sometimes differed. In Experiment 1, after training, discriminative stimuli were either removed (by lighting both keys white) or reversed. Accuracy was lower when discriminative stimuli were reversed than when they were removed. Experiment 2 showed that after training with discriminative stimuli, a history of reinforcement without discriminative stimuli was sufficient for the response sequence to emerge at high levels of accuracy when the discriminative stimuli were reversed.

Results suggest a parsimonious explanation for why highly predictive discriminative stimuli sometimes fail to control behavior based on behavioral history. 33  
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**Keywords** Feature-positive effect · S-R compatibility · Motor skill learning · Stimulus control · Behavior chain · Pigeons 36  
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Traditionally, each response in a response sequence (i.e., a behavior chain) is thought to be jointly controlled: A discriminative stimulus sets the occasion for the response. A stimulus change reinforces the response and sets the occasion for the subsequent response in the sequence. Correctly executing the entire response sequence is reinforced after the terminal response. For example, a simple response sequence in a rodent operant chamber might be: left light illuminated (discriminative stimulus)→left lever press (response)→left light extinguished/right light illuminated (discriminative stimulus)→right lever press (response)→right light extinguished/food delivered (reinforcer). Behavioral researchers have long been interested in how consequences for responding (i.e., reinforcement) affect behavior in response sequences (e.g., Reed et al. 1991). An important research question that has not been addressed until recently is how learned response sequences are affected by changes to discriminative stimuli that were present during acquisition of the response sequence. 38  
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Researchers have begun to investigate how changing or removing the discriminative stimuli that "guide" the response sequence during acquisition affect skill maintenance (e.g., Reid et al. 2010). Changes in discriminative stimuli can be highly disruptive—even when new discriminative stimuli are highly predictive of reinforcement. In fact, changes to equally predictive discriminative stimuli can be more disruptive than removing discriminative stimuli altogether (Reid et al. 2013). If particular changes in the way consequences are signaled reduce the frequency with which the reinforced response 56  
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Portions of these data were presented at the Southeastern Association for Behavior Analysis annual meeting in Columbia, SC in 2012.

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Q2

66 sequence occurs, specifying those changes would help behav- 119  
67 ioral scientists develop methods for maintaining response- 120  
68 sequence accuracy at high levels in dynamic, unpredictable 121  
69 circumstances when discriminative stimuli may be changed or 122  
70 removed. Researchers might also begin to develop better 123  
71 theoretical accounts for why such disruptions occur, and most 124  
72 importantly, why some stimuli that are highly predictive of 125  
73 reinforcement don't control behavior. A better understanding 126  
74 of how changes to discriminative stimuli affect learning has 127  
75 far-reaching implications for teaching and maintaining motor 128  
76 skills in humans. The objectives of the two experiments that 129  
77 follow were to a) further test a theoretical explanation that has 130  
78 been used explain the disruptiveness of reversing discrimina- 131  
79 tive stimuli associated with an acquired response sequence 132  
80 (Experiment 1), and b) reduce the extent to which the reversal 133  
81 in discriminative stimuli disrupts response-sequence accuracy 134  
82 by manipulating behavioral histories with the discriminative 135  
83 stimuli in question (Experiment 1). 136

84 Previous response-sequence learning studies have focused 137  
85 on how reinforcement can organize behavior and create re- 138  
86 sponse units (e.g., Bachá-Méndez et al. 2007; Reed et al. 139  
87 1991; Schneider and Davison 2005; Schneider and Morris 140  
88 1992). Other research has investigated how choice and timing 141  
89 behavior adjust in dynamic environments when discriminative 142  
90 stimuli do not change, but the contingencies of reinforcement 143  
91 do (e.g., Kyonka and Grace 2007, 2008). In all of these 144  
92 general circumstances, behavior changes in ways that are 145  
93 highly adaptive for maximizing rate of reinforcement. 146

94 Researchers are becoming more interested in how changes 147  
95 in discriminative stimuli affect behavior when the reinforced 148  
96 response sequence remains unchanged. In several experi- 149  
97 ments, Reid and colleagues have evaluated how response 150  
98 sequences develop and are affected by changes in discrimina- 151  
99 tive stimuli. For example, Reid et al. (2001) found that if a 152  
100 tone was presented at the beginning and end of a response 153  
101 sequence, acquisition was faster than when the same response 154  
102 sequence was learned without the tones. 155

103 Reid et al. (2010) exposed a group of rats to a "Follow-the- 156  
104 Light" task. Under this procedure, left-right (L-R) lever-press 157  
105 response sequences were reinforced with food. The illumina- 158Q4/Q5  
106 tion of lights above each lever served as discriminative stimuli 159  
107 for each response. At the start of each trial the light above the 160  
108 left lever was lighted. The programmed consequence of a 161  
109 press to that lever was that the light was extinguished and 162  
110 the light above the right lever was lighted. If the rat then 163  
111 pressed the right lever, all lights were extinguished and food 164  
112 was delivered. Once all rats produced the L-R sequence on at 165  
113 least 80 % of trials (i.e., performed at above 80 % accuracy), 166  
114 they were split into two groups. The lights were eliminated for 167  
115 the "No-Lights" group. For the "Reversed-Lights" group the 168  
116 lights above the non-active lever in the sequence – right-left – 169  
117 were lit. For both groups, the L-R response-sequence contin- 170  
118 gency remained in place. 171

119 After five sessions in the No-Lights condition, response- 120  
121 sequence accuracy in the No-Lights group was approximately 122  
123 60 %—lower than at the end of the Follow-the-Light condi- 124  
125 tion, but still well above chance (25 %). However, after five 126  
127 sessions in the Reversed-Lights condition, response-sequence 128  
129 accuracy in the Reversed-Lights group was 5 % across sub- 130  
131 jects. Most of the response sequences during the Reversed- 132  
133 Lights condition were R-L, indicating responding was con- 134  
135 trolled by the discriminative properties of the lights. The 136  
137 authors concluded there was "stronger stimulus control by 138  
139 the 'misleading' lights and weaker control by the history of 140  
141 the subjects' own behavior" (p. 514–515). In other words, the 142  
143 authors suggested two potential sources of behavioral control: 144  
145 *environmental cues* (panel lights) and *practice cues*, which are 146  
147 the result of repeating the same sequence many times (Lattal 148  
149 1975; Shimp 1981, 1982). They explained the results in terms 150  
151 of an overshadowing effect—the panel lights overshadowed 152  
153 control by practice cues when the lights were reversed. 154  
155

156 Two theoretical accounts have been considered as expla- 157  
158 nations for why switching from 'Follow-the-Lights' to 'Re- 159  
160 versed-Lights' is particularly disruptive of response-sequence 161  
162 accuracy. The spatial S-R compatibility effect (Fitts and 163  
164 Seeger 1953; Hommel 1995, 2011; Kiernan et al. 2012; 165  
166 Proctor and Reeve 1990) holds that reaction times should be 167  
168 faster when the discriminative stimulus and the correct re- 169  
170 sponse are spatially compatible, or adjacent, because a reflex 171  
172 or a "spatial code" orients behavior toward the source of 173  
174 stimulation. The Simon Effect is a more complex version of 175  
176 S-R compatibility in which stimulus position is irrelevant 177  
178 (Simon 1969; Urcuioli et al. 2005). Applied to the two-lever 179  
180 response sequence in Reid et al.'s (2010, 2013) experiments, 181  
182 both versions of this theory predict response sequences will be 183  
184 more accurate and faster when the illuminated light is above 184  
185 the lever on which a response was required than when it is 185  
186 above the lever to be avoided. Therefore, it can adequately 186  
187 account for disruptions in response-sequence accuracy during 187  
188 transitions from Follow-the-Lights to Reversed-Lights. 188  
189

189 The other theoretical explanation that has been considered 190  
191 is feature-positive discrimination bias (Hearst 1991; Jenkins 191  
192 and Sainsbury 1969, 1970; Lotz et al. 2012; Nallan et al. 1984; 192  
193 Sainsbury 1973). It is a tendency for organisms to discriminate 193  
194 the presence or addition of a stimulus more readily than the 194  
195 absence or removal of a stimulus. A feature-positive arrange- 195  
196 ment is one in which the presence of a stimulus signals 196  
197 reinforcement and a feature-negative arrangement is one in 197  
198 which the absence of a stimulus signals reinforcement. In Reid 198  
199 et al.'s (2010, 2013) experiments, the Follow-the-Lights con- 199  
200 dition could be considered a feature-positive condition, while 200  
201 the Reversed-Lights condition could be considered a feature- 201  
202 negative condition. The theory follows that the presence of the 202  
203 feature-positive lights will prevent control by the other dis- 203  
204 criminative stimuli that are present, such as practice cues from 204  
205 repeating the same L-R sequence. The theory predicts that 205

172 responses will be biased toward the feature-positive lights and  
 173 can explain why response-sequence accuracy was below  
 174 chance in Reid et al.'s Reversed-Lights conditions.

175 Reid et al. (2013) considered the major strengths and  
 176 limitations of each of these potential explanations. They con-  
 177 cluded that both explanations could account for most of Reid  
 178 et al.'s (2010, 2013) simple binary transitions from one con-  
 179 dition to another, but neither could account for other aspects of  
 180 their data, especially in ABA procedures. One limitation of the  
 181 S-R compatibility explanation is that it cannot account, with-  
 182 out the addition of post-hoc assumptions, for Reid et al.'s  
 183 (2013, Experiment 3) contrary finding that illuminating both  
 184 lights produced slower and less responding (approximately  
 185 30 % fewer trials per session) than when neither light was  
 186 illuminated. Spatial S-R compatibility explicitly predicts  
 187 faster responding when the spatial locations of the stimulus  
 188 and response are in agreement, as they were when both lights  
 189 were illuminated.

190 **Experiment 1**

191 As mentioned, the feature-positive discrimination bias can  
 192 explain some of the previous response-sequence rat data  
 193 (Reid et al. 2010, 2013). By using pigeons as subjects and  
 194 illuminated keys as stimuli in Experiment 1, the feature-  
 195 negative conditions were eliminated and the adequacy of the  
 196 feature-positive bias explanation was further tested. If  
 197 response-sequence accuracy is similarly disrupted in an *all-*  
 198 *feature positive* reversed-cues condition as it was in Reid  
 199 et al.'s Reversed-Lights condition, then the feature-positive  
 200 discrimination bias theory cannot account for the disruption.

201 In Experiment 1, pigeons were exposed to a left-peck,  
 202 right-peck response sequence contingency and effects of  
 203 changes in discriminative stimuli were assessed. Specifically,  
 204 the experiment was designed to assess how experience with  
 205 stimuli formerly correlated with extinction (S- stimuli) might  
 206 affect behavior in the presence and absence of stimuli former-  
 207 ly correlated with reinforcement (S+ stimuli) when the under-  
 208 lying response sequence (left peck-right peck) necessary for  
 209 reinforcement remained unchanged. In Experiment 1, all S+  
 210 and S- stimuli in all conditions were positive features: lighted  
 211 response keys of differing colors.

Q6 212 **Method**

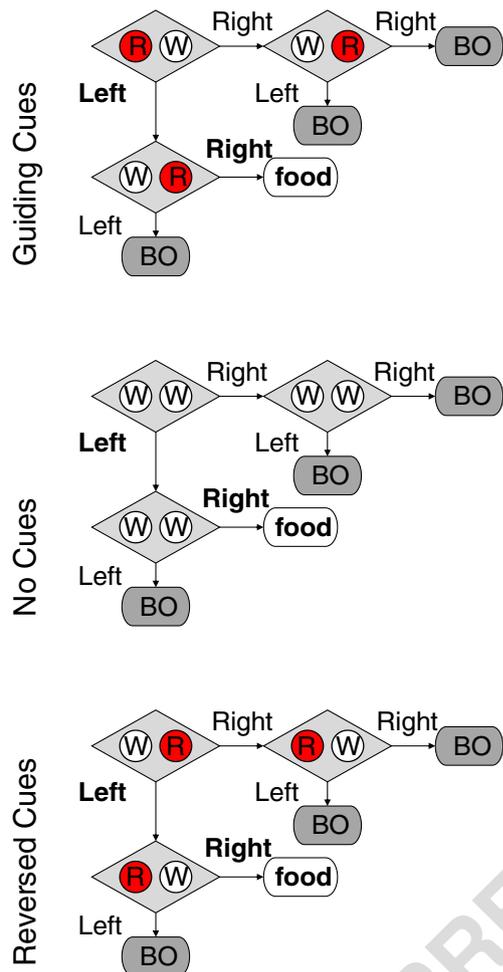
213 *Subjects* This research was approved by West Virginia  
 214 University's Animal Care and Use Committee. Four pigeons  
 215 numbered 301 to 304 maintained at 85 % of their free-feeding  
 216 body weight via appropriate post-session feedings served as  
 217 subjects for Experiment 1. Pigeons were housed individually  
 218 in a vivarium with a 12-hr light:dark cycle with continuous

free access to water and intermittent access to grit. All pigeons 219  
 had previous experience pecking keys for access to food in a 220  
 variety of schedules of reinforcement. 221

*Apparatus* Four standard operant chambers (25.5 cm deep X 222  
 32 cm wide X 33.5 cm high) enclosed in sound-attenuating 223  
 boxes equipped with ventilation fans were used. Each cham- 224  
 ber contained three response keys arranged 6 cm apart and 225  
 24 cm above the floor of the chamber. Response keys could be 226  
 lighted red, green, or white. A grain hopper (5.5 cm high X 227  
 6 cm wide) was located below the middle response key and 228  
 5.5 cm from the floor. A house light was located at the top of 229  
 the chamber on the wall opposite of the response keys. 230  
 The grain hopper aperture was lighted during reinforcer 231  
 presentation and the hopper contained mixed grain. A 232  
 force of approximately 0.15 N was required to register 233  
 a response on any key. All experimental events were 234  
 controlled through a computer and MED-PC<sup>®</sup> interface 235  
 located in an adjacent room. 236

*Procedure* Because all pigeons had previous experience 237  
 pecking lighted keys for food, training began immediately. 238  
 All sessions lasted for 72 trials or 60 min, whichever came 239  
 first. All four pigeons were first trained on a left key (L)-right 240  
 key (R) response sequence, in which red lights served as S+ 241  
 stimuli for two sessions. Pigeon 303 received eight additional 242  
 sessions of this training because of a failure to acquire the L-R 243  
 sequence at above 80 % accuracy. During the training period, 244  
 only the red lights were present on the active key in the L-R 245  
 sequence. A peck to the red left key extinguished it and lighted 246  
 the right key red. If the next peck was to the lighted right red 247  
 key, it resulted in access to food. However, if the next peck 248  
 was to the left key, it resulted in a 10-s blackout followed by 249  
 presentation of a new trial. 250

After training, all four pigeons were exposed to the 251  
 Guiding-Cues condition. Figure 1 is an event-sequence sche- 252  
 matic for the Guiding-Cues, Reversed-Cues, and No-Cues 253  
 conditions described below. At the start of a trial, the house 254  
 light was lighted, the left key was lighted red and the right key 255  
 was lighted white. If the first peck was to the right key, the 256  
 color of the right key was changed from white to red and the 257  
 color of the left key from red to white. The next peck on either 258  
 key resulted in a 10-s blackout during which all lights were 259  
 extinguished, followed by the start of the next trial. If the first 260  
 peck in a trial was on the left key, the color of the left key was 261  
 changed from red to white and the right key from white to red. 262  
 A second peck on the left key resulted in a 10-s blackout 263  
 during which all lights were extinguished, followed by the 264  
 start of the next trial. A peck on the right key following a peck 265  
 on the left key resulted in 3-s access to grain, during which all 266  
 the lights in the chamber were extinguished, and the grain 267  
 aperture was lighted. The subsequent trial followed immedi- 268  
 ately. There were four possible two-peck response sequences: 269



**Fig. 1** Event sequence for trials in Guiding-Cues, No-Cues and Reversed-Cues. Circles at each decision point show stimuli—either white (W) or red (R) lights—presented on the left and right keys in the operant chamber. “Left” and “Right” refer to keys pecked. The sequence that produced access to food (*in bold*) was always the same, but the relationship between color and correct key differed depending on condition. All other response sequences produced a 10-s blackout (BO)

270 L-R, R-L, L-L, R-R. Only the L-R sequence was reinforced  
271 with access to food.

272 Mastery of the L-R sequence in the presence of the guiding  
273 cues was defined as at least 80 % accuracy in each session for  
274 five consecutive sessions, with no increasing or decreasing  
275 trends in accuracy. Once mastery was reached in the Guiding-  
276 Cues condition, Pigeons 301 and 303 experienced the No-  
277 Cues condition for five sessions, and Pigeons 302 and 304  
278 experienced the Reversed-Cues condition for five sessions. In  
279 the No-Cues condition, the cues provided by the red lights  
280 were removed; both lights were lighted white throughout a  
281 trial. The L-R response requirement remained. In the  
282 Reversed-Cues condition, the arrangement of red and white  
283 lights was reversed but the response requirement remained the  
284 same. At the start of a trial, the left key was lighted white and  
285 the right key red. After the first peck to either key, the color of

the right key was changed from red to white and the color of  
the left key from white to red. For the No-Cues and Reversed-  
Cues conditions, the L-R peck sequence was reinforced with  
access to food and immediate presentation of the next trial. All  
other two-peck sequences produced a 10-s blackout. The only  
programmed difference was that in No-Cues, there were no  
discriminative stimuli to “follow” and in Reversed-Cues,  
pecks were required to “follow” the white key light instead  
of following the red key light to obtain reinforcement. Table 1  
shows the order of conditions and number of sessions per  
condition for each pigeon.

Results

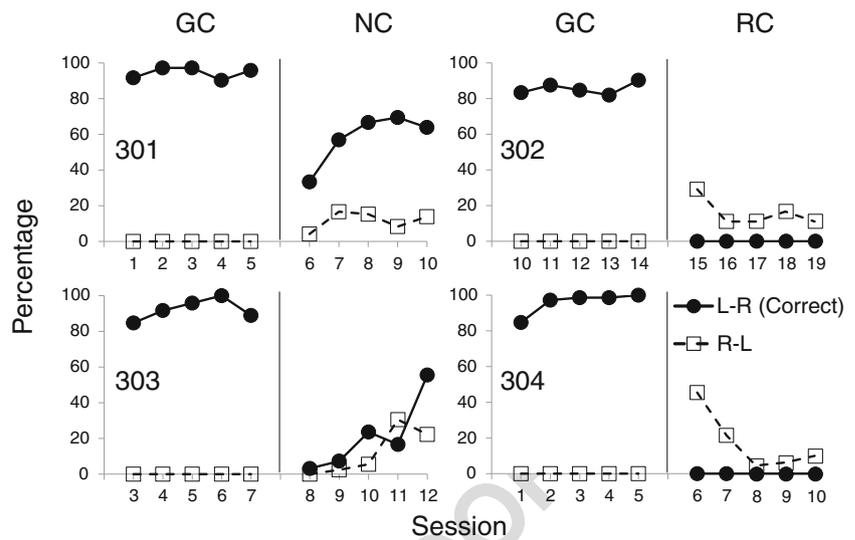
Figure 2 shows the percentage of L-R response sequences and  
R-L response sequences during the last five sessions of the  
Guiding-Cues condition and all five sessions of the second  
condition for each pigeon. All pigeons acquired the L-R  
response sequence at above 80 % accuracy in the presence  
of the guiding cues. Accuracy for Pigeons 301 and 304 met  
the mastery criteria in the minimum five sessions. Accuracy  
for Pigeons 302 and 303 met the mastery criteria in 14 and  
seven sessions, respectively.

In the subsequent condition, Pigeons 301 and 303 were  
exposed to the No-Cues condition. Both keys were lighted  
white and the L-R response sequence contingency remained  
in effect. In the first session of the No-Cues condition, the  
proportion of accurate L-R response sequences dropped from  
above 80 % to 33 % and 3 % for Pigeons 301 and 303,  
respectively. Accuracy increased over five sessions for both  
pigeons in the No-Cues condition. In the final session, accu-  
racy was 64 % (46 correct trials) and 56 % (40 correct trials)  
for Pigeons 301 and 303, respectively. Binomial sign tests on  
number of L-R sequences with Bonferroni-adjusted alphas to  
correct for multiple tests were conducted to test whether 1)  
accuracy was significantly greater than chance, 25 %; and 2)  
accuracy was significantly less than mastery, 80 %. Sign tests  
revealed that in the fifth session of the No-Cues condition,  
accuracy was significantly greater than chance ( $ps < 0.001$ ) for

**Table 1** Condition orders for pigeons in Experiment 1 with number of sessions per condition in parentheses

Pigeon				
301	302	303	304	
Red Only (2)	Red Only (2)	Red Only (6)	Red Only (2)	t1.4
Guiding Cues (5)	Guiding Cues (14)	Guiding Cues (2)	Guiding Cues (5)	t1.5
No Cues (5)	Reversed Cues (5)	Red Only (4)	Reversed Cues (5)	t1.6
		Guiding Cues (5)		t1.7
		No Cues (5)		t1.8

**Fig. 2** Percent correct L-R sequences recorded in Guiding-Cues (GC) and No-Cues (NC) conditions for Pigeons 301 and 303 (*left graphs*) and in Guiding-Cues and Reversed-Cues (RC) conditions for Pigeons 302 and 304 (*right graphs*) in Experiment 1. The L-R sequence re-emerged within five sessions when discriminative stimuli were removed, but not when they were reversed



323 both pigeons, and not significantly less than mastery ( $p >$   
 324 0.99) for either. Greater-than-chance accuracy by the end of  
 325 the No-Cues condition suggests that pigeons learned other  
 326 discriminative stimuli (e.g., location) related to the response  
 327 sequence in addition to the red-light cues during the Guiding-  
 328 Cues condition.

329 Neither pigeon in the Reversed-Cues condition produced  
 330 any correct L-R sequences in the presence of the reversed  
 331 guiding cues. Pigeon 302 continued to complete all 72 trials in  
 332 the five Reversed-Cues sessions. Of those trials, 15.8 % were  
 333 the R-L “follow red” sequence. Pigeon 304 finished 22, 14,  
 334 22, 16 and ten trials in the five consecutive Reversed Cues  
 335 sessions, respectively—an indication that responding may  
 336 have been undergoing extinction in the presence of the re-  
 337 versed cues. Of those completed trials, 17.5 % were the R-L  
 338 sequence.

339 To compare changes in accuracy for pigeons in the two  
 340 groups, the difference between the number of accurate re-  
 341 sponse sequences on the last day of the Guiding-Cues con-  
 342 dition and the number of accurate response sequences on the  
 343 fifth day of the No-Cues or Reversed-Cues condition was  
 344 computed for each pigeon. An independent-samples  $t$ -test  
 345 revealed that accuracy decreased significantly more in the  
 346 Reversed-Cues condition than the No-Cues condition,  $t(2) =$   
 347 12.73,  $p = 0.006$ . The L-R sequence reemerged when discrim-  
 348 inative stimuli were removed in the No-Cues condition, but  
 349 not when they were reversed in the Reversed-Cues condition.

350 **Discussion**

351 Pigeons’ performance was similar to rats’ performance report-  
 352 ed by Reid et al. (2010) and Reid et al. (2013). Performance in  
 353 comparable conditions was similar across studies and species.  
 354 Accuracy in the feature-positive No-Cues condition was compar-  
 355 able to accuracy in Reid et al.’s (2010) feature-negative

No-Lights condition. In both studies, accuracy dropped from  
 above 80 % in the previous condition to approximately 60 %  
 when discriminative stimuli were removed for five sessions.

When the guiding cues were reversed in the Reversed-Cues  
 condition, Reid et al.’s (2010) rats’ accuracy fell to approxi-  
 mately 5 %. A feature-positive discrimination bias was one  
 potential explanation for the large decrease in accuracy: a  
 propensity to respond to feature-positive discriminative stim-  
 uli may have prevented control over responding by practice  
 cues. When Pigeons 302 and 304 were switched from the  
 Guiding-Cues condition to the Reversed-Cues condition in  
 Experiment 1, the correct L-R response sequence did not  
 change. The signaling functions of the red and white lights  
 switched, but the correct sequence still followed a feature-  
 positive cue. No correct sequences were recorded for either  
 pigeon in the Reversed-Cues condition of Experiment 1. Even  
 under what amounted to extinction conditions for Pigeon 304,  
 the red-light stimuli still controlled behavior, or at least  
 prevented control by the white lights and practice cues asso-  
 ciated with the previously reinforced L-R sequence.

**Experiment 2**

Results of Experiment 1 cannot be attributed to a feature-  
 positive discrimination bias because all stimuli in all  
 conditions were feature-positive. The primary objective  
 in Experiment 2 was to determine whether, after initial train-  
 ing with discriminative stimuli, establishing a reinforcement  
 history without discriminative stimuli would allow behavior  
 to adapt to the reversal in discriminative stimuli in the  
 Reversed-Cues condition. Specifically, we hypothesized that  
 a history of access to food as a consequence of pecking white  
 keys in a No-Cues condition, thus creating a history in which  
 white keys signaled reinforcement, would facilitate behavior

388 to come under control of the white key light in the Reversed-  
 389 Cues condition—causing sequence accuracy to increase in the  
 390 Reversed-Cues condition. Reid et al. (2013) showed that the  
 391 extent to which a change in discriminative stimuli disrupted  
 392 sequence accuracy depended in large part on whether or not  
 393 their rats had been exposed to certain conditions prior to the  
 394 transition. Experiment 2 further explored the possibility that  
 395 the relative disruptiveness of a transition is in part controlled  
 396 by an organism’s history with the discriminative stimuli in  
 397 question.

398 Four pigeons were exposed to a series of Guiding-Cues,  
 399 No-Cues, and Reversed-Cues conditions and replications with  
 400 the expectation that creating a history in which the white lights  
 401 signaled reinforcement in the No-Cues condition would facil-  
 402 itate sequence-accuracy maintenance/recovery when discrim-  
 403 inative stimuli were reversed. This signal-food history hypoth-  
 404 esis yielded two empirical predictions for Experiment 2. First,  
 405 as in Experiment 1, L-R response sequences would not occur  
 406 with initial exposure to a Reversed-Cues condition. However,  
 407 if a history of reinforcement for pecking the white key had  
 408 been established in the interim, L-R response sequences  
 409 would emerge in a replication of the Reversed-Cues condition.  
 410 Second, L-R response sequences would be observed during  
 411 initial exposure to a Reversed-Cues condition, provided a  
 412 history of reinforcement for pecking the white key in the  
 413 No-Cues condition.

414 **Method**

415 *Subjects* Four pigeons numbered 205 to 208 maintained at  
 416 85 % of their free-feeding body weight via appropriate post-  
 417 session feedings served as subjects for Experiment 2. Pigeons  
 418 were housed individually in a vivarium with a 12-hr light:dark  
 419 cycle with continuous free access to water and intermittent  
 420 access to grit. All had a prior experimental history with fixed-  
 421 interval (FI) and response-initiated fixed-interval (RIFI)  
 422 schedules in the presence of both red and green key lights  
 423 (Fox and Kyonka 2013).

424 *Apparatus* The apparatus was the same as in Experiment 1.

*Procedure* All four pigeons were trained on an L-R response  
 sequence during which red lights served as discriminative  
 stimuli for two sessions. During this training period, only the  
 red lights were present on the active key in the L-R sequence.  
 A peck to the left red key extinguished it and lit the right red  
 key. A subsequent peck to the right red key resulted in the  
 delivery of reinforcement, and a subsequent peck to the left  
 key resulted in a 10-s blackout.

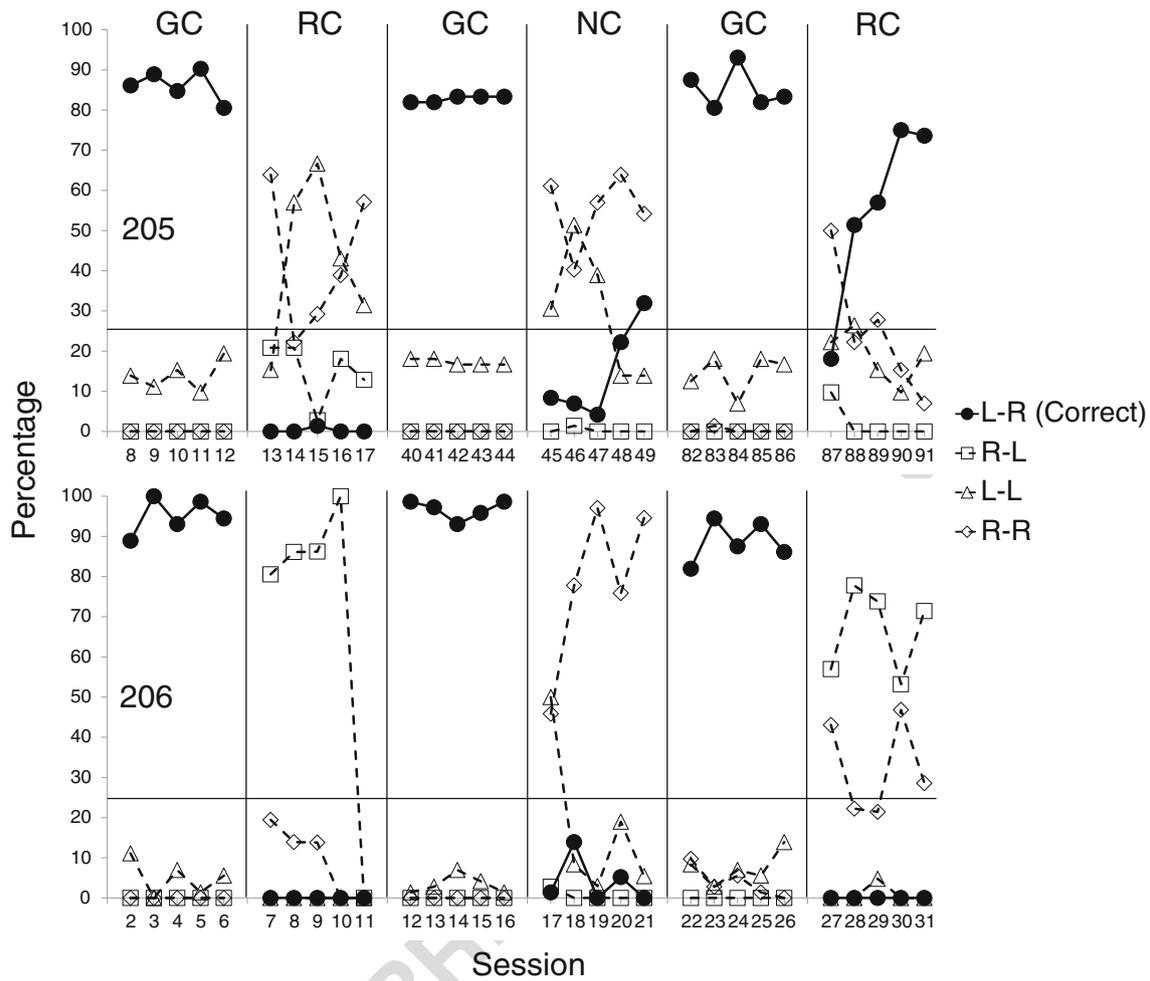
After training, all four pigeons were exposed to the  
 Guiding-Cues condition. The white lights (S-) were added  
 for the Guiding-Cues condition. All Guiding-Cues, No-Cues  
 and Reversed-Cues conditions were the same as described in  
 Experiment 1 (see Fig. 1). After initial Guiding-Cues training,  
 Pigeons 205 and 206 were exposed to conditions in the  
 following order: Reversed-Cues, Guiding-Cues, No-Cues,  
 Guiding-Cues, Reversed-Cues. After initial Guiding-Cues  
 training Pigeons 207 and 208 were exposed to conditions in  
 the following order: No-Cues, Guiding-Cues, No-Cues,  
 Guiding-Cues, Reversed-Cues. All Reversed-Cues and No-  
 Cues conditions lasted five sessions. Guiding-Cues conditions  
 lasted until accuracy was above 80 % for five consecutive  
 sessions, and there were no increasing or decreasing trends in  
 accuracy. As in Experiment 1, the L-R sequence was rein-  
 forced and all other sequences (R-L, R-R, and L-L) resulted in  
 a 10-s blackout in all conditions, regardless of the discrimina-  
 tive stimuli present. Table 2 shows the order of conditions and  
 number of sessions per condition for each pigeon.

**Results**

Figure 3 shows the percentage of correct L-R response se-  
 quences for Pigeons 205 and 206. Both met the mastery  
 criterion of 80 % accuracy in all Guiding-Cues conditions.  
 Pigeon 205 required 12, 27 and 37 sessions for mastery in the  
 initial Guiding-Cues condition and each replication, respec-  
 tively. Pigeon 206 initially met the mastery criterion in six  
 sessions and then within the minimum five sessions for both  
 replications. Consistent with the results of Experiment 1,  
 accuracy fell to 0.001 % (one L-R sequence was recorded  
 for Pigeon 205 in Session 15) in the first Reversed-Cues

t2.1 **Table 2** Condition orders for  
 t2.2 pigeons in Experiment 2 with  
 t2.3 number of sessions per condition  
 in parentheses

Pigeon	205	206	207	208
t2.4	Red Only (2)	Red Only (2)	Red Only (2)	Red Only (2)
t2.5	Guiding Cues (12)	Guiding Cues (6)	Guiding Cues (6)	Guiding Cues (5)
t2.6	Reversed Cues (5)	Reversed Cues (5)	No Cues (5)	No Cues (5)
t2.7	Guiding Cues (27)	Guiding Cues (5)	Guiding Cues (5)	Guiding Cues (5)
t2.8	No Cues (5)	No Cues (5)	No Cues (5)	No Cues (5)
t2.9	Guiding Cues (37)	Guiding Cues (5)	Guiding Cues (5)	Guiding Cues (5)
t2.10	Reversed Cues (5)	Reversed Cues (5)	Reversed Cues (5)	Reversed Cues (5)



**Fig. 3** Percentage of each response sequence recorded across conditions for Pigeons 205 and 206 in Experiment 2. The reinforced L-R sequence was observed reliably in the No-Cues condition and the second Reversed-

Cues condition for Pigeon 205, but not for Pigeon 206. Sessions on the X-axis are individually scaled and are non-consecutive for Pigeon 205. Note: GC=Guiding Cues; RC=Reversed Cues; NC = No Cues

463 condition. In the No-Cues condition that followed, accuracy  
 464 was initially below chance for Pigeon 205 but increased in the  
 465 final three sessions and was 32 % in the final session of the  
 466 condition. Across the five sessions of the No-Cues condition  
 467 (Sessions 17–21), mean accuracy ranged from 1 to 14 % for  
 468 Pigeon 206. In addition, Pigeon 206 finished 72, 72, 68, 58  
 469 and 37 trials in Sessions 17 through 21, respectively—indicating that pecking was potentially undergoing extinction. In  
 470 the first session of the second Reversed-Cues condition, accu-  
 471 racy was below chance for Pigeons 205 and 206. However,  
 472 accuracy increased across the five sessions for Pigeon 205. In  
 473 the fourth and fifth sessions of the Reversed-Cues condition,  
 474 accuracy was 75 % and 74 %, respectively, suggesting that the  
 475 history of reinforcement in the No-Cues condition was  
 476 sufficient for high levels of response-sequence accuracy  
 477 to emerge in the Reversed-Cues condition. Accuracy was  
 478 0 % across all five sessions in the final Reversed-Cues  
 479 condition for Pigeon 206. The majority of response sequences  
 480

recorded in the Reversed-Cues conditions for Pigeon 206  
 were R-L—an indication that the red lights were controlling  
 responding.

For a quantitative assessment of accuracy, binomial sign  
 tests on number of L-R sequences were conducted for the last  
 session in both Reversed-Cues conditions and the No-Cues  
 condition for each pigeon. Bonferroni-adjusted alphas were  
 used to correct for multiple tests asking whether accuracy was 1)  
 greater than chance and 2) less than mastery. Sign tests re-  
 vealed that, for both pigeons, accuracy in the fifth session of  
 the first Reversed-Cues condition and the fifth session of the  
 No-Cues condition, was significantly less than mastery ( $ps <$   
 $0.001$ ), but not significantly greater than chance ( $ps \geq 0.11$ ).  
 Similarly, because no L-R sequences were recorded for Pi-  
 geon 206 in the second Reversed-Cues condition, accuracy  
 was significantly less than mastery and not greater than  
 chance. However, sign tests revealed that for Pigeon 205,  
 accuracy in the fifth session of the second Reversed-Cues

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499 condition was significantly greater than chance ( $p < 0.001$ ) and  
 500 not significantly less than mastery ( $p = 0.12$ ).

501 Figure 4 shows the percentage of correct L-R response  
 502 sequences for Pigeons 207 and 208. The mastery criterion of  
 503 80 % accuracy in the initial Guiding-Cues condition required  
 504 six sessions for Pigeon 207. Pigeon 208's accuracy was consistently  
 505 below the 80 % criteria upon initial exposure to the  
 506 first Guiding-Cues condition. The response sequences recorded  
 507 for Pigeon 208 were predominantly L-L sequences with  
 508 very brief inter-response times, likely due to key reverberation  
 509 following pecks of greater than the minimum-required force.  
 510 For this reason, a 0.01-s "buffer" was programmed for Pigeon  
 511 208. After any peck to any key, no pecks were recorded on  
 512 that same key until 0.01 s had elapsed. After the buffer was  
 513 added to the computer program, Pigeon 208 met the 80 %  
 514 criteria in five sessions. In the No-Cues condition that follow-  
 515 ed, accuracy increased across the five sessions for Pigeon 207,  
 516 but remained below 40 %. Accuracy in each No-Cues session  
 517 was at or below 6 % for Pigeon 208. Upon re-presentation of

the Guiding-Cues stimuli in the third condition, accuracy was  
 518 above 80 % for both pigeons in the minimum five sessions. In  
 519 the second No-Cues condition, accuracy showed no trend at a  
 520 mean of 47.4 % for Pigeon 207. Overall, accuracy in the  
 521 second No-Cues condition for Pigeon 208 was a mean of  
 522 9.6 %, lower than in Guiding-Cues, but higher than in the  
 523 previous No-Cues. In the final session of the second No-Cues  
 524 condition, accuracy was 22 % for Pigeon 208. Accuracy in the  
 525 third Guiding-Cues condition was above 80 % for both pigeons  
 526 for the minimum five sessions. In the sixth and final  
 527 condition, which was the sole presentation of the Reversed-  
 528 Cues condition for Pigeons 207 and 208, accuracy in the first  
 529 session was 29 % for Pigeon 207 and 1 % for Pigeon 208.  
 530 Accuracy for both pigeons increased across the five sessions.  
 531 By the fifth session, accuracy in the Reversed-Cues condition  
 532 was comparable to accuracy observed in the Guiding-Cues  
 533 conditions, finishing at 92 % for both Pigeons 207 and 208.

534 For a quantitative assessment of accuracy, binomial sign  
 535 tests on number of L-R sequences with Bonferroni-adjusted  
 536

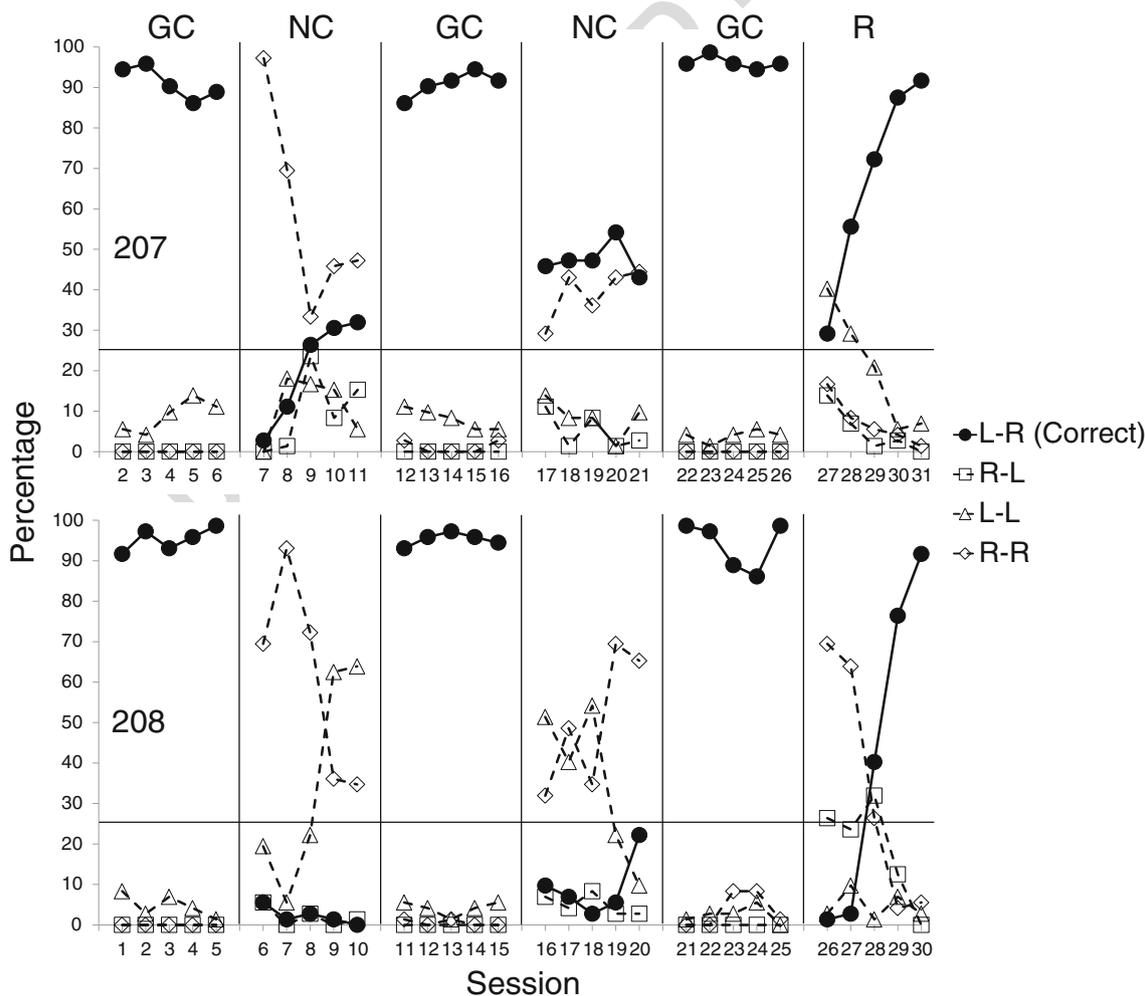


Fig. 4 Percentage of each response sequence recorded across conditions for Pigeons 207 and 208 in Experiment 2. The reinforced L-R sequence was observed in the Reversed-Cues condition for both pigeons. Note: GC=Guiding Cues; RC=Reversed Cues; NC = No Cues

