Perspectives on Observational Learning in Animals

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Observational learning is presumed to have occurred when an organism copies an improbable action or action outcome that it has observed and the matching behavior cannot be explained by an alternative mechanism. Psychologists have been particularly interested in the form of observational learning known as imitation and in how to distinguish imitation from other processes. To successfully make this distinction, one must disentangle the degree to which behavioral similarity results from (a) predisposed behavior, (b) increased motivation resulting from the presence of another animal, (c) attention drawn to a place or object, (d) learning about the way the environment works, as distinguished from what we think of as (e) imitation (the copying of the demonstrated behavior). Several of the processes that may be involved in observational learning are reviewed, including social facilitation, stimulus enhancement, several kinds of emulation, and various forms of imitation.

Keywords: imitation, observational learning, social facilitation, stimulus enhancement, emulation

Several reviews of observational learning have appeared in the past 20 years, including those by Galef (1988b), Whiten and Ham (1992), Zentall (1996), Whiten, Horner, Litchfield, and Marshall-Pescini (2004), Huber et al. (2009), and Hoppitt and Laland (2008). The purpose of the present review is not only to distinguish among the various kind of social influence, social learning, and learning by nonsocial means (e.g., emulation) but also to examine several variables that appear to be important in determining whether a particular behavior will be copied. In addition, an attempt will be made to identify several kinds of complex social learning that may be unique to humans.

Observational learning can be defined as a change in behavior that follows the observation of another (typically a conspecific) perform a similar behavior, the products of the behavior, or even the products alone. In theory, whether learning is involved depends on the novelty of the behavior. If the behavior were already in the repertoire of the observer, it would be considered performance rather than learning. However, in practice, it is difficult to identify novel behavior because some aspect of any behavior that the observer is capable of performing is likely to have been present in some form prior to its observation. Thus, the term "observational learning" will be used whenever performance of the observed behavior is very unlikely to have occurred in the absence of a model prior to its observation.

If one examines the literature on observational learning, one is struck by the fact that there are two very different approaches to its study. One approach can be characterized as the biological or ecological approach, which focuses primarily on the adaptive advantage of such learning. The other approach can be characterized as the psychological approach, which focuses more on identifying the mechanisms or processes that underlie observational learning.

Researchers who consider its adaptive value are interested in the degree to which achieving a goal, such as finding food or escaping from a predator, is facilitated (or the cost of achieving the goal is reduced) by observing others. For these researchers, the means by which the information is transmitted is not as important as the degree to which the information is useful (to survival or reproductive success). For example, if a fish is placed on one side of a transparent partition with food on the other side, following another fish to the food side through a small hole in the partition is sufficient to demonstrate the value to the observing fish of the social context if, later, the original observing fish will swim through the hole on its own (Laland & Williams, 1997).

Interestingly, an approach that focuses on adaptive value would predict that there are conditions under which observational learning has less value than individual learning (Laland, 2004). For example, observational learning might be less valuable when individual learning is not costly, when the current behavior of the observer is productive, and when outcomes are certain. Furthermore, this approach predicts that the identity of the model is likely to be important. Thus, social learning is more likely to occur when the model is related to the observer, when the model is successful, or when the model is older (see Rendell et al., 2011, for additional conditions under which social learning would be advantageous over individual learning).

On the other hand, given the same scenario, a psychologist would typically be more interested in *how* the observer fish learned how to get to the food. Did the observer have a natural tendency to affiliate with others and thus follow others through the opening in the partition? If it did, it may have learned incidentally where the hole was and that the other side was safe. The psychologist might ask whether learning would occur if the observer were not permitted to follow. Would it still learn about the opening by attending to the other fish as they passed through the opening such

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that it could find the opening at a later time? This would suggest more than a following response accompanied by incidental learning. But even if such learning could be demonstrated, the psychologist would not be inclined to call this kind of behavior imitation. Rather, a psychologist might attribute this behavior to learning facilitated by local enhancement (attention to a location) or stimulus enhancement (attention to an object, such as the hole).

But why does a psychologist care about the nature of the process by which the observer learns? To answer this question, one must see how imitation has been viewed in the human psychological literature. For example, imitation by young children has been viewed, by some, as an instrumental conditioning process in which behavior that happens to match the behavior of a model is selectively reinforced (e.g., Horne & Erjavec, 2007; Zukow-Goldring & Arbib, 2007), by others as an acquired understanding of the relation between one's own felt body parts and the observed body parts of others (e.g., Guillaume, 1926/1971; Mitchell, 1987), and by still others as a cognitive process reflecting an understanding or assimilation of the relation between one's own body parts and those of others (imagine an adult human walking with his hand clasped behind his back and being followed by a young child with his hands also clasped behind his back). According to this view, imitation can be an intentional, conscious process involving the ability to take the perspective of another (Whiten, 2000). Kurdek and Rodgon (1975) call this *perceptual* perspective taking, especially when the observer cannot easily see itself perform the behavior. When imitation is this of kind, it is has been referred to as imitation of invisible actions (Piaget, 1962) or as opaque imitation (Heyes, 2002). If it can be shown that animals are capable of such imitation, it might be argued that those animals have a relatively advanced representational system. However, it should be noted that a simpler learning model, which will be discussed later, has been proposed to account for opaque imitation (Heyes & Ray, 2000; Ray & Heyes, 2011).

