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Imitation of Conditional Discriminations in Pigeons (*Columba livia*)

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In the present experiments, the 2-action method was used to determine whether pigeons could learn to imitate a conditional discrimination. Demonstrator pigeons (*Columba livia*) stepped on a treadle in the presence of 1 light and pecked at the treadle in the presence of another light. Demonstration did not seem to affect acquisition of the conditional discrimination (Experiment 1) but did facilitate its reversal of the conditional discrimination (Experiments 2 and 3). The results suggest that pigeons are not only able to learn a specific behavior by observing another pigeon, but they can also learn under which circumstances to perform that behavior. The results have implications for proposed mechanisms of imitation in animals.

Imitative learning is a type of social learning in which an individual learns a specific motor behavior from watching another individual perform that behavior. Although demonstrating that animals are able to imitate may seem straightforward, facilitated acquisition can be produced by nonimitative social influence. For example, the mere presence of another animal (social facilitation) may affect the motivational state of an observer, which in turn can affect the rate of acquisition of a new response. Similarly, the movement of the manipulandum (stimulus enhancement) can draw the observer's attention to it and can increase the likelihood that contact is made. Finally, the pairing of movement of the manipulandum and the sight of food can establish a Pavlovian association between the two, leading to observational conditioning (or autoshaping).

Early imitation research showed that primates could learn to open a box in different ways depending on how a model opened it (Whiten & Custance, 1996) or that budgerigars could learn to remove the lid from a container of food in the same way as they had seen a model remove the lid (Dawson & Foss, 1965). However, in each of these experiments, the different means of obtaining a reward involved differential movement of a part of the model's environment. Thus, the observers may have learned what change in the environment was needed for a reward to be obtained (i.e., what Tomasello, 1996, referred to as the emulation of affordances) rather than what response topography is required. (For a complete discussion of the various factors that must be controlled before a researcher can conclude that imitation has occurred, see Galef, 1988; Whiten & Hamm, 1992; Zentall, 1996.) To demonstrate imitative learning, it is important to show that the specific behavior of the demonstrator has caused the observer to perform the same response. With a procedure in which the only difference between two groups is the specific behavior of the demonstrator, Zentall, Sutton, and Sherburne (1996) showed imitative learning in pigeons in the absence of other types of facilitation. Observer pigeons observed demonstrator pigeons either pecking at or stepping on a treadle (that moved in the same way with either response) to obtain food. Then the observers were allowed access to the treadle, and all responses to the treadle were reinforced. The only difference between the two groups was the specific behavior of the demonstrator. Zentall et al. found that there was a significant correlation between the behavior observed and the behavior performed. Such imitative learning also has been shown in Japanese quail (Akins & Zentall, 1996, 1998; Dorrance & Zentall, 2001).

The predominant view of imitative learning is that it represents the understanding of how the behavior of another relates to one's own behavior (Whiten & Custance, 1996; Whiten & Hamm, 1992). If pigeons are able to learn what to do to obtain a reward on the basis of what a model is doing, then they also may be able to understand that a reward can be obtained in one of two different ways, depending on which conditional cue is present. If imitative learning involves a form of cognitive functioning beyond simple instrumental learning or released behavior, then it may be possible for pigeons to show the kind of flexibility needed for them to integrate two different response topographies with the conditional cues that signal which one is appropriate.

Experiment 1

In Experiment 1, demonstrator pigeons were trained to perform a conditional discrimination in which two distinct behaviors were performed, each under a different condition. For example, when the houselight was white, stepping was reinforced, whereas when it was green, pecking was reinforced. If pigeons are able to imitate the specific response in the presence of a specific cue, then observers that are subsequently trained to perform the same discrimination as the demonstrator should learn more quickly than observers that are subsequently trained to perform the reverse discrimination. A trial and error group that observed a demonstra-

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tor eating was included in order to assess the rate of learning the task in the absence of a demonstrator performing a behavior to the treadle.

Method

Subjects

Sixteen white Carneaux pigeons (*Columba livia*) obtained from the Palmetto Pigeon Plant (Sumter, SC) served as subjects. The pigeons were housed in individual cages, were maintained at 80% of their free-feeding weight, and were given free access to grit and water. All pigeons were naive to the experimental apparatus and procedure.

Apparatus

The apparatus consisted of two large modular test chambers (Coulbourn Instruments, Lehigh Valley, PA) that were placed side by side. Each chamber measured 30.5 × 25.5 × 28.0 cm. The side walls of the chamber were made of Plexiglas, which allowed the observers to view the demonstrator's chamber. Located on the front panel of the demonstrator's chamber were two shielded houselights (28.0 V, 0.1 A), one that provided white light and one that provided green light, and an opening that provided access to a rear mounted feeder. Reinforcement consisted of 2-s access to mixed grain. A feeder light was turned on whenever reinforcement was available. A response treadle (3.8 × 3.8 cm) was located at the front panel, 1 cm from the common wall between the two chambers and 1.3 cm above the wire mesh floor. The observers' chamber was similar to the demonstrators' chamber but it had no houselight, feeder, or treadle. A computer controlled the sequence of events in the experimental chamber. A schematic of the experimental apparatus is presented in Figure 1.