537 alphas were conducted for the last session in both No-Cues  
538 conditions and the Reversed-Cues condition for Pigeons 207  
539 and 208. Sign tests revealed that, for both pigeons, accuracy in  
540 the fifth session of both No-Cues conditions were significantly  
541 less than mastery ( $ps < 0.001$ ). Accuracy was also significantly  
542 greater than chance for Pigeon 207 in the second No-Cues  
543 condition ( $p = 0.001$ ). After a history of food reinforcement as  
544 a consequence of pecking the white key had been established  
545 in the No-Cues conditions, accuracy was significantly greater  
546 than chance ( $ps < 0.001$ ) and not significantly less than mas-  
547 tery (accuracy was in fact greater than mastery) for both  
548 pigeons in the Reversed-Cues condition. The improvement  
549 in accuracy indicates that the white lights may have acquired  
550 S+ properties for both pigeons during exposure to the No-  
551 Cues conditions.

552 The critical between-groups comparison for Experiment 2  
553 was whether changes in accuracy were different upon initial  
554 exposure to the Reversed-Cues condition (condition 2 for  
555 Pigeons 205 and 206; condition 6 for Pigeons 207 and 208).  
556 The difference between the number of accurate response  
557 sequences on the last day of the preceding Guiding-Cues  
558 condition and the number of accurate response sequences on  
559 the fifth day of the Reversed-Cues condition was computed  
560 for each pigeon. An independent-samples *t*-test revealed that  
561 accuracy decreased significantly more for Pigeons 205 and  
562 206 than it did for Pigeons 207 & 208,  $t(2) = 11.57$ ,  $p = 0.007$ .  
563 Evidently, a history of reinforcement for the L-R sequence in  
564 the presence of white lights on both keys made it possible for  
565 the response sequence to come under the control of the white  
566 keys as discriminative stimuli in the Reversed-Cues condition,  
567 even though they were presented concurrently with previous  
568 S+ stimuli (the red lights).

569 All of the non-L-R response sequences in all Guiding-Cues  
570 conditions were L-L sequences. Although pecking the key  
571 with enough force to register a response produced auditory  
572 feedback and (in Guiding-Cues and Reversed-Cues condi-  
573 tions) a visual stimulus change, it is possible that pigeons  
574 did not always discriminate that the first peck was registered.  
575 Interestingly, when the L-R sequence did not occur in  
576 Reversed-Cues conditions, no other sequence occurred reli-  
577 ably across pigeons and the R-L (follow-red) sequence only  
578 occurred reliably for one pigeon—Pigeon 206.

## 579 Discussion

580 Accuracy in the final Reversed-Cues session of Experiment 2  
581 was almost as high for Pigeon 205 as it was for Pigeons 207  
582 and 208, which suggests that initial exposure to the No-Cues  
583 condition immediately prior to the Reversed-Cues condition  
584 was not necessary for recovery of the L-R sequence. However,  
585 it is not clear what stimuli were controlling behavior in the  
586 final Reversed-Cues condition for those three pigeons. Stimuli  
587 unrelated to the key lights, such as “practice cues,” may have

588 acquired control over behavior once the L-R sequence had  
589 been reinforced without discriminative stimuli: The red lights  
590 no longer overshadowed control by these other stimuli in the  
591 Reversed-Cues condition. It is also possible that the white  
592 lights in the Reversed-Cues condition may have taken on the  
593 same S+ function as the red lights in the Guiding-Cues con-  
594 dition after pecking white keys was reinforced in the No-Cues  
595 condition.

596 Once the L-R sequence had been reinforced in the absence  
597 of discriminative stimuli, the sequence was maintained or  
598 recovered independently of discriminative stimuli. Neverthe-  
599 less, there was some evidence in Experiment 2 that key-light  
600 discriminative stimuli continued to exert stimulus control over  
601 response sequences. For three out of four pigeons, percent  
602 accuracy in the final session of the last Reversed-Cues condi-  
603 tion was comparable to accuracy in Guiding Cues conditions,  
604 but accuracy in No-Cues conditions was always lower. Both  
605 Guiding Cues and Reversed Cues were effective discrimina-  
606 tive stimuli. It is possible that after additional experience  
607 switching back and forth between the Guiding-Cues and  
608 Reversed-Cues conditions, accurate sequences might be main-  
609 tained at above 80 % and not initially decline following a  
610 transition. Reid et al. (2014) also observed maintained or  
611 improved accuracy during repeated shifts between conditions  
612 in pigeons completing L-R response sequences.

613 The additional experience in the No-Cues replication prior  
614 to any exposure to a Reversed-Cues condition apparently  
615 facilitated L-R sequences in the final Reversed-Cues condition  
616 for Pigeons 207 and 208. The fact that accuracy in the fifth  
617 session of the Reversed-Cues replication was near mastery for  
618 Pigeon 205 suggests, however, that the specific number and  
619 presentation order of conditions was not strictly necessary.  
620 Pigeon 205 experienced the No-Cues condition only once and  
621 finished at 74 % accuracy in the final Reversed-Cues session.  
622 Pigeons 207 and 208 experienced the No-Cues condition for  
623 five more sessions than Pigeons 205 and 206, and finished the  
624 final Reversed-Cues condition at 92 % accuracy. Additional  
625 experience for Pigeon 206 in the No-Cues condition would  
626 not necessarily have improved performance in the Reversed-  
627 Cues condition, because responding appeared to be undergo-  
628 ing extinction in the No-Cues condition. Alternatively, the  
629 disruption of the L-R sequence in the first Reversed-Cues  
630 condition may have interfered with any facilitative effects of  
631 the No-Cues condition for Pigeons 205 and 206.