Another perspective on the cognitive implications of imitation has been proposed by Bandura (1969), who noted a difference between simple imitation, the copying of behavior occurring at about the same time as it is observed, and deferred imitation or observational learning, in which performance of the observed behavior occurs at a later time. Bandura's (1969) distinction is based on the premise that being able to defer imitation requires one to have a representation of the observed behavior that can be retrieved and performed at a later time when the model is no longer present. The potential value of deferred imitation is that it can function as a tool that can be used flexibly at an appropriate time after observation of the behavior. Of course, in a sense, all imitation can be thought of as deferred because it always occurs after observation, but a useful, if not precise, distinction can be made between a delay that is no longer than working memory (seconds) and one that is minutes or more long (Cowan, Wood, Nugent, & Treisman, 1997).

Bandura's (1969) distinction between deferred imitation and imitation that occurs at or about the time of observation, what Byrne and Russon (1998) have referred to as response facilitation, rests on the assumption that immediate imitation involves a simpler process. But referring to imitation as response facilitation implies that the ability to copy the behavior of another is automatic and reflexive. However, describing the immediate copying of behavior as reflexive fails to explain how the observation of the

model's behavior translates into the performed behavior by the observer, especially if the observer's own behavior is opaque. Thus, if one is interested in how organisms understand and reproduce observed behavior, distinguishing among the various contributions to learning from others is a meaningful endeavor.

In the present review, I will start with several examples of social influence, where behavior is influenced by the presence of others, but for which either learning is not involved or learning is a side effect of the behavior of the other animal. I will then consider several examples of simple social learning in which the other animal plays an important role in facilitating the same behavior in the observing animal but associative learning processes by the observer are sufficient to account for the learning. Finally, I will address the possibility that, under certain conditions, animals may perform an observed behavior that requires a more cognitive explanation. Such a process, by which the behavior of others is translated into one's own behavior, may not involve what Piaget (1962) referred to as perspective taking nor what Bandura (1969) viewed as a case of mental representation. Yet it would be difficult to account for such behavior as that is predisposed, induced by increased motivation, enhanced by attention, or readily subsumed under the rubric of trial-and-error learning involving a social stimulus. Although the processes involved in these more complex examples of imitation may be difficult to disentangle from simpler motivational, attentional, and trial-and-error processes, because, in nature, they do not typically occur in isolation, they do have theoretical implications for the conceptual capacities of animals.

Social Influence

Social influence occurs when the presence of other members of the same species (a) results in a reflexive response (contagion), (b) affects the motivation of the observing animal (mere presence), or (c) causes the observing animal to direct its attention to a place or object (local or stimulus enhancement).

Contagion

Predisposed tendencies to match specific behaviors of a conspecific (a member of the same species) are often referred to as contagious behaviors, mimesis, response facilitation, or response priming. Contagion can be used to describe certain elicited courtship displays, antipredator behavior (such as mobbing), and social eating. These behaviors are often reflexive species-typical responses to the behavior of another animal. For example, a chicken that is provided with food until it has eaten its fill and has stopped eating will often begin eating again if one introduces a hungry chicken that begins eating (Tolman, 1964). In this case, the behavior of one animal appears to serve as a releaser for the natural, unlearned behavior of others (Thorpe, 1963) and is unrelated to the copying of more instrumental behavior.

Motivational Influences

Social factors that affect the general arousal or motivation of an animal may affect its general activity, which may, in turn, affect the probability that it will make a matching response.

Social facilitation/Social enhancement. The mere presence of another animal, irrespective of that animal's behavior, may

increase (or decrease) arousal, a phenomenon called social facilitation or social enhancement. Increased arousal can lead to increased activity, leading to increased contact with environmental contingencies. For example, if the presence of another animal increases a rat's general exploratory activity, that rat may discover (on its own) a lever that, when pressed, leads to reinforcement (Zajonc, 1965). Alternatively, in a novel environment, the presence of a conspecific may lead to a decrease in fear, which may lead to a decrease in arousal and increased general exploratory activity (Moore, Byers, & Baron, 1981).

Incentive motivation. Reinforcement provided to the observer during the demonstration of a response may also play a role in the rate at which the response is acquired by way of incentive motivation (see Caldwell & Whiten, 2003). That is, being in the presence of another animal that is eating may increase motivation still further.

Observation of aversive conditioning. The copying of a response being acquired or being performed by a demonstrator that is motivated by the avoidance of painful stimulation (e.g., electric shock) may result from the induction of motivation in the observer. Emotional cues of pain or fear provided by a conspecific, either escaping from or avoiding shock, may instill fear in the observer. For example, John, Chesler, Bartlett, and Victor (1968) found that cats that had observed a demonstrator being trained to jump over a hurdle to avoid footshