

Action imitation in birds

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Action imitation, once thought to be a behavior almost exclusively limited to humans and the great apes, surprisingly also has been found in a number of bird species. Because imitation has been viewed by some psychologists as a form of intelligent behavior, there has been interest in how it is distributed among animal species. Although the mechanisms responsible for action imitation are not clear, we are now at least beginning to understand the conditions under which it occurs. In this article, I try to identify and differentiate the various forms of socially influenced behavior (species-typical social reactions, social effects on motivation, social effects on perception, socially influenced learning, and action imitation) and explain why it is important to differentiate imitation from other forms of social influence. I also examine some of the variables that appear to be involved in the occurrence of imitation. Finally, I speculate about why a number of bird species, but few mammal species, appear to imitate.

The idea of a natural scale of intelligence has been around for some time, and remarkably, it is still quite popular (see Nakajima, Arimitsu, & Lattal, 2003). Although it has long been recognized that there are specialized cognitive abilities in animals (e.g., navigation by pigeons, scent tracking by dogs, spatial memory in rats, and food caching by birds), these abilities have often been discounted, perhaps because their specificity suggests that they may be genetically predisposed. Also, they have been discounted because they represent abilities that are not particularly well developed in humans, and we often judge the intelligence of animals relative to human measures.

Action imitation, the copying of another's behavior that can be seen, is one of those behaviors for which humans show great proficiency (see, e.g., Meltzoff, 1996). Thus, not surprisingly, it is considered by some to be an important indicator of human cognitive development (Piaget, 1962). But if imitation is considered a form of intelligent behavior, it must first be distinguished from other socially influenced behavior that may be controlled by simpler motivational, perceptual, and learning processes.

For many years, researchers have worked to develop designs and procedures that might adequately distinguish among these processes (Zentall, 2001). However, as procedures have been refined and data from a number of species have been collected, it has become clear that there are serious problems with theories that have represented attempts to order animal species according to intelligence and to view action imitation as a behavioral index of intelligence. Although several phylogenetically close primate species (e.g., chimpanzees and orangutans)¹ show good evidence of imitative learning (see, e.g.,

Whiten & Custance, 1996), perhaps the best evidence for imitation in nonape species comes, not from other primates, but from birds (e.g., parrots; Moore, 1996), some of which are not known for their remarkable intelligence (e.g., pigeons and Japanese quail; Zentall, 2003).

BIOLOGICAL FUNCTION VERSUS PSYCHOLOGICAL MECHANISM

The preceding discussion may make more sense to psychologists than to biologists, because researchers in the two fields tend to ask different questions about behavior. A biologist's interest in imitation stems not from its implications for a theory of intelligence, but from its potential function for the organism. For example, Boyd and Richerson (1988) have proposed that there are two major evolutionary strategies that regulate behavior, each of which has its drawbacks. First, and most universal, is species-typical behavior, which is primarily under genetic control. The benefit of species-typical behavior is its relative certainty. Birds do not have to rely on trial-and-error learning to build a nest. They are genetically predisposed or programmed to build them. On the other hand, there is a cost to such inflexible behavior. Should the environment change in a way that is inconsistent with an animal's predispositions, it may not be able to survive.

The response to this problem has been the evolution of flexible behavior in the form of (trial-and-error) learning. For example, in an unpredictable environment where ideal foods may not be available or where other animals may compete for that food, an animal may be predisposed to follow a more general rule: *If it looks like it might be food, try it. If the consequences are good, eat more. If the consequences are bad, stop eating it.* Learning by experience, this second evolutionary strategy, allows for rapid adaptation to a rapidly changing environment.

But learning by experience has its cost as well. For an animal to learn what not to eat, it must sometimes risk

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negative consequences that may result in sickness or even death. Thus, the evolutionary dilemma: Species-typical behavior may not be flexible enough, but learning may be dangerous.

The answer, according to Boyd and Richerson (1988), is social learning—learning from observation of the behavior of others. Social learning provides much of the flexibility of individual learning, with considerably less potential cost. Not only is it more efficient, in the sense that less time is lost making errors, but it is also less dangerous, in the sense that one does not have to suffer the consequences of those errors.

Thus, a biologist is more interested in how social learning contributes to the animal's survival and reproductive success than in the psychological mechanisms responsible for the behavior. Biologists may understand the distinctions that psychologists often make among different kinds of social-learning mechanisms, but they may not appreciate why those distinctions are often the focus of psychologists' attention.

