

# Imitation and Affordance Learning by Pigeons (*Columba livia*)

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The bidirectional control procedure was used to determine whether pigeons (*Columba livia*) would imitate a demonstrator that pushed a sliding screen for food. One group of observers saw a trained demonstrator push a sliding screen door with its beak (imitation group), whereas 2 other groups watched the screen move independently (possibly learning how the environment works) with a conspecific either present (affordance learning with social facilitation) or absent (affordance learning alone). A 4th group could not see the screen being pushed (sound and odor control). Imitation was evidenced by the finding that pigeons that saw a demonstrator push the screen made a higher proportion of matching screen pushes than observers in 2 appropriate control conditions. Further, observers that watched a screen move without a demonstrator present made a significantly higher proportion of matching screen pushes than would be expected by chance. Thus, these pigeons were capable of affordance learning.

Imitative learning can be described as a form of social learning that involves the acquisition of motor behavior that is facilitated by observing the performance of another organism. Although it is difficult to define imitation more precisely than that, one can more easily distinguish between imitation and other forms of social learning.

## Nonimitative Forms of Social Learning

### *Contagion*

Particular species-typical behaviors can be released when an animal observes an animal of the same species (a conspecific) engage in the behavior (Thorpe, 1963). Examples of contagious behavior include laughing and yawning in humans and mobbing and flocking in several bird species. Because contagious behavior is automatically released, it is not considered to be imitative. In studying imitation, contagion can be avoided by focusing research on the copying of arbitrary or improbable behaviors and by separating the period of observation from the period of observer performance.

### *Mere Presence*

Even if a behavior is not contagious, the mere presence of another animal can alter an animal's motivation (social facilitation), thus affecting subsequent behavior (Zajonc, 1965). In general, the presence of another animal seems to enhance performance of well-learned tasks but hinder performance when the task is

difficult or unfamiliar. Although the mechanisms underlying mere presence effects are not well understood, Zajonc (1965) hypothesized that the presence of an audience may increase arousal by activating the endocrine systems and elevating hydrocortisol levels. Such effects can be controlled for in imitation experiments by including a group of observers that view a conspecific that does not perform the target behavior. In this way, both experimental and control animals should experience the same level of social facilitation.

### *Local and Stimulus Enhancement*

The activity of a conspecific at a particular location may draw an observer's attention to that location. This effect, known as local enhancement, may result in an increased likelihood that the observer will approach the same area (Roberts, 1941). Similarly, the activity of a conspecific toward a particular object may draw an observer's attention to the object. This effect, known as stimulus enhancement, may result in an increased likelihood that the observer will contact the object (Spence, 1937). Controlling for local enhancement and stimulus enhancement effects is more complex than controlling for contagion and social facilitation because the location and the stimulus are often integral to the target task. For this reason, controls for local enhancement and stimulus enhancement are discussed later.

### *Learned Affordances*

Tomasello (1990) proposed that emulation (or affordance learning) could account for many reported instances of animal imitation. According to Tomasello (1996), when an animal observes the behavior of another animal, it may not learn about the observed behavior but rather it may learn only about the changes in the environment that result from the observed behavior. For example, if an animal watches another animal open a nut by hitting it against a rock, the observer could learn that nuts can be opened to obtain food and that when a rock makes sharp contact with a nut, the nut may open, rather than learning about the nut-opening behavior of the demonstrator.

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Thus, in principle, affordances can be learned in the absence of a demonstrator. For example, if an animal sees a nut fall from a tree and break when hitting a rock, the observer could learn from this observation that nuts break and that rocks break nuts. Therefore, a study that attempts to separate affordance learning from imitation might include a group of observers that see an object move in the absence of a demonstrator or in the presence of an animal that is not demonstrating. In this way, one can differentiate between affordance learning and imitation.

### Testing for Imitation

#### *Two-Action Procedure*

An approach that provides an unconfounded test for imitation is the two-action procedure. With this procedure, observer animals are exposed to a demonstrator performing one of two different behaviors involving an object (e.g., something to be manipulated). This procedure places the focus of the study on the behavior, rather than on the outcome. Thus, the two-action procedure controls for local enhancement, stimulus enhancement, and learned affordances because although the observed behaviors are different, the object moves in the same manner (e.g., up and down) and its movement has the same consequence (raising the feeder). Therefore, merely learning how the object moves and the consequence of its movement should not lead observers to use the same behavior as the demonstrator.

Zentall, Sutton, and Sherburne (1996) exposed observer pigeons to a demonstrator either pecking at or stepping on a small platform (treadle) for a food reward. Observers were then allowed to manipulate the treadle. Evidence for imitation was found when observers showed a significant tendency to make the treadle response in the same way that they saw it performed by the demonstrator. Similar results were found with Japanese quail (Akins & Zentall, 1996, 1998).

#### *Bidirectional Control Procedure*

A variation of the two-action procedure, called the bidirectional control procedure, was developed by Heyes and Dawson (1990). In Heyes and Dawson's version of the bidirectional control procedure, observer and demonstrator rats were placed in separate chambers, facing each other, with a clear wall between them. Observer rats were exposed to a demonstrator that pushed an overhead pole consistently in one direction (to the left or to the right) for a food reward (see Figure 1). After the demonstrator was removed, observers were placed in the demonstrator's chamber and were allowed to push the pole in either direction for food. Heyes and Dawson found that observer rats pushed the pole significantly more often in the same direction as their demonstrators, even though, during test, observers had to move the pole in the opposite direction, relative to their own bodies during observation. To control for learned affordances, Heyes, Dawson, and Nokes (1992) manipulated the spatial location of the pole between observation and performance (they moved the pole to a perpendicular wall within the chamber) and found that observer rats continued to push the pole in the same relative direction as their demonstrators. The bidirectional control procedure has the advantage that it allows for the comparison of symmetrical behaviors

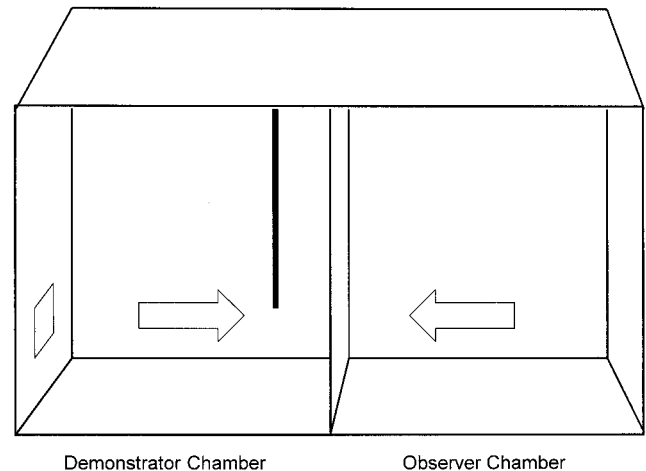


Figure 1. Diagram of the apparatus used by Heyes and Dawson (1990). Adapted from "A Demonstration of Observational Learning in Rats Using a Bidirectional Control," by C. M. Heyes and G. R. Dawson, 1990, *Quarterly Journal of Experimental Psychology: Comparative and Physiological Psychology*, 42(B), p. 63. Copyright 1990 by Psychology Press. Adapted with permission.

(behaviors that differ only in direction) that are of comparable difficulty (presumably, it is just as easy to move the pole to the right as it is to move the pole to the left).

Recently, however, Mitchell, Heyes, Gardner, and Dawson (1999) discovered that odor cues left on the pole by the demonstrator rats were probably responsible for the similarity between the demonstrators' and observers' behaviors. When observer rats saw a demonstrator push the pole in one direction but were then tested with the pole rotated 180° on its central axis (i.e., twisted), observer rats failed to imitate the demonstrator. Instead, they tended to push the pole in the opposite direction. In spite of the apparent problem with odor cues, if an appropriate control group is included, the bidirectional control procedure still may provide a useful test for imitation, particularly in an avian species, such as the pigeon, for which odor cues are not likely to be important (Mitchell et al., 1999).

Recently, Akins, Klein, and Zentall (2002), using an adapted version of the bidirectional control procedure, found evidence for imitation in Japanese quail. Akins et al. exposed quail observers to a demonstrator pushing a sliding screen to the left or to the right to obtain food. Quail in a control group observed a demonstrator that stood away from the screen as it was moved to the left or to the right by a hidden experimenter. Observers that saw a demonstrator push the screen made a significantly greater proportion of screen pushes in the direction that they saw it pushed than observers that saw the screen move independently of the demonstrator.