Procedure

Demonstrator training. Four pigeons were trained as demonstrators. At the beginning of a trial, one of the houselights was illuminated for 20 s, followed by a 10-s intertrial interval (ITI). For 2 of the demonstrators, each step on the treadle was reinforced in the presence of the green, but not the white, houselight, and each peck at the treadle was reinforced in the presence of the white, but not the green, houselight. For the other 2 demonstrators, the contingencies were reversed. The demonstrators had previously been reinforced for stepping in the presence of one houselight and for refraining from stepping in the presence of the other houselight. During this experiment, they continued to be reinforced for stepping during one houselight, but in addition, they were trained to peck during the other houselight by the method of successive approximations. Each session consisted of 24 trials, 12 of each houselight condition. Demonstrators were trained until they were making no incorrect responses in a session.

Observer pretraining. Observers were trained to eat from the feeder and were habituated to each of the two chambers for approximately 10 min during a session. Pretraining consisted of 10 to 12 daily sessions of 24 trials each. At the beginning of each trial, the houselight was illuminated for 10 s, followed by the lifting of the grain feeder, which remained lifted for 2 s after the pigeon broke a photobeam and began eating. On half of the sessions, the houselight during the ITI was white, and on the other half of the sessions, the houselight during the ITI was green. To decrease the novelty of observation of the demonstrator, each observer observed another pigeon eating from the feeder for two sessions. During pretraining, the treadle was removed from the chamber.

Observation–test phase. During the observation–test phase, a demonstrator was placed in the demonstrator's chamber while an observer was placed in the observer's chamber. Each observer observed the same demonstrator during each session. Four pigeons observed a demonstrator pecking during the white houselight and stepping during the green houselight, whereas 4 pigeons observed a demonstrator stepping during the white houselight and pecking during the green houselight. Following observation, the experimenter left the room while a second experimenter entered, removed the demonstrator, and placed the observer in the demonstrator's chamber. This enabled each experimenter to remain unaware of which pigeons were in the consistent group and which pigeons were in the inconsistent group. The observer's performance session started immediately (approximately 30 s after the end of the demonstrator's session). Half of the observers in each group were reinforced for performing the same discrimination as the demonstrator (consistent group, $n = 4$). The remaining observers were reinforced for performing the discrimination with the contingencies reversed (inconsistent group, $n = 4$). That is, pigeons trained

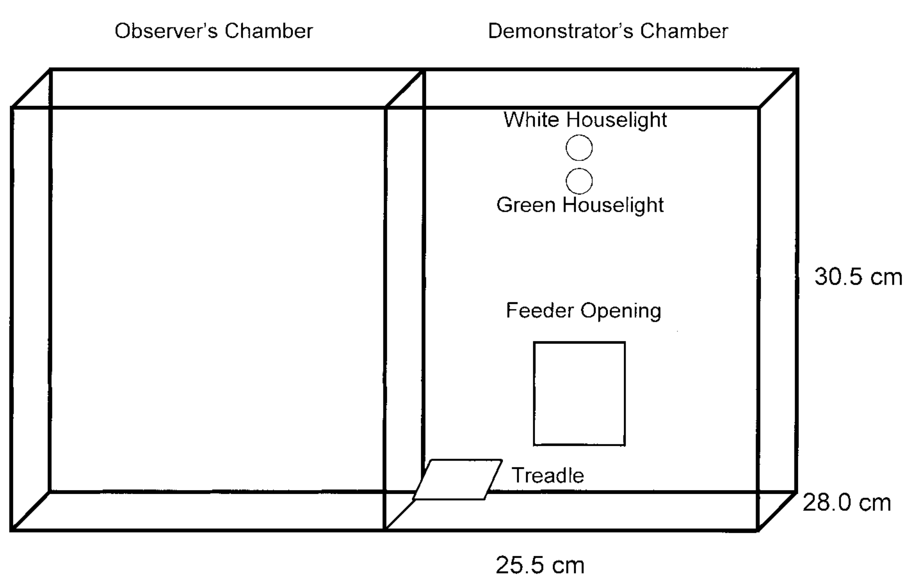

Figure 1. A diagram of the apparatus used in the present experiments.

inconsistently, for example, observed stepping during the white houselight and pecking during the green houselight but were then trained to peck during the white houselight and to step during the green houselight. Pigeons in the trial and error group ($n = 4$) observed a demonstrator eating during presentations of the white and green houselights. The treadle was removed from the chamber during these sessions. Then the treadle was replaced and 2 of the observers in the trial and error group were reinforced for performing one discrimination, whereas 2 of the observers were reinforced for performing the other discrimination. The demonstrator was fed a mean of eight times per trial, a rate comparable with that of the demonstrators that responded to the treadle. All other aspects of the observation−test phase were the same as those of the other groups. In each session, an observer was exposed to an observation session, followed by a training session, until the observer reached a proportion of correct responses of at least .90 during each houselight condition during one session. The design of Experiment 1 is presented in Table 1.

Results and Discussion

The proportion of correct responses was calculated by dividing the number of correct responses by the number of total responses on each trial. The mean proportion of correct responses over sessions made by demonstrators in the presence of observers was .99 (SE = .00). The mean number of steps per trial made by demonstrators was 10.94 (SE = 0.55), and the mean number of pecks was 5.28 (SE = 0.65).

Most of the observer pigeons learned to step on the treadle more quickly than they learned to peck at it. One pigeon in the trial and error group showed no signs of learning to peck during the correct houselight, and training was stopped after 20 sessions. For the purpose of the analysis, this pigeon was assigned a score of 20 sessions. The number of sessions it took for each pigeon to acquire the stepping and pecking discriminations is presented in Table 2. The mean number of sessions to reach criterion during both houselight conditions for the consistent group was 7.50 (SE = 2.40), for the inconsistent group was 6.25 (SE = 0.85), and for the trial and error group was 16.00 (SE = 1.87). These data are presented in Figure 2. An analysis of variance (ANOVA) performed on the sessions-to-criterion scores revealed a significant effect of group, $F(2, 9) = 8.46$, $p < .01$. To make comparisons among the three groups, we used the Bonferroni method to ensure that the overall p was less than .05 (i.e., for each individual comparison, p must be less than .012). With this procedure, the difference between the consistent and the inconsistent groups was not significant, $t(6) = 0.49$, the difference between the consistent and the trial and error groups was marginally significant, $t(6) = 2.80$, $p < .05$, and the difference between the inconsistent and the trial and error groups was significant, $t(6) = 4.74$, $p < .01$. Furthermore, the mean of the consistent and inconsistent groups combined was significantly different from the trial and error groups, $t(10) = 4.25$, $p < .01$.

Table 1
Design of Experiment 1

Group	Counterbalancing	Conditions observed	Conditions trained
Consistent	White/Step	White→Step Green→Peck	White→Step Green→Peck
	White/Peck	White→Peck Green→Step	White→Peck Green→Step
Inconsistent	White/Step	White→Peck Green→Step	White→Step Green→Peck
	White/Peck	White→Step Green→Peck	White→Peck Green→Step
Trial and error	White/Step		White→Step Green→Peck
	White/Peck		White→Peck Green→Step

Table 2
Number of Sessions for Each Pigeon to Acquire Pecking and Stepping in Experiment 1

	Trial type		
Group and pigeon	Peck	Step	Both
Consistent			
1	2	1	2
2	5	11	11
3	5	1	5
4	2	12	12
M (SE)	3.5 (1.7)	6.2 (6.1)	7.5 (5.2)
Inconsistent			
1	4	4	4
2	5	1	6
3	5	2	7
4	6	1	8
M (SE)	5.0 (0.8)	2.0 (1.4)	6.2 (1.7)
Trial and error			
1	20	6	20
2	9	1	16
3	10	6	11
4	17	1	17
M (SE)	14.0 (5.4)	3.5 (2.9)	16.0 (3.7)

The number of sessions for each group to acquire each behavior separately was also analyzed. The number of sessions to acquire pecking differed among the groups, $F(2, 9) = 11.97$, $p < .01$; t tests showed that acquisition of pecking did not differ between the consistent and the inconsistent groups, $t(6) = 1.57$, *ns*, but acquisition of pecking differed between the consistent and the trial and error groups, $t(6) = 3.73$, $p = .01$, and differed marginally (according to the Bonferroni method) between the inconsistent and the trial and error groups, $t(6) = 3.33$, $p = .02$. The number of sessions to acquire stepping did not differ significantly among the groups, $F(2, 9) = 1.18$. There were no significant effects of counterbalancing variables, and for this reason, they have not been reported.

The results of Experiment 1 indicated that both the consistent and the inconsistent groups acquired the task more quickly than the trial and error group. This result suggests that the demonstration of pecking and stepping facilitated learning of the discrimination regardless of whether that demonstration was the same or the reverse discrimination from what the observer was trained to perform. However, if pigeons are able to learn by observing another pigeon to peck under one condition and to step under another condition, then pigeons in the consistent group should have learned significantly faster than pigeons in the inconsistent group because the consistent group was reinforced for performing the same discrimination as that performed by the demonstrator,

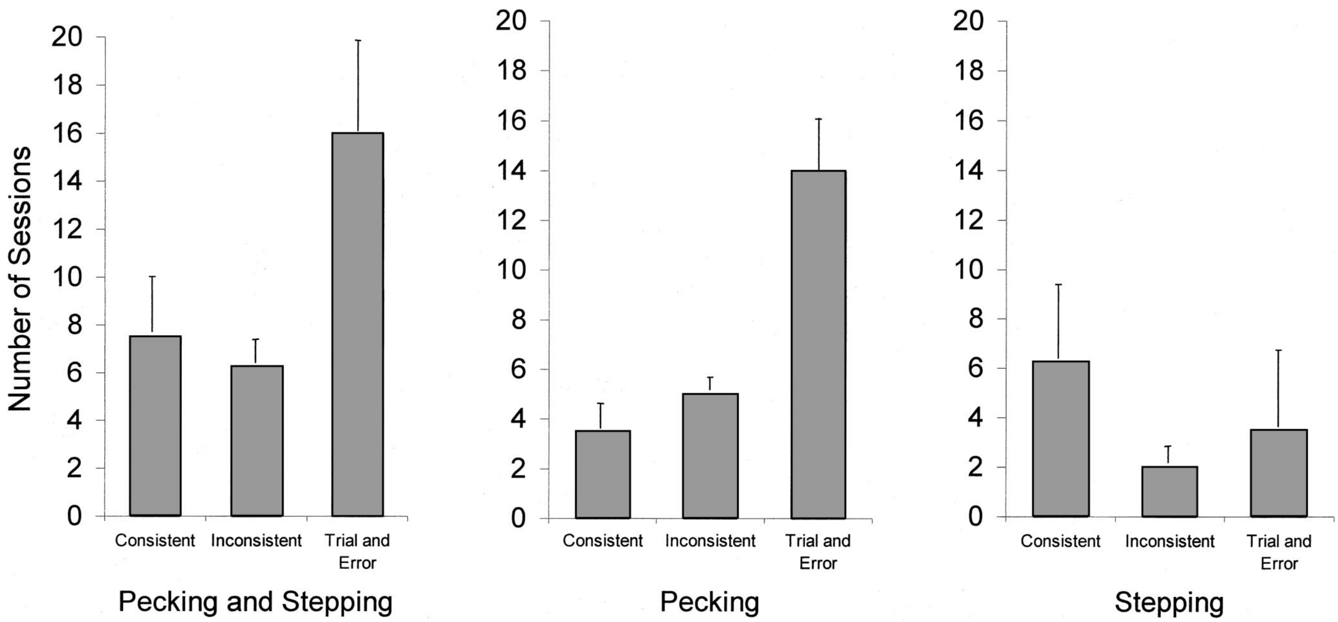

Figure 2. The number of sessions to reach criterion during both cues and during the stepping and pecking cue individually in Experiment 1.

whereas the inconsistent group was reinforced for performing the opposite discrimination as that performed by the demonstrator. The present results do not show evidence that the pigeons learned to perform a specific behavior under a specific condition. Furthermore, the trial and error group may have learned more slowly because of several factors. Not only did this group not observe the specific behaviors of pecking at and stepping on the treadle, but this group also did not see the treadle move (possible stimulus enhancement) and did not see the movement of the treadle followed by food (possible observational conditioning). Therefore, comparing the trial and error group with the consistent and the inconsistent groups cannot tell us whether or not the latter two groups imitated the behaviors of pecking and stepping because there may have been differential stimulus enhancement and observational conditioning.

Experiment 2

In Experiment 1, acquisition of a conditional discrimination was not significantly affected by the observation of a demonstrator. It is quite likely that individual (i.e., within-group) differences in rates of learning the discrimination were large enough to obscure imitative learning. Therefore, in Experiment 2, two manipulations were introduced. First, after training observers to step in the presence of one houselight and to peck in the presence of the other houselight, the observers were exposed to a demonstrator performing either the same discrimination (consistent group) or the reverse discrimination (inconsistent group). If pigeons naturally imitate, then those exposed to a demonstrator performing the reverse discrimination should show disrupted performance as compared with those exposed to a demonstrator performing the same discrimination. Second, the observers were then trained to perform the reverse discrimination. The advantage of a reversal procedure over an acquisition procedure is that the observers would already have had experience pecking at and stepping on the treadle. Thus, relative to pigeons that have never learned to peck or step, these pigeons should be stepping and pecking at comparable rates at the start of the reversal. Any differences in the initial probability of stepping and pecking that may have played a role in initial acquisition should be greatly reduced in acquiring the reversal. Thus, if pigeons can learn through observation, acquisition of the reversal should be faster for the former inconsistent group (now the consistent reversal group) than for the former consistent group (now the inconsistent reversal group; see Table 3).

Method

Subjects and Apparatus

Eight white Carneaux pigeons similar to those used in Experiment 1 served as observers. Two of the demonstrators from Experiment 1 served as demonstrators. The experimental chamber was the one used in Experiment 1.

Procedure

Observer pretraining and training. Observers were pretrained to eat from the feeder and were habituated to both chambers, as in Experiment 1. Then, the observers were shaped by the method of successive approximations to step during one houselight and to peck during the other houselight. For half of the observers, stepping was reinforced in the presence of the white houselight, and pecking was reinforced in the presence of the green houselight. For the other half of the observers, stepping was reinforced in the presence of the green houselight, and pecking was reinforced in the presence of the white houselight. All other aspects of the training sessions

Table 3
Design of Experiment 2

	Training	Observation–Test Phase	Observation–Reversal Training	
Group	Conditions trained	Conditions observed	Conditions observed	Conditions trained
Consistent/inconsistent reversal	White→Step Green→Peck	White→Step Green→Peck	White→Step Green→Peck	White→Peck Green→Step
Inconsistent/consistent reversal	White→Step Green→Peck	White→Peck Green→Step	White→Step Green→Peck	White→Step Green→Peck

were the same as those from Experiment 1. Each observer was trained until it reached a proportion of correct to total responses of at least .90 during each houselight condition for one session.

Observation−test phase. During this phase, for one session, a demonstrator that was placed in the demonstrator's chamber performed the task on which it had been trained, and an observer was placed in the observer's chamber. For half of the observers, the demonstrator performed the same discrimination that the observers had learned (consistent group). For the remaining observers, the demonstrator performed the discrimination with the contingencies reversed from those of the observers (inconsistent group). Following observation, the demonstrator was removed and the observer was placed in the demonstrator's chamber. For the first six trials (three in each houselight condition), the observer was reinforced for any response it made to the treadle.

Retraining. Following those six trials, the observers were retrained. That is, during the last 18 trials of the session, the pigeons were reinforced for performing the task as they had originally acquired it. Observers were then retrained for an additional session or until the proportion of their correct responses during a session was .90. For all but one pigeon, retraining lasted for two sessions.

Observation−reversal training. The day after retraining, each observer again observed the same demonstrator it had previously observed. Then, the demonstrator was removed and the observer was placed in the demonstrator's chamber, but the observer was no longer reinforced for performing the discrimination it had previously acquired; rather, it was reinforced for performing the task with the contingencies reversed (e.g., if it had been trained to step during white and peck during green, it was now reinforced for pecking during white and stepping during green). For half of the pigeons, the demonstrator performed the discrimination that was consistent with the task that the observer had been trained to perform previously but a discrimination that was inconsistent with what the observer was now being trained to perform (inconsistent reversal group). For the remaining pigeons, the demonstrator performed the discrimination that was inconsistent with the task that the observer had been trained to perform previously but was consistent with what the observer was now being trained to perform (consistent reversal group). Each observer experienced an observation session followed immediately by a test session each day until the conditional discrimination had reversed to a proportion of at least .90 correct responses for one session.

Results and Discussion

Training

The mean number of sessions to criterion for the consistent group was 11.50 (SE = 2.25) and for the inconsistent group was 10.75 (SE = 4.53). The difference between the groups was not statistically significant, $F(1, 6) < 1.00$.

Test

Table 4 shows the proportion of correct responses for each pigeon during the last session of training before observation and performance during the first two and first six trials that followed the first observation session. On the last session of training, the mean proportion of correct responses for the consistent group was .99 (SE = .01) and for the inconsistent group was 1.00 (SE = .00). Following the first observation session, performance during the first two trials for the consistent group was .98 (SE = .02) and for the inconsistent group was .88 (SE = .12). Although the difference in performance between the consistent group and the inconsistent group was in the expected direction, only one pigeon in the inconsistent group showed disruption, and none of the pigeons in the consistent group showed disruption. Thus, the difference was not statistically significant, $F(1, 6) < 1.00$. Apparently, once the discrimination was acquired, observation of an inconsistent discrimination did not significantly disrupt the pigeons' performance.

Reversal Training

The number of sessions to reverse for each pigeon is presented in Table 5. The mean number of sessions to reverse for the consistent reversal group was 5.25 (SE = 1.25) and for the inconsistent reversal group was 8.00 (SE = 0.41). Sessions-to-criterion scores, overall, as well as sessions-to-criterion scores for each component of the conditional discrimination are presented in Figure 3. The difference between the groups was not quite significant, $F(1, 6) = 4.37$, $p = .08$. As previously mentioned, 1 pigeon showed disruption in performance following the test (performance

Table 4
Mean Proportion of Correct Responses for Each Pigeon in Each Group During the Last Training Session and During the First Two and First Six Trials Following Observation in Experiment 2

	Proportion correct		
Group	Last training session	First two trials[a]	First six trials[a]
Consistent			
	.99	.95	.95
	1.00	1.00	1.00
	1.00	1.00	1.00
	1.00	1.00	1.00
Inconsistent			
	1.00	.50	.75
	1.00	1.00	1.00
	.97	1.00	.96
	1.00	1.00	1.00

[a] Following observation.

Table 5
Number of Sessions to Reverse Each Trial Type for Each Pigeon in Experiment 2

	Trial type		
Group and pigeon	Peck	Step	Both
Consistent			
1	4	6	9
2	4	4	4
3	4	4	4
4	3	4	4
M (SE)	3.8 (0.5)	4.5 (1.0)	5.2 (2.5)
Inconsistent			
1	4	6	7
2	7	4	9
3	7	6	8
4	8	6	8
M (SE)	6.5 (1.7)	5.5 (1.0)	8.0 (0.8)

dropped from 1.00 to 0.50 during the first two trials following observation and recovered to only 0.75 by the end of the first block of six trials). When the overall sessions-to-criterion data were analyzed without that pigeon, the mean number of sessions to reverse for the consistent reversal group was 4.00 ($SE = 0.00$), which was significantly lower than the sessions to reverse for the inconsistent reversal group, $F(1, 5) = 68.57$, $p < .001$. Although the data from this pigeon cannot be ignored, it is interesting that without this pigeon's data, the results suggest that observers' reversal performance was affected by the demonstrators' behavior.

The number of sessions to acquire each behavior separately was also analyzed. When the data from all pigeons were considered, the consistent reversal group acquired pecking significantly faster than the inconsistent reversal group, $F(1, 6) = 9.31$, $p < .05$. However, the consistent reversal group did not acquire stepping significantly faster than the inconsistent reversal group, $F(1, 6) = 2.00$, *ns*. Again, when data from the pigeon whose performance was disrupted during the test was excluded from the analysis, the consistent reversal group acquired both pecking and stepping more quickly than the inconsistent reversal group, $F(1, 5) = 7.11$, $p < .05$, and, $F(1, 5) = 6.43$, $p = .05$, respectively.

Experiment 3

Although the test following observation in Experiment 2 did not affect the observers' performance significantly, that manipulation may have affected the observers' subsequent reversal performance. Each observer that was exposed to a demonstrator whose behavior was consistent with the test was later exposed to a demonstrator whose behavior was inconsistent with the reversal task. Exposure to a demonstrator performing the reversal at a time when the reversal was incorrect could have encouraged pigeons in the consistent reversal group to ignore the behavior of the demonstrator and diminish the magnitude of the effect found. Consistent with this hypothesis, the pigeon that showed the most disruption following the first test in Experiment 2 was also the pigeon that subsequently reversed most slowly. The purpose of Experiment 3 was to replicate the effects of observation of discrimination consistent with or inconsistent with reversal learning as in Experiment 2 but without the prior test, which occurred at the end of acquisition (the first test). Experiment 3 was similar to Experiment 2 except that the first test and retraining phases were omitted in Experiment 3.

Method

Subjects and Apparatus

Eight white Carneaux pigeons similar to those used in Experiments 1 and 2 served as observers. The 2 demonstrators from Experiment 2 served as demonstrators. The experimental chamber used in Experiments 1 and 2 was used.

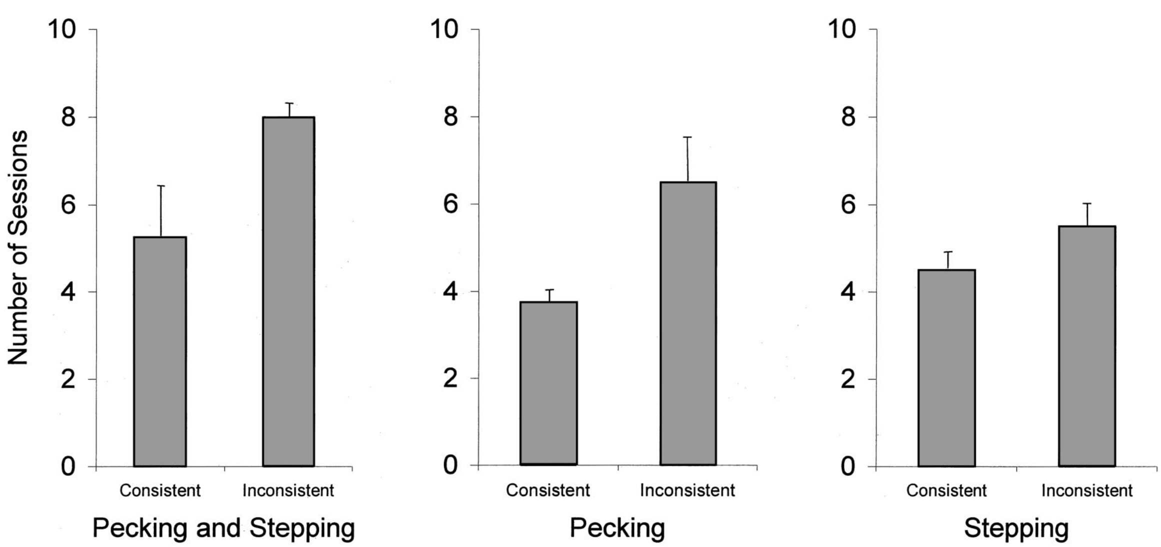

Figure 3. The number of sessions to reach criterion during both cues and during the stepping and pecking cue individually in Experiment 2.

Procedure

The procedure was identical to the procedure of Experiment 2, except that the observation–test and retraining phases were omitted. As in Experiment 2, observers were trained to step in the presence of one houselight and to peck in the presence of the other houselight and then were exposed to an observation–reversal phase similar to that of Experiment 2.