The reason that psychologists devote so much attention to the various mechanisms that may underlie imitation is that imitation (especially where direct visual matching of behavior is not possible) has been viewed as an intelligent process that may be indicative of the higher level process known as perspective taking (the ability to imagine oneself in the place of another; Piaget, 1962). Alternatively, cross-modal matching has been suggested as a possible mechanism (Meltzoff, 1996). In cross-modal matching, the visual information provided by the model is actively compared with the proprioceptive feedback from the observer's own movements. Thus, if imitation were to be found, not just among our close primate relatives, but in a variety of species, it would require either that the capacity for perspective taking or cross-modal matching be attributed to a much broader range of species or that other mechanisms be proposed to account for imitation.

In the section that follows, I will attempt to outline the various kinds of social influence and learning and provide evidence for imitation in birds. Finally, I will speculate about why birds may be better imitators than many mammalian species.

SOCIAL INFLUENCE AND SOCIAL LEARNING BY BIRDS

Early research on social learning by birds did not distinguish among a number of underlying motivational, perceptual, and learning processes. In order to isolate the direct evidence for imitation, I will present some of the findings and identify some of the alternative mechanisms that might be involved.

Bird Song

The acquisition of song dialect by some birds can be viewed as a form of imitation, but most researchers place it in the category of vocal mimicry, rather than imitation, because of the special unimodal characteristic of the audi-

tory stimulus and response (see, e.g., Fritz & Kotrschal, 2002). Even when dialects are acquired only after a listener hears adult birds sing (Petrinovich, 1988), the song produced by the demonstrator and that produced by the listener are quite similar to the listener. That is, to the listener, the two behaviors show considerable sensory correspondence. This is the case because they both occur in the auditory modality. To put this attribute of bird song in more concrete terms, the listener can match the sound that it hears to the sound that it makes. Thus, bird song can be viewed as a special case of within-modality stimulus matching. In this form of stimulus matching, from the perspective of the animals doing the matching, the stimuli to be matched are perceptually similar to each other (see, e.g., Mowrer, 1960; Zentall, Edwards, & Hogan, 1983). To say that stimulus matching may account for certain kinds of imitation is not to depreciate these examples, because the ability to match stimuli implies the ability to use a generalized matching rule that can be acquired in one context and then applied in a different context.

A remarkable extension of song learning in birds has been demonstrated in grey parrots (e.g., Pepperberg, 2002). Pepperberg has shown not only that parrots can produce English speech sounds, but also that they can use what they learn appropriately to answer questions. An important characteristic of this kind of social learning that distinguishes it from other forms of vocal copying is that the copied sounds are clearly novel and cannot be specifically predisposed, as might be the case in the copying of songs that are merely variations of species-typical songs. Although this characteristic of vocal copying in parrots may warrant calling it imitative learning, the fact that it all occurs within a single modality puts it in a class that is conceptually different from the cross-modal matching that occurs when the visual appearance of the modeled behavior to the observer is quite different from the visual appearance of the observer's own behavior when it imitates. Imitation that must be described in terms of cross-modal matching or perspective taking is of particular theoretical interest because it appears to require a more cognitive explanation than do other examples of imitation. In recognition of the unique aspect of this form of imitation, Nehaniv and Dautenhahn (2002) have referred to it as the *correspondence problem*.

Contagious Behavior

Birds sometimes act in concert when they flock or attack a predator as a group (mobbing). These are species-typical defensive reactions shown by all members of the species. These behaviors are considered contagious because naturally occurring behavior is released by the sight of others engaged in that activity. Similarly, social-eating behavior may be considered contagious when it occurs in an animal presumed to be sated (as evidenced by its refraining from eating) but that resumes eating when a hungry animal is introduced. The term *contagion* is appropriate when the target behavior is clearly species typical and when the effect on the observer persists only

while the performing demonstrator is present. The term *contagion* has been used sometimes to indicate any behavior that may have been performed in the past (i.e., behavior that is not novel; see, e.g., Fritz & Kotschal, 2002). However, in practice, it may be impossible to determine whether or not a behavior is novel. For example, when a child imitates, how do we know that the child has never performed a similar behavior in the past? To the contrary, I think one can assume that it would be difficult to find a truly novel response, because in most cases, imitated behavior falls within the existing response repertoire of the observer (Whiten & Cusance, 1996).