The purpose of the present experiment was two-fold: first, to replicate with pigeons the results obtained by Akins et al. (2002) while controlling for learned affordances as well as other nonimitative social effects and, second, to extend the findings of Akins et al. by determining whether pigeons can demonstrate affordance learning. Specifically, one group of observers saw a trained demonstrator pigeon push a sliding screen door either to the left or to the right with its beak (imitation group), whereas two other groups

of observers watched the screen move independently with a conspecific either present (affordance learning with mere presence) or absent (affordance learning). A fourth group could not see the screen being pushed (sound and odor control). The measure of interest was the effect of group assignment on the proportion of screen pushes made by the observers during test that matched the direction they saw the screen move.

If pigeons imitate the direction in which the screen is pushed, then observers that watch a demonstrator push the screen should make a significantly higher proportion of screen pushes in the same direction as their demonstrator, as compared with observers that see the screen move in the presence of a nonpushing demonstrator (these two conditions are equated for mere presence effects).

Although pigeons that see the screen move in the presence of a nonpushing demonstrator will not have another pigeon to imitate, they do have the benefit of seeing the screen move (affordance learning). However, according to Zajonc's (1965) theory (see also Zentall & Levine, 1972), it may be that observers that watch a nonpushing demonstrator will show impaired acquisition relative to similar observers that have no demonstrator present because of mere presence effects. In this case, observers that watch a screen move in an empty chamber may match screen pushes observed more than observers that see a screen move independently, with a nonperforming conspecific present. To assess the effects of pure affordance learning, we compare response-matching behavior by pigeons in the affordance condition with no demonstrator present with chance because there is no appropriate comparison group for this condition.

Finally, sound and odor cues are not expected to play a role for pigeons, but to determine if they might account for imitation effects, we compare the performance of observers that cannot see their demonstrator push the screen with those in the imitation condition.

## Method

### Subjects

Fifty-eight White Carneaux pigeons (*Columba livia*) of unknown sex served as subjects. Originally, 40 birds were randomly selected to serve as observers and 6 as demonstrators. However, 12 observers did not make any responses during test. Therefore, an additional 12 pigeons were added as observers to obtain an equal number of responders in each group. The pigeons were retired breeders obtained from the Palmetto Pigeon Plant (Sumter, SC). The pigeons were individually caged and maintained at 80% of their free-feeding body weights for the duration of the experiment. The birds had free access to water and grit in their home cages. The pigeon colony room was maintained under a 12-hr light-dark cycle. The pigeons' care was in accordance with University of Kentucky institutional guidelines.

### Apparatus

The apparatus used in the experiment was the same as that used by Akins et al. (2002). The apparatus consisted of two Large Modular Test Chambers (Model E10-10, Coulbourn Instruments, Lehigh, PA) placed side by side (see Figure 2). Each chamber measured 30.5 cm high, 25.5 cm wide, and 28.0 cm long. The sidewalls of each chamber were made of clear Plexiglas, which allowed observers to view the demonstrator. Doors on the outside sidewalls of each chamber allowed access to the chambers. The

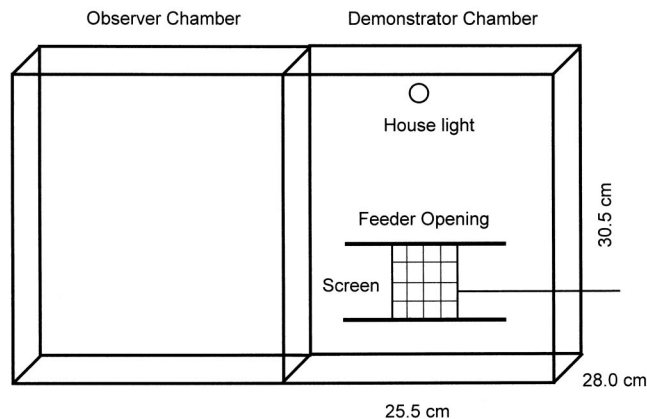


Figure 2. Schematic of the imitation box.

front wall of the demonstrator chamber included a rectangular feeder opening, a feeder light, and a white house light that provided general illumination. The feeder opening could be covered with a 7.6 cm high  $\times$  5.0 cm wide sliding screen with holes measuring 2.5 cm high  $\times$  1.5 cm wide. The screen was attached to a stiff wire that extended outside of the demonstrator chamber and allowed the experimenter to push or pull the screen in front of or to either side of the feeder opening. Pigeons could access food (Purina Pro Grains) through the feeder opening when the feeder tray was raised and the screen was pushed to either side. Whenever the feeder was raised, the feeder light was turned on. The observer chamber did not contain a feeder opening, a feeder light, or a house light.

### Procedure

All pigeons were trained to eat from the feeder when it was raised. Pigeons were considered feeder trained when they would eat from the feeder 24 times within a 10-min session for 10 consecutive sessions. During feeder training, the pigeons were allowed 2-s access to food before the feeder tray dropped and the pigeon experienced a 10-s intertrial interval (ITI). During feeder training, the screen was secured in an open position to the left or right of the feeder opening (alternated daily) prior to the start of the session.

**Demonstrator training.** Following feeder training, 2 demonstrators were trained to access food by pushing the screen to the left, and 2 different demonstrators were trained to access food by pushing the screen to the right. To ensure that observers in the no-push condition would not attribute the screen movement to a demonstrator, we trained two additional demonstrators to stand back from the feeder while the experimenter moved the screen to the left or to the right. Once the screen was moved to one side, the demonstrators were allowed 2-s access to food. During the ITI, the screen was repositioned in front of the feeder. For the demonstrators, the screen was prevented from moving in a direction other than the one specified by the demonstrator's assigned condition. Demonstrators were considered trained when they were able to complete 48 trials within 20 min for 10 consecutive days. During training, a bird otherwise not involved in the experiment was placed in the observer chamber to allow the demonstrators to habituate to the presence of an observer.

**Observer pretraining.** After feeder training, observers were habituated to the observer chamber during ten 10-min sessions with no demonstrator present. Observers were randomly assigned to one of four conditions (push, no push, no demo, or vision blocked). Originally, 10 birds were assigned to each condition. However, once birds were added to replace nonresponders, there was a total of 10 birds in the push condition, 15 birds in the no-push condition, 15 birds in the no-demo condition, and 12 birds in the vision-blocked condition. Within each condition, the screen moved to the

left for half of the birds and to the right for the remaining birds. If an observer did not make any responses during test, then the replacement bird saw the screen move in the same direction as the bird it replaced.

**Observer training.** For all observers, training consisted of a 48-trial observation period in the observer chamber. The experimental design described below for each group is shown in Table 1.

**Push condition.** The push condition tested for imitation. During observation, observers in the push condition were exposed to a demonstrator performing its push-left or push-right response for one 48-trial session. Five observers in the push condition saw a demonstrator push the screen to the right (away from the observer), whereas 5 other observers saw a demonstrator push the screen to the left (toward the observer). By pushing the screen, demonstrators obtained 2-s access to food reward followed by a 10-s ITI.

**No-push condition.** The no-push condition allowed for affordance learning while controlling for the presence of a demonstrator. Nine observer pigeons in the no-push condition were exposed to a demonstrator that stood away from the feeder as the experimenter used the stiff wire to move the screen to the right. For the remaining 6 no-push observers, the screen moved to the left. Once the screen was moved, the demonstrator pigeon was allowed to eat for 2 s followed by a 10-s ITI.

**No-demo condition.** Observers in the no-demo condition were not exposed to a demonstrator. Instead, 7 observer pigeons in the no-demo condition were allowed to watch the screen being pushed to the right by the experimenter. Eight other no-demo observers were allowed to watch the screen being pushed to the left. During each trial, the no-demo observers could see the feeder rise and the screen move. The feeder remained up for 2 s followed by a 10-s ITI. The no-demo condition allowed for pure affordance learning in the absence of another pigeon.

**Vision-blocked condition.** The vision-blocked condition controlled for the effects on the observers of any possible odor cues left on the screen and for possible auditory cues that may have been produced by the demonstrator. Observers in the vision-blocked condition were not able to see their demonstrator because a cardboard partition was placed between the observer and demonstrator chambers. For 7 observer pigeons in the vision-blocked condition, the demonstrator pushed the screen to the right and received 2-s access to food followed by a 10-s ITI. For 5 vision-blocked observers, a demonstrator pushed the screen to the left for the same outcome.

**Observer test.** Immediately following the observation period, the demonstrator (if present) was removed from the demonstrator chamber. The screen was unblocked so that it could move freely in either direction, and the screen was centered over the feeder opening. The observer was then placed in the demonstrator chamber for a 20-min test session. Observers in all conditions were allowed to move the screen to an open position in either direction. All screen pushes, regardless of direction, were reinforced with 2-s access to food, followed by a 10-s ITI. As with the demonstrators, during the ITI, the screen was repositioned in front of the feeder. Pushes

were defined as moving the screen sufficiently to the left or to the right of the feeder opening to allow the observer to eat. During test, the experimenter recorded the frequency of left and right pushes.

Comparison of the push and no-push conditions provided a measure of imitation. Comparison of the no-demo and no-push conditions provided a measure of the effects of the mere presence of another pigeon. Comparison of the no-demo condition to chance provided a measure of pure affordance learning. Comparison of the push and vision-blocked conditions provided a measure of the contribution of sound and odor cues to response matching.

## Results

All observers in the push condition pushed the screen at least once during test. However, only 10 of the 15 observers in the no-push condition, 10 of the 15 observers in the no-demo condition, and 10 of the 12 observers in the vision-blocked condition made at least one push during test.

For those pigeons that made at least one response during test, the proportion of matching pushes (pushes made in the same direction as demonstrated) was calculated by dividing the number of pushes made in the same direction as the screen moved during the observation period by the total number of pushes. Because proportion scores are typically not normally distributed, the proportions were transformed using the arcsine transformation. A two-way analysis of variance (ANOVA) was conducted to evaluate the effects of condition (push, no push, no demo, and vision blocked) and direction (left vs. right) on the proportion of matching pushes. The means and standard deviations for the proportion of matching pushes as a function of the two factors are presented in Table 2.

The ANOVA performed on the transformed scores indicated there was a significant main effect of condition,  $F(3, 32) = 3.15$ ,  $p < .05$ . However, there was not a significant main effect of direction,  $F(1, 32) = 2.88$ ,  $p > .05$ , nor was there a significant Condition  $\times$  Direction interaction,  $F(3, 32) = 1.02$ ,  $p > .05$ . To further investigate the main effect of condition, we pooled the data over direction, and the mean proportions of matching responses made by observers in selected conditions were compared.

### Imitation

To test for imitation, we compared the performance by observers in the push and no-push conditions. Observers in the push condition made a significantly higher proportion of matching pushes (.84) than observers in the no-push condition (.58),  $t(18) = 3.26$ ,  $p < .01$  (see Figure 3).

### Mere Presence

To test for the effects of mere presence, we compared performance by observers in the no-demo and no-push conditions. Although observers in the no-demo condition made a higher proportion of consistent screen pushes (.74) than observers in the no-push condition (.58), this difference was not statistically significant,  $t(18) = 1.69$ ,  $p > .05$  (see Figure 3).

### Affordance Learning

To test for affordance learning, we compared the proportion of matching screen pushes made by observers in the no-demo condition (.72) to chance. A one-sample  $t$  test revealed that perfor-

Table 1  
Experimental Design

Group	Observation	Cues present
Push	Demonstrator pushing screen left or right	Demonstrator behavior, affordances, mere presence, odor, auditory
No push	Demonstrator standing away from screen while screen moves left or right	Affordances, mere presence
No demo	Screen moving left or right	Affordances
Vision blocked	Visual access blocked	Odor, auditory

Table 2  
*Mean Proportion of Matching Pushes and Standard Deviations for Each Condition*

Condition	Screen moved left				Screen moved right			
	Untransformed		Transformed		Untransformed		Transformed	
	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>
Push	0.826	0.167	1.020	0.274	0.864	0.116	1.120	0.306
No push	0.588	0.262	0.685	0.401	0.572	0.135	0.616	0.164
No demo	0.588	0.407	0.708	0.517	0.900	0.119	1.670	0.235
Vision blocked	0.488	0.329	0.555	0.417	0.698	0.314	0.825	0.390

Note.  $N = 10$ .

mance by observers in the no-demo condition was significantly different from chance,  $t(9) = 2.91$ ,  $p < .05$ .

### Sound and Odor Cues

To investigate whether sound and odor cues could be responsible for the matching screen-pushing behavior of the imitation group, we compared the performance by observers in the vision-blocked and push conditions. Observers in the push condition made a significantly higher proportion of matching screen pushes (.84) than observers in the vision-blocked condition (.59),  $t(18) = 2.41$ ,  $p < .05$  (see Figure 3).

### First Response

Analyses based on the proportion of matching screen pushes in each condition provide the best measure of response matching.

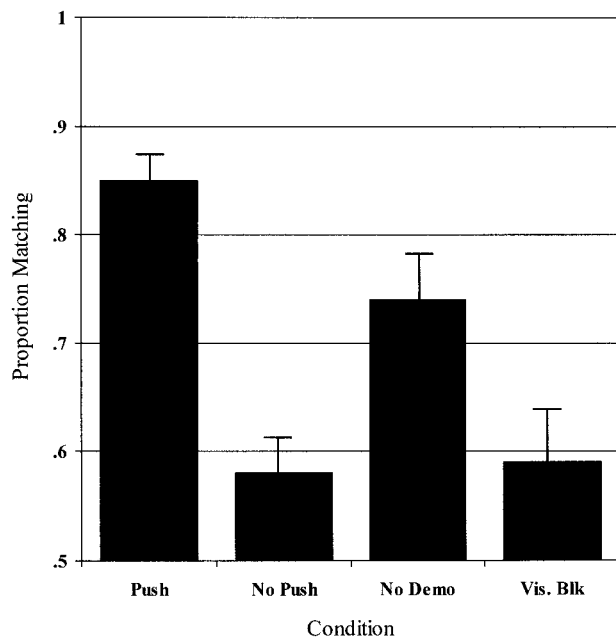


Figure 3. Mean proportion of matching screen pushes for each condition (untransformed). Error bars indicate standard errors of the means. Push = imitation condition; No Push = mere presence plus learned affordances condition; No Demo = learned affordances condition; Vis. Blk = vision-blocked (odor and auditory control) condition.

However, one can also ask about the direction of the first screen push. Given that there were only 10 birds in each condition that made at least one screen push, a nonparametric test, such as the chi-square statistic, must be used. Although the chi-square statistic does not provide a very powerful test, its power can be improved by combining the data from the two conditions that showed little evidence of screen-push matching (no-push and vision-blocked conditions) and comparing the number of birds in these two conditions that matched the direction of their first screen push with each of the other two conditions (push condition and no-demo condition). For the two control conditions, the first screen push matched the direction of the demonstrator for only 8 out of 20 birds, whereas for the push and no-demo conditions, the first screen push matched the direction of the demonstrator for 8 out of 10 birds in each condition. For each of these analyses,  $\chi^2(1, N = 30) = 7.29$ ,  $p < .01$ . Thus, relative to the two control groups, the first screen push showed significant evidence of both imitation and affordance learning.

Finally, a one-way ANOVA conducted on data obtained for all observers examining the effect of condition on the total number of screen pushes was not significant,  $F(3, 48) < 1$ ,  $p > .05$ . Table 3 presents the mean number of pushes for each condition.

### Discussion

Observers in the push condition made a significantly higher proportion of matching pushes than observers in the no-push conditions. This result is consistent with the result Akins et al. (2002) obtained with Japanese quail and provides evidence for imitative learning in pigeons. The no-push condition is the appropriate comparison group for the push condition because it controls for the presence of a conspecific.

Although the difference was not significant, the fact that pigeons in the no-demo condition showed a higher proportion of matching

Table 3  
*Mean Number of Pushes and Standard Deviations for Each Condition*

Condition	<i>N</i>	<i>M</i>	<i>SD</i>
Push	10	30.6	19.3
No push	15	32.0	26.8
No demo	12	33.9	26.7
Vision blocked	15	29.0	20.4

screen pushes than those in the no-push conditions is consistent with Zajonc's (1965) theory of social facilitation. Zajonc proposed that the acquisition of novel behavior could be impaired by the presence of a conspecific. It is interesting to note that observers in the push condition should have experienced the same mere presence effects that observers in the no-push condition did; however, it appears that the facilitation produced by the opportunity to imitate in the push condition overcame the possible inhibitory effects of the presence of another pigeon in the no-push condition. If mere presence of a conspecific prior to performance does inhibit the learning of affordances, it may be possible to reduce those effects by imposing a delay between observation and subsequent testing. In this way, the presumed arousal caused by the presence of a demonstrator should have a chance to dissipate. Such a delay could result in some memory loss; however, any loss attributable to forgetting should be comparable for all groups. Furthermore, previous research (Dorrance & Zentall, 2001) has shown that Japanese quail will imitate even after a 30-min delay between observation and performance.

Another important result of this experiment was that observers in the no-demo condition made a significantly higher proportion of consistent screen pushes than would be expected by chance. The results for the no-demo condition suggest that pigeons are capable of learning affordances through observation. To our knowledge, this is the first report of affordance learning by pigeons.