Results and Discussion

The mean number of sessions to acquire the overall discrimination for the consistent reversal group was 12.00 ($SE = 6.42$) and for the inconsistent reversal group was 14.00 ($SE = 2.92$). This difference was not statistically significant, $F(1, 6) < 1.00$.

The number of sessions to reverse the discrimination for each pigeon is presented in Table 6. The mean number of sessions to reverse for the consistent reversal group was 5.25 ($SE = 0.48$) and for the inconsistent reversal group was 12.00 ($SE = 2.28$). Overall session-to-criterion scores for each group as well as sessions-to-criterion scores for each component of the conditional discrimination appear in Figure 4. The difference in sessions to reverse between the groups was statistically significant, $F(1, 6) = 8.44$, $p < .05$. Therefore, pigeons that observed a demonstration of the reversal that was consistent with what had to be performed acquired the reversal faster than pigeons that observed a demonstration that was inconsistent with what had to be performed. When the number of sessions to reach criterion for each behavior was analyzed separately, the consistent reversal group acquired stepping significantly faster than the inconsistent reversal group, $F(1, 6) = 9.42$, *ns*. However, the consistent reversal group did not acquire pecking significantly faster than the inconsistent reversal group, $F(1, 6) = 1.74$, *ns*.

As in the other experiments, proportion correct did not differ between the groups during the first block of trials following the first observation session, and it did not differ during the first session following observation (both *t*s < 1). If the pigeons' reversal was affected by observation, the two groups might show a difference in performance immediately following observation. That is, the consistent reversal group might show relatively more improvement after observation than the inconsistent reversal group. In fact, the inconsistent reversal group might even be expected to perform worse after observation. Sessions were divided into four blocks of six trials each. To measure the change in performance following observation, we compared blocks immediately after observation with blocks immediately before observation (the last six trials from the previous session). A mixed, repeated measures ANOVA was performed to determine whether the proportion of correct responses during the blocks immediately preceding observation differed from the blocks immediately following observation as a function of group (see Table 7). *Before trials* included the last six trials of each session, whereas *after trials* included the first six trials of each session, which were those trials that immediately followed observation of a demonstrator. For example, Block Position 1 refers to the last six trials of the first session of reversal training (before trials) and the first six trials of the second session of reversal training (after trials). Therefore, after trials should be those trials that were most affected by observation. A three-way, mixed, repeated measures ANOVA with group (consistent reversal vs. inconsistent reversal), block type (blocks immediately preceding observation vs. blocks immediately following observation), and block position (four pairs of before and after blocks) as factors revealed significant main effects of block type, $F(1, 6) = 6.47$, $p < .05$, and of block position, $F(3, 18) = 12.72$, $p < .001$. Furthermore, a significant Group × Block Type interaction indicated that the consistent reversal group's performance increased more following observation than the inconsistent reversal group's performance, $F(1, 6) = 9.41$, $p < .05$. Finally, a significant Group × Block Position interaction showed that over the four six-trial blocks, the consistent reversal group's performance improved more quickly than the inconsistent reversal group's performance, $F(3, 18) = 5.63$, $p < .01$. Therefore, the performance of the observers was significantly affected by the behavior of the demonstrators.

Table 6
Number of Sessions to Reverse Each Trial Type for Each Pigeon in Experiment 3

Group and pigeon	Trial type		
	Peck	Step	Both
Consistent			
1	4	3	5
2	4	4	4
3	6	5	6
4	6	5	6
M (SE)	5.0 (1.2)	4.2 (1.0)	5.2 (1.0)
Inconsistent			
1	7	9	9
2	2	8	8
3	16	6	18
4	11	13	13
M (SE)	9.0 (5.9)	9.0 (2.9)	12.0 (4.5)

General Discussion

The results of the present experiments suggest that pigeons are able to learn from observing the specific conditional discrimination behaviors of other pigeons. In Experiment 1, pigeons observed demonstrators stepping in the presence of one cue and pecking in the presence of another cue, but when the observers were trained to perform either the same or the opposite discrimination, acquisition was not significantly affected by observation. In Experiments 2 and 3, observation did appear to affect reversal of the conditional discrimination.

During the reversal phase of the experiment, although each of the required behaviors, pecking at and stepping on the treadle, was not novel, the conditions under which those behaviors would be reinforced had never been experienced by the pigeons before. The fact that the present task involved a conditional discrimination that tested performance following (rather than simultaneously with) observation should be sufficient to rule out contagion as a mechanism responsible for the present results.

The requirement that a behavior must be novel to be truly imitative (Moore, 1992, 1996) was originally suggested by Thorpe (1963) to avoid considering various contagious behaviors as imitative learning. If novelty of behavior is used as a necessary criterion for imitation, then it is not clear how it could ever be

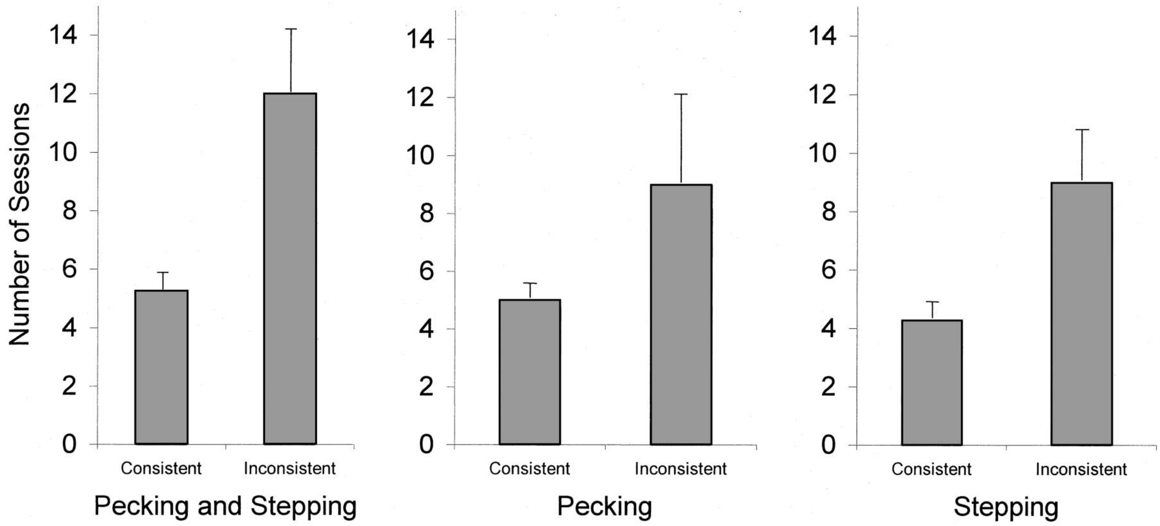

Figure 4. The number of sessions to reach criterion during both cues and during the stepping and pecking cue individually in Experiment 3.

ensured that the target behavior is actually novel. In fact, it can be argued that any form of training can only increase the probability of behavior that already exists in an animal's repertoire (although often with a very low probability). Rather than requiring that a behavior be novel, it makes more sense to require that a behavior have a relatively low probability of occurrence under the conditions being tested. Such a requirement is satisfied in the present experiments.

How are pigeons capable of imitating the behavior of others? One proposed mechanism is that the sight of an animal performing a behavior is a releaser for the same behavior in another animal (Meltzoff, 1996). That is, the sight of a demonstrator pecking at a treadle releases pecking at the treadle by the observer, and the sight of a demonstrator stepping on a treadle releases stepping on the treadle by the observer. This account requires that there is a genetically predisposed tendency to peck when other pigeons are pecking and to step when other pigeons are stepping. Furthermore, these tendencies must extend beyond the period of observation to a time when the demonstrators are no longer there and the observers are moved to the demonstrator's compartment. In fact, these releasers must be capable of releasing behavior as long as 30 min after observation (Dorrance & Zentall, 2001). In addition, the present results suggest that the released behavior is conditionally affected by the color of the houselight in effect at the time of observation during each of the two responses. To attribute such an effect to released behavior stretches the notion of a releaser well beyond that intended by those who use the term to indicate an immediate, elicited behavior (e.g., see Hinde, 1970, p. 240).

In contrast to this relatively simple mechanism, a perspective-taking mechanism has been suggested as underlying imitation in humans (Piaget, 1962). According to this account of imitation, in order to imitate, an observer must be able to take the perspective of the demonstrator and have knowledge that the demonstrator's actions are the same as the observer's own. Although it would seem that any evidence showing that pigeons can use their imitative abilities flexibly would suggest that pigeons are not simply responding reflexively to the pecking or stepping of the demonstrators; it also does not seem likely that pigeons are able to take the perspective of others. Thus, an adequate explanation of imitative learning is not presently available.

The results of the present experiments suggest that imitative learning by pigeons is quite flexible. Although individual differences in the rate of acquiring the conditional discrimination involving two different responses likely masked differences in the rate of acquisition for the consistent and inconsistent conditions, when the conditional discriminations were reversed, the pigeons benefited from the opportunity of observing a model perform the appropriate conditional discrimination. The results of the present

Table 7
Mean Proportion Correct Before and After Observation for Consistent Reversal and Inconsistent Reversal Groups in Experiment 3

	Block Position 1		Block Position 2		Block Position 3		Block Position 4	
Group	Before	After	Before	After	Before	After	Before	After
Consistent	.10 (.05)	.25 (.06)	.19 (.08)	.24 (.11)	.40 (.04)	.68 (.12)	.73 (.13)	.90 (.03)
Inconsistent	.18 (.11)	.17 (.11)	.27 (.15)	.46 (.10)	.36 (.23)	.21 (.21)	.46 (.17)	.37 (.16)

Note. Standard errors are presented in parentheses.

experiments extend the findings of earlier research using the two-action method to include more complex learning tasks.

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