Motivational Factors

Social facilitation. It has been shown that the mere presence of another animal may affect the motivation or arousal of the observer (Zajonc, 1965). An increase in motivation may cause the animal to be more active, and thus, because it is more likely to interact with its environment, it may be more likely to acquire a new response through individual learning. Similarly, in a novel fear-inducing environment, the mere presence of another animal may have a fear-reducing effect, and fear reduction can also lead to increased activity (Morrison & Hill, 1967).

Incentive motivation. Being in the presence of a demonstrator that is eating may increase arousal and activity beyond the level induced by a demonstrator's mere presence (see Zentall & Levine, 1972). A change in incentive motivation may also occur when the behavior to be acquired through observation is motivated by avoidance of an aversive effect. In this case, the motivation of the demonstrator may transfer to the observer either directly as a consequence of the demonstrator's contact with the aversive event (e.g., shock) or indirectly through behavioral evidence of the demonstrator's fear (John, Chesler, Bartlett, & Victor, 1968). Such transfer of fear may sensitize the observer to the aversive event, thus increasing its effect, which, in turn, could facilitate the acquisition of the avoidance response.

Perceptual Factors

When the observation of a demonstrator draws attention to the consequences of a response (e.g., a leverpress), it may alter the salience of the lever (stimulus enhancement) or the place where the lever is located (local enhancement).

Local enhancement. Local enhancement refers to the facilitation of learning that results from drawing attention to a locale or place associated with reinforcement (Roberts, 1941). For example, Lorenz (1935) noted that ducks enclosed in a pen may not react to a hole large enough for them to escape unless they happen to be near another duck as it is escaping from the pen. The sight of a duck passing through the hole in the pen may serve to draw attention to the hole.

Local enhancement has also been implicated in the finding that puncturing the top of milk bottles by great tits spread in a systematic way from one neighborhood to another (Fisher & Hinde, 1949). The technique of peck-

ing through the top of the bottle may be learned through observation; however, the mere presence of birds feeding from the bottles appears to be sufficient for observer birds to acquire the milk-bottle-opening behavior (Sherry & Galef, 1990).

Similarly, Zentall and Hogan (1976) found that pigeons that observed another pigeon pecking at a response key for food were more likely to peck that key, when given the opportunity, than were pigeons that had observed another pigeon not pecking at the key but eating from the feeder. Attention to the demonstrator's response key may have been sufficient to account for this facilitation of response acquisition by the observers.

Stimulus enhancement. When the activity of the demonstrator draws the attention of the observer to a particular *object* (e.g., something that must be the manipulated), such facilitation of responding is referred to as *stimulus enhancement*. Often, the stimulus object is at a particular location, so local and stimulus enhancement effects are confounded. For this reason, the term *stimulus enhancement* is used primarily when there are two similar objects to be manipulated, one for the demonstrator and the other for the observer, and they appear in different locations (e.g., the duplicate chamber; Zentall & Levine, 1972). Under these conditions, although attention to the location of the demonstrator's object should remove the observer's attention from its own object, the similarity between the two may result in attention to the observer's object as well (by means of stimulus generalization).

Stimulus enhancement is likely to have been involved in the spread of leaf chewing in a free-living flock of greylag geese (Fritz, Bisenberger, & Kotschal, 1999). Initially, 3 geese were observed to bite through and chew the stems of butterbur leaves, but within 2 years, 95 of the 130 individuals in the flock had acquired this behavior, and it appeared to spread particularly fast within families. Although it is difficult to isolate the mechanisms responsible for this spread of leaf chewing in this natural environment, it is quite likely that the observers were drawn to the leaves when they saw them being chewed by others. Stimulus enhancement probably was also responsible for the finding by Fryday and Greig-Smith (1994) that house sparrows preferred a particular colored food patch after having observed a trained demonstrator feed from the same colored patch more than they did when they saw it feed from a patch of a different color.

Social Learning

Observational conditioning. The observation of a performing demonstrator can do more than merely draw attention to the object being manipulated (e.g., a colored food patch). Because the observer's orientation to the object is often followed immediately by access to food being provided to the demonstrator, a Pavlovian association may be established. This form of conditioning, in which the observer learns the relation between some part of an environment and a reinforcer (e.g., an initially neutral stimulus and an aversive event [Cook, Mineka,

Wolkenstein, & Laitsch, 1985] or depression of a lever and the food that follows [Heyes, 1994]) has been called *observational conditioning*, or *valence transformation*. Although such conditioning would have to take the form of higher order conditioning (because the observer would not actually experience the unconditioned stimulus), there is evidence that such higher order conditioning can occur even in the absence of a demonstrator. For example, if the onset of a localizable light is soon followed by the presentation of inaccessible grain, pigeons will often peck at the light (Zentall & Hogan, 1975). The presence of a demonstrator drawing additional attention to the object (by pecking at it) and to the reinforcer (by eating it) may further enhance associative processes in the absence of imitative learning. What characterizes observational conditioning is that the associative process makes it more likely that the observer will approach the conditioned stimulus (the lever or response key) and activate it by chance.

Emulation, or learning affordances. A form of learning that is similar to observational conditioning is emulation (also called *object movement reenactment*). Emulation involves reproducing the *results* of a demonstrator's actions. For example, it is possible for an observer to learn about the consequences of the actions of the demonstrator without actually learning about the actions themselves. This kind of learning has sometimes been referred to as learning about the affordances of the task (Tomasello, 1996). For example, if a pigeon sees another pigeon pulling the stopper from a tube to obtain grain from the tube (Beauchamp, Giraldeau, & Dugatkin, 1994), the observer may learn that stoppers can be removed from tubes to get the grain inside without learning how to remove the stopper from the tube. Tomasello (1990) has argued that reproducing results does not necessarily imply an understanding of the *behavior* that led to those results. A clear example, attributable to emulation, has been provided by Meltzoff (1988). In his experiment, young children who were shown a toy that could be pulled apart by the experimenter pulled the toy apart themselves more often than did control children who were shown the toy but did not see it pulled apart. The problem is, seeing that the toy comes apart is apparently sufficient for the child to make the pulling-apart response (Huang, Heyes, & Charman, 2002; Meltzoff, 1995).

It should be noted, however, that learning about the affordances of the environment, although different from imitation, may not be a less complex process. In fact, the translation of an observed environmental relationship into behavior that produces the same consequence is a quite remarkable ability (see Klein & Zentall, 2003). I will return to the implications of emulation later.

Emulation is also likely to have been involved in an experiment reported by Huber, Rechberger, and Taborsky (2001), in which keas (a New Zealand parrot) observed a demonstrator removing several locking devices to open a box. Although, following observation, the observers were

not successful in opening the box, they explored the devices more and succeeded in unlocking more devices than did birds that had not observed demonstrators.

IMITATION

Imitation is a form of social learning that remains when one has ruled out or controlled for all of the alternative mechanisms that might contribute to the higher probability of a copied response. Although this is a negative definition of imitation, because it identifies what imitation is not, more positive definitions are accompanied by more serious problems. For example, Tomasello (1990) has proposed that an imitating observer understands that the demonstrator used particular actions with a particular goal in mind. Such inferences are difficult to make with human children and may be impossible to make with animals.

Action Imitation

To control for nonimitative factors, in most imitation research, an attempt is made to include comparison conditions that do not involve imitation (e.g., a social facilitation control). But it may not be possible to control adequately for all of the nonimitational factors that have been described by a process of elimination (e.g., by including a group that is not exposed to a performing demonstrator but controlling for the stimulus enhancement that may result from observation of a moving manipulandum). An alternative approach is to demonstrate different specific body movements to different observers. For example, Moore (1992) would wave his hand at his grey parrot while saying "caio" and found that the parrot waved back while saying "caio." Similarly, Moore would say "look at my tongue" while sticking out his tongue, and the parrot would do the same. Because these behaviors were not explicitly reinforced and were produced on cue, Moore concluded that they demonstrated imitation.

The Two-Action Procedure

The idea of action imitation can be incorporated into a better controlled design by defining different responses to be imitated that have individual topographies but have the same consequence. Ideally, the responses should have comparable probabilities of occurrence (i.e., they should be equally likely to occur by chance), but that is not critical. Half of the observers are exposed to one of the topographies, and the other half are exposed to another. Following observation, the observers are able to perform either topography to obtain reinforcement. The question is, what is the correlation between the topography of the response performed by the demonstrator and that performed by the observer?

The strength of this design lies in the fact that it controls for each of the alternative mechanisms described earlier. Because both groups have similar experiences with a demonstrator and with vicarious reinforcement, their motivational levels should be comparable. Because

the consequences of both topographies are the same, local and stimulus enhancement should be comparable for the two groups. And finally, because the results of the demonstrator's responses, and their relationship to reinforcement, should be the same for the two groups, emulation should be comparable as well. Thus, when this design is used, the only distinguishing feature between the two groups should be the two response topographies.

The first study in which a design of this type was used was reported by Dawson and Foss (1965). But rather than define two response topographies, they allowed demonstrators to discover on their own how to obtain reinforcement from a loosely covered container. By chance, the 5 demonstrators learned to remove the lid in three quite different ways, 2 by pushing the lid back with the beak, 2 by twisting the lid off with the beak, and 1 by pulling it off with the foot. Each of the demonstrators was observed by an observer, and when the observers were then presented with the covered containers, they removed the lid in the same way that they had seen it removed. Although a later attempt to replicate this effect (Galef, Manzig, & Field, 1986) produced weaker evidence of imitation, the potential strength of the design was recognized.

A similar approach was used by Campbell, Heyes, and Goldsmith (1999). Starlings, in the presence of conspecific observers, selected one of two distinctly colored stoppers and either pushed it into a container or pulled it out of the container, to obtain a food reward. When the observers were given the opportunity, they selected the same color, and they acted on it in the same way as their demonstrators (see also Fritz & Kotrschal, 1999; Heyes & Saggerson, 2002). However, in this particular experiment, selecting the same color can be explained in terms of stimulus enhancement. Furthermore, repeating the push or the pull action may have been influenced by the two different outcomes—the stopper moving into the container, in one case, or out of the container, in the other (i.e., differential emulation; see Fawcett, Skinner, & Goldsmith, 2002).

Heyes and Dawson (1990) developed a variation on the two-action procedure, which they called the *bidirectional control*. In this procedure, rats observed demonstrators that were expressly trained to push a vertical overhead pole either to the left or to the right. When the observers were then given access to the pole, Heyes and Dawson found that the rats tended to push the pole in the same direction as their demonstrators had pushed it. Remarkably, the observers matched the demonstrators' behavior despite the fact that, because the observers had faced the demonstrators during the period of observation, the direction of pole motion during observation (relative to the observer's body) had been opposite that of the pole's motion when the observers performed.

Later research suggested, however, that olfactory cues, specific to the side of the pole against which the demonstrators had pushed, were probably responsible for this response-matching effect (Heyes & Ray, 2000; Mitchell, Heyes, Gardner, & Dawson, 1999). Olfactory cues were

implicated because, when the pole was rotated 180° around its central axis following demonstration, the observers tended to push the pole in the direction opposite to that pushed by the demonstrators.

Recently, evidence for response matching has been found with the bidirectional control procedure in an experiment using Japanese quail (Akins, Klein, & Zentall, 2002). In this experiment, a screen that could be pushed either to the left or to the right was placed in front of the feeder, and demonstrators were trained to push the screen in one direction or the other. After each demonstrator performed the screen-pushing response for the observer, the observer was given access to the screen. As with the rat experiments, the Japanese quail showed a significant tendency to push the screen in the same direction that they had seen it pushed. Akins et al. also included control groups that saw the screen being moved either to the left or to the right by the experimenter by means of a stiff wire that projected outside the chamber. To control for the possible effects of the presence of other animals, an inactive demonstrator was also present. These *ghost controls* allow one to assess the effect on screen movement matching of merely seeing the screen move in one direction or the other (i.e., learning affordances). The birds in these groups showed no evidence of matching the direction in which they had seen the screen move when they were given access to the screen.

In a more recent experiment (Klein & Zentall, 2003), the results of the screen-pushing task were replicated with pigeons. Furthermore, Klein and Zentall included a group of observers that were exposed to screen-pushing demonstrators (either left or right), but with their view of the demonstrator being blocked. These groups served as a control for the contribution of possible olfactory and auditory cues to response matching. When these pigeons were then given access to the screen, they showed no evidence of response matching. Thus, olfactory and auditory cues are insufficient to account for the response matching that was found.

It should be noted, however, that the bidirectional control procedure suffers from an inherent interpretational problem. Because the manipulated object (i.e., the overhead pole, the stopper, or the feeder screen) moves in a different direction for the two observation groups, it is possible that response matching is facilitated by emulation of the movement of the object, rather than by imitation of the demonstrator's screen-pushing response. To rule out differential emulation, ideally, the object should move in the same way independently of the differential response made to it. A refined version of the two-action procedure, developed by Zentall, Sutton, and Sherburne (1996) for use with birds, met this requirement. To preclude differential learning about the environmental consequences of the two responses, the manipulated object, a treadle located just above the floor of the operant chamber, was constrained in how it could be moved. The treadle moved down only; similar to a rat lever, it was spring loaded to come back up. One group of demonstrators

was trained to depress the treadle with the beak, whereas another group was trained to depress the treadle with the foot. Thus, the only variable manipulated in this experiment was the topography of the demonstrator's response.

Following observation, when the observers were given access to the treadle, Zentall et al. (1996) found a significant correlation between the topography used by the observers and that used by their respective demonstrators. Furthermore, when control pigeons were exposed either to demonstrators that were not depressing the treadle at all or to an empty demonstrator compartment, there was no tendency for the observers to either peck at or step on the treadle (Kaiser, Zentall, & Galef, 1997). Even better evidence for observer/demonstrator matching behavior was found in a similar experiment conducted with Japanese quail (Akins & Zentall, 1996).

Two important points should be made about this procedure. First, the environmental consequences of stepping and pecking were the same, so the only difference between the behaviors was the two response topographies. Second, there is likely to have been very little similarity between the visual stimulus seen by the observer during observation and that seen by the observer during its own performance of that response. Specifically, to the observer, the demonstrator's beak on the treadle must have appeared quite different from the observer's own beak on the treadle. Similarly, although perhaps not so obviously, when a bird stepped on the treadle (located at the front of the chamber, near the common wall between the demonstrator and the observer), it pulled its head back and thrust its body forward. Thus, it could not see its foot making contact with the treadle. Once again, to the observer, the demonstrator's response to the treadle must have appeared quite different from the observer's own response to the treadle. It is quite implausible that visual stimulus matching could account for the imitation effects found in these experiments.

Demonstrator's incentive. If imitation is a cognitive process that reflects the observer's understanding of the behavior of the demonstrator and its consequences (Tomasello, 1990), whether the demonstrator's behavior is reinforced may be important to the observer. That is, one might expect that the observer would be more likely to imitate if the demonstrator's behavior resulted in reinforcement. Alternatively, it may be that imitation is a reflexive behavior that will occur independently of demonstrator reinforcement.

This hypothesis was tested in an experiment with Japanese quail (Akins & Zentall, 1998). Demonstrators were trained on either a rich schedule of continuous reinforcement for treadle pecks or treadle steps or a lean variable-interval schedule in which reinforcement for either pecking or stepping was provided for the first response that occurred after an unpredictable amount of time (which averaged 2 min). Because reinforcement was unpredictable, this lean schedule ensured that the demonstrators would respond for well over 2 min without reinforcement. To ensure a high rate of responding

by the nonreinforced demonstrators, the observers were exposed successively to 2 demonstrators performing the same response (either stepping or pecking), each for 2.5 min. The observers exposed to reinforced demonstrators also observed 2 demonstrators for 2.5 min each, but these demonstrators received reinforcement for each response (either pecking or stepping). The results indicated clear response matching for the groups that observed demonstrators that were reinforced for responding, but no response matching for those that observed the demonstrators responding but not receiving reinforcement. These results are consistent with a cognitive account of imitation. If the observer sees the demonstrator responding but not receiving reinforcement, the observer does not imitate.

Alternatively, it may be that seeing the food or seeing the demonstrator eating may increase the motivational level of the observer and that the higher level of motivation may encourage imitation. Although this hypothesis may appear to be similar to the motivational factors described earlier (e.g., social facilitation), it is different. The effects described earlier may have resulted in the increased probability of a particular response (e.g., pecking), but this could not account for the differential effect—both increased pecking by the observe-pecking group and increased stepping by the observe-stepping group. Thus, such a manipulation of motivation may have enhanced the imitation effect, but it cannot explain it.

It also may be that observational conditioning plays a role in this selective imitation effect. The pairing of treadle movement and the sight of food may result in second-order Pavlovian conditioning. However, once again, this mechanism does not provide an alternative to imitation, because it cannot account for the differential responses produced by the two observation groups (pecking by one, stepping by the other). Observational conditioning may explain why the observer approaches the treadle (it may be associated with the sight of food), but it cannot explain why the response elicited is different for the two groups.

Observer's motivation. A manipulation that is perhaps related to demonstrator reinforcement is the degree to which the observer has been food deprived. That is, does the degree to which the demonstrator's reinforcer is relevant to the motivational state of the observer at the time of observation affect the likelihood of response matching? In an experiment in which an attempt was made to answer this question, demonstrator Japanese quail either pecked at or stepped on a treadle in the presence of observers that were or were not food deprived. When the observers that were not food deprived were later tested (to induce levels of motivation sufficient to ensure performance), they showed little evidence of imitation (Dorrance & Zentall, 2001). However, those quail that observed while food deprived showed good evidence of imitation. Although it is difficult to identify the mechanism responsible, these results are consistent with the hypothesis that, for attention to a demonstrator's behavior to be promoted, it is necessary that the demon-

strator should be responding to a reinforcer relevant to the observer. It would be of interest to know whether observers that were motivated by a different reinforcer (e.g., if they were water deprived) would show the same absence of imitation. If similar results were to be obtained when the demonstrator's reinforcement was inconsistent with the object of the observer's deprivation, it would suggest that the observer may be capable of judging the relations among the demonstrator's behavior, the outcome to the demonstrator, and the observer's own motivational state—a more cognitive mechanism of control. On the other hand, it may be that any heightened motivational state would be sufficient to encourage the observer to attend to the demonstrator's behavior.

Conditional discriminations. Under appropriate conditions, the two-action method appears to have been useful in demonstrating imitation in at least two bird species. When imitation has been demonstrated in human children and in chimpanzees, however, it often has involved the acquisition of a more complex response (Whiten & Custance, 1996). Although there are various approaches to studying the effects of observation of multiple responses, Dorrance and Zentall (2002) investigated the observation and later performance of a conditional discrimination. Given that pigeons appear to imitate treadle pecking and treadle stepping, Dorrance and Zentall (2002) asked whether pigeons' acquisition of a conditional discrimination involving both responses would be facilitated by the prior observation of a demonstrator performing the same conditional discrimination (consistent group), as compared with a demonstrator performing a different (incompatible) conditional discrimination (inconsistent group). The conditional discriminations consisted of acquiring both treadle pecking and treadle stepping, conditional on the color of the houselight (green or white). Although significant differences in acquisition were not found between pigeons in the consistent and the inconsistent groups (within-group variability due to large individual differences in the rate of acquisition appears to have masked imitation effects in acquisition), both groups acquired their conditional discriminations significantly more quickly than a control group that acquired the conditional discrimination without prior demonstration of the treadle-pecking and treadle-stepping responses.

More encouraging were the results of a discrimination reversal for the two groups. When the conditional discriminations for each group were reversed, prior demonstration of the to-be-reversed conditional discrimination significantly facilitated the reversal, relative to prior demonstration of the original conditional discrimination (the rate of reversal learning was less variable than the rate of acquisition). Thus, once a conditional discrimination involving two different response topographies has been acquired, its reversal can be facilitated through observation of a demonstrator performing the reversal.

Deferred imitation. Bandura (1969) made a distinction between imitation that occurred at the same time as demonstration (or immediately thereafter) and observa-

tional learning that occurred some time after demonstration of the target behavior. Those who make this distinction consider immediate response matching to be of a simpler kind, released as a form of contagious behavior or produced reflexively in response to a demonstration. On the other hand, according to this view, deferred imitation cannot be reflexive but must represent the internalization of the demonstrator's behavior, and thus it exemplifies a higher level of cognitive behavior.

As part of a larger study in which the effects of observer motivation at the time of observation were investigated, Dorrance and Zentall (2001) included a group that observed the demonstration of treadle pecking or treadle stepping while hungry; these pigeons were then fed immediately after the observation experience in order to equate their level of motivation with that of another group that had been fed immediately prior to observation. A half hour later, when both groups were allowed access to the treadle, whereas the group satiated prior to observation showed no sign of response matching, the group that was satiated following observation showed response matching that was comparable to that of a standard imitation group that had been food deprived prior to observation and had been tested immediately after. Thus, Japanese quail show deferred imitation when up to a half hour occurs between observation and performance. Whether deferred imitation reflects a higher level of cognitive behavior than immediate imitation or not, deferred imitation does serve to rule out contagion or the elicitation of a reflexive response in the presence of the demonstrator's behavior as explanations of the response matching found in these studies.