632 Another possible contributor to the re-emergence of the L-  
633 R sequence in the final Reversed-Cues condition for Pigeon  
634 205 is increased experience in the Guiding-Cues condition.  
635 The mastery criterion of greater than 80 % accuracy in the  
636 Guiding-Cues condition was met in the minimum five ses-  
637 sions for Pigeons 206, 207 and 208 after the first Guiding-  
638 Cues condition. Pigeons 206, 207 and 208 spent a total of 16,  
639 16 and 15 sessions in the Guiding-Cues condition, respective-  
640 ly (after programming the buffer for Pigeon 208). Pigeon 205

641 spent 76 sessions in the Guiding-Cues condition because of a  
642 failure of accuracy to meet the mastery criterion. This additional  
643 experience performing the sequence may have been  
644 responsible for increased accuracy in the last Reversed-Cues  
645 condition for Pigeon 205 compared to Pigeon 206. However,  
646 Pigeons 207 and 208 experienced the Guiding-Cues condition  
647 an equal or lesser number of times compared to Pigeon 206,  
648 suggesting that it was the experience in the No-Cues condition  
649 that facilitated higher levels of accuracy in the final Reversed-  
650 Cues condition and not more experience in the Guiding-Cues  
651 condition.

652 Pigeons' performance in the final Reversed-Cues condition  
653 of Experiment 2 suggests that either the red or white lights  
654 could function as discriminative stimuli to "guide" the L-R  
655 response sequence. Higher accuracy and therefore more rein-  
656 forcers delivered in the presence of just the white lights in the  
657 No-Cues condition prior to the final Reversed-Cues condition  
658 was correlated with higher accuracy in the final Reversed-  
659 Cues condition. Pigeon 206 was the only pigeon that never  
660 produced the L-R sequence in the final Reversed-Cues condi-  
661 tion after experiencing the No-Cues condition. Pigeon 206  
662 also earned the fewest reinforcers in the No-Cues condition  
663 and the two white keys may have signaled extinction, or at  
664 least a very low probability of reinforcement. Furthermore, for  
665 the three pigeons in which the L-R response sequence  
666 emerged at levels near or above mastery in the final  
667 Reversed-Cues condition, response-sequence accuracy in-  
668 creased across the five sessions in the No-Cues condition that  
669 preceded it. Together, these findings suggest that accurate  
670 predictions of how changes in discriminative stimuli will  
671 affect response-sequence accuracy can be made based on an  
672 inspection of the organism's behavioral history with the dis-  
673 criminative stimuli in question.

## 674 General Discussion

675 In Experiment 1, pigeon response-sequence accuracy in-  
676 creased and decreased in the same way as previously reported  
677 in rats (Reid et al. 2010) when discriminative stimuli signaling  
678 correct responses changed. In the No-Cues condition, the  
679 discriminative function of the key lights was removed by  
680 lighting both side keys white and the percent of correct se-  
681 quences decreased for Pigeons 301 and 303. In the Reversed-  
682 Cues condition, the discriminative functions of the red and  
683 white lights were reversed; the correct L-R sequence required  
684 pecking the white keys. Correct L-R sequences never occurred  
685 in the Reversed-Cues condition. In Experiment 2, for three out  
686 of four pigeons, exposure to the No-Cues condition prior to  
687 the Reversed-Cues condition effectively enabled recovery of  
688 the L-R sequence in the Reversed-Cues condition.

689 Neither a feature-positive discrimination bias nor the S-R  
690 compatibility theory can explain results of all guiding-cues

691 experiments published to date. The S-R compatibility theory 691  
692 cannot account for the results from Reid et al.'s (2013) 692  
693 Experiment 3, and the feature-positive bias effect cannot 693  
694 account for the results from Experiment 1 or the replication 694  
695 in the first two conditions of Experiment 2 described above. 695  
696 Reid et al. (2013) concluded that behavioral history may play 696  
697 an important role in how changes in discriminative stimuli 697  
698 affect behavior. The results of Experiment 2 show that an 698  
699 account of behavioral histories can in part explain why 699  
700 response-sequence accuracy may or may not be disrupted— 700  
701 specifically, the results of Experiment 2 suggest that a previ- 701  
702 ous history with a stimulus as an S+ is sufficient for it to 702  
703 function as an effective "guiding cue" in the future, even if the 703  
704 organism has a history with that same stimulus as an S- in 704  
705 other contexts. So far, a behavioral history explanation of 705  
706 guided-skill learning and disruption caused by changes in 706  
707 discriminative stimuli is more parsimonious and predictive 707  
708 than the other two explanations. 708

709 The fact that exposure to previous experimental conditions 709  
710 profoundly impacted the disruptiveness of transitions between 710  
711 conditions is not new. It is more broadly known as "path 711  
712 dependence" in associative learning (e.g., Brown-Su et al. 712  
713 1986; Miller et al. 1995). Both Experiment 2 and Reid 713  
714 et al.'s (2013) Experiment 4 illustrate the importance of path 714  
715 dependence in guided skill learning experiments. In 715  
716 Experiment 2, the notion of path dependence is illustrated by 716  
717 the relative disruptiveness of the Guiding-Cue → Reversed- 717  
718 Cue transition. If the transition was preceded by exposure to 718  
719 the No-Cues condition, it was relatively undistruptive for three 719  
720 of four pigeons: by the end of five sessions, response- 720  
721 sequence accuracy was at or near levels observed in the 721  
722 Guiding-Cues conditions. However, if the transition was not 722  
723 preceded by the No-Cues condition, it resulted in profound 723  
724 disruption of response-sequence accuracy. In the context of 724  
725 operant conditioning and guided-skill learning, major ques- 725  
726 tions remain. What factors contribute to the influence that 726  
727 experience has on current transitions? How much experience 727  
728 is necessary and what specific conditions must be present in 728  
729 the learning history for certain transitions to become less 729  
730 disruptive in the future? How do "environmental cues" (e.g., 730  
731 key lights) and "practice cues" interact or compete for control 731  
732 of a response sequence, and how do transitions affect control 732  
733 by these two potential sources? These are not easy questions 733  
734 to answer, but the "guiding-cues" framework has proven 734  
735 useful in starting to analyze some of the relevant variables. 735

736 Future research using this experimental preparation should 736  
737 include a stimulus change in the No-Cues conditions when a 737  
738 peck is recorded—for example, the lights could blink when a 738  
739 response is recorded. The lack of a visual change in these 739  
740 conditions may produce more L-L or R-R sequences because 740  
741 the "registering" of a response is not signaled, although res- 741  
742 sponses in Experiments 1 and 2 did produce an audible "click" 742  
743 when the key micro-switch was closed. 743

744 The behavioral framework used here and by Reid and  
 745 colleagues (2010, 2013, 2014) provides a useful tool for  
 746 investigating the variables that affect motor-skill learning  
 747 and for studying path dependence in operant conditioning.  
 748 The behavioral-histories explanation provided here for why  
 749 discriminative stimuli that are highly predictive of reinforce-  
 750 ment don't control behavior is predictive and testable. Cogni-  
 751 tive models and descriptions of motor-skill learning and tech-  
 752 niques for improving motor-skill acquisition and maintenance  
 753 (e.g., Schmidt 1975) are largely descriptive and do not provide  
 754 predictions for how skills are maintained under changing  
 755 conditions (Gluck et al. 2008; Reid et al. 2010). Future re-  
 756 search might also test human performance using the current  
 757 framework, thus potentially extending the framework's scope  
 758 of potential applications. This motor-skill learning paradigm  
 759 might also be useful for testing effects of drugs on motor-skill  
 760 acquisition, maintenance, and resistance to change.

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 762 computer programming.

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