Finally, pigeons, unlike rats, do not appear to use odor cues (if there are any) left by a demonstrator to guide their behavior during test, nor do they appear to use auditory cues. These results support the hypothesis that the bidirectional control procedure is a viable means of testing for imitation in pigeons.

The results of this experiment are consistent with previous experiments assessing the imitative ability of pigeons. The results provide clear evidence for imitative learning in pigeons using the bidirectional control procedure. In addition, the results indicate that in the absence of a demonstrator, pigeons may be able to learn affordances.

The fact that imitation has been distinguished from affordance learning should not be taken to mean that affordance learning is an inferior phenomenon. In fact, to say that an animal learns how the environment works on the basis of an observation of that environment does not explain how, for example, seeing the screen move to the left causes the observer to move the screen to the left. One could posit the development of a Pavlovian association between a left-moving screen and food (sometimes referred to as observational conditioning; see Zentall, 1996), which might explain a preference for left-moving screens, but it does not explain how the observer learns to push the screen to the left. Learning about affordances may be different from imitation, but it is certainly not explained in simple learning terms. In fact, the ability of an animal

to learn affordances suggests an underlying mechanism that may be just as complex as imitation.

## References

- Akins, C. K., Klein, E. D., & Zentall, T. R. (2002). Imitative learning in Japanese quail using the bidirectional control procedure. *Animal Learning & Behavior*, *30*, 275–281.
- Akins, C. K., & Zentall, T. R. (1996). Imitative learning in male Japanese quail using the two-action method. *Journal of Comparative Psychology*, *110*, 316–320.
- Akins, C. K., & Zentall, T. R. (1998). Imitation in Japanese quail: The role of reinforcement of demonstrator responding. *Psychonomic Bulletin & Review*, *5*, 694–697.
- Dorrance, B. R., & Zentall, T. R. (2001). Imitative learning in Japanese quail depends on the motivational state of the observer quail at the time of observation. *Journal of Comparative Psychology*, *115*, 62–67.
- Heyes, C. M., & Dawson, G. R. (1990). A demonstration of observational learning in rats using a bidirectional control. *Quarterly Journal of Experimental Psychology: Comparative and Physiological Psychology*, *42*(B), 59–71.
- Heyes, C. M., Dawson, G. R., & Nokes, T. (1992). Imitation in rats: Initial responding and transfer evidence. *Quarterly Journal of Experimental Psychology: Comparative and Physiological Psychology*, *45*(B), 81–92.
- Mitchell, C. J., Heyes, C. M., Gardner, M. R., & Dawson, G. R. (1999). Limitations of a bidirectional control procedure for the investigation of imitation in rats: Odour cues on the manipulandum. *Quarterly Journal of Experimental Psychology: Comparative and Physiological Psychology*, *52*(B), 193–202.
- Roberts, D. (1941). Imitation and suggestion in animals. *Bulletin of Animal Behavior*, *1*, 11–19.
- Spence, K. (1937). Experimental studies of learning and high mental processes in infrahuman primates. *Psychological Bulletin*, *34*, 806–850.
- Thorpe, W. H. (1963). *Learning and instinct in animals* (2nd ed.). Cambridge, MA: Harvard University Press.
- Tomasello, M. (1990). Cultural transmission in the tool use and communicatory signaling of chimpanzees? In S. Parker & K. Gibson (Eds.), *Language and intelligence in monkeys and apes: Comparative developmental perspectives* (pp. 274–311). Cambridge, England: Cambridge University Press.
- Tomasello, M. (1996). Do apes ape? In C. M. Heyes & B. G. Galef (Eds.), *Social learning in animals: The roots of culture* (pp. 319–346). San Diego, CA: Academic Press.
- Zajonc, R. B. (1965, July 16). Social facilitation. *Science*, *149*, 269–274.
- Zentall, T. R. (1996). An analysis of imitation learning in animals. In C. M. Heyes & B. G. Galef (Eds.), *Social learning in animals* (pp. 221–243). New York: Academic Press.
- Zentall, T. R., & Levine, J. M. (1972, December 15). Observational learning and social facilitation in the rat. *Science*, *178*, 1220–1221.
- Zentall, T. R., Sutton, J. E., & Sherburne, L. M. (1996). True imitative learning in pigeons. *Psychological Science*, *7*, 343–346.

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