Emulation. When an animal has learned through observation how the environment works, this has been referred to as *emulation* (Tomasello, 1990), *learning affordances* (Zentall, 2003), or *object-movement reenactment* (Akins et al., 2002). Emulation has been distinguished from imitation because emulation does not require that the specific action of the demonstrator be matched, but only that the same goal outcome be obtained. Thus, imagine a child standing in a room in which the door is latched with an unusual device never previously experienced by the child. Leaving the room would certainly be facilitated by observing someone else operate the latch to open the door. But one would not necessarily attribute that facilitation to imitation. Rather, the child might learn how the latch worked by seeing how it operated. In principle, seeing the latch operate in the absence of a demonstrator might well be sufficient to facilitate opening the door.

Although it is clear that emulation is conceptually different from imitation, the means by which such learning is translated into the appropriate behavior is not trivial. For example, if I observe that the downward movement of an operant lever is always followed by the delivery of a pellet of food, I may develop a Pavlovian association between the lever movement and the sight of food. Such learning should increase my attention to the lever and, perhaps, cause me to salivate whenever I see the lever

depressed, but it is not clear how that learning would necessarily lead me to depress the lever. It is not a trivial distinction to say that learning an association between the movement of an object and an appetitive outcome is different from causing that movement to occur for the purpose of obtaining the appetitive outcome. And in the absence of explicit instrumental training, it is not clear how observing the stimulus–reinforcement relationship can lead directly to response acquisition.

As part of a larger study in which the bidirectional control procedure with pigeons was investigated, Klein and Zentall (2003) included a group of observers that were exposed to an empty chamber; periodically, a lit feeder was raised behind a wire mesh screen. After a few seconds, the experimenter moved the screen either to the left (for some birds) or to the right (for others) by means of a stiff wire that projected outside the chamber. Thus, the agent of the movement could not be seen. When the observers were then placed in the chamber and the feeder was raised, they showed a significant tendency to push the screen in the same direction that they had seen it pushed. Presumably, they had learned that access to food could be gained by pushing the screen in the direction that had been observed.

Why Imitation in Birds?

Earlier, it was noted that clear evidence of imitation comes primarily from humans and other closely related species. Evidence for imitation in monkeys, for example, is often absent (Visalberghi & Fragaszy, 2002). Nevertheless, good evidence for imitation can be found in several bird species. Behavioral ecologists see no problem with this discontinuity among species, because they see the evolution of particular abilities to be naturally selected for and, thus, imitation should be found in species for which the capacity enhances the survival and reproductive success of individuals that have it. Although this account may well be true, it is somewhat unsatisfactory, because it tends to be circular: Animals have an ability because it is good for them, and it must be good for them because they have the ability.

The alternative approach is to look for species differences that might account for the differential use of imitation. Some obvious differences are probably not uniquely responsible for the discontinuity in the use of imitation among species. First, although most bird species are known to have excellent visual acuity, many mammalian species do not (e.g., rodents). Visual acuity would be needed to detect a demonstrated behavior. On the other hand, there is currently no evidence that mammals that do have good visual acuity (e.g., monkeys and most mammalian predators) imitate. Second, many bird species are social, and therefore, their close proximity to others might encourage the evolution of imitation. However, pigeons are not particularly social, yet they imitate, and monkeys generally are social, but they do not. A third possibility is that the benefits of imitation (particularly of the type assessed in the research presented here) depend on the need for animals to learn how to obtain food

from the environment. Many monkey species eat primarily fruit, and once it is found, it is easily acquired. Monkeys may not need to learn how to get to the edible portion of the fruit by observing others. On the other hand, birds often need to remove shells from seeds, and different seeds may require different shell-removing techniques. An attempt to understand why birds appear to be reasonably good imitators should prove to be quite useful in trying to understand how such a capacity has evolved independently in a number of taxa and why it is less widespread than its apparent utility would suggest. It is also possible that the capacity for imitation is present in many species and that prior social experience has either reinforced or extinguished attention to or reproduction of the behavior of others. Thus, it may be that certain animals learn to imitate, whereas others learn not to imitate.

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NOTE

1. Dolphins, which are not particularly close to us phylogenetically, may be a notable exception, because there is evidence that they too can imitate (Herman, 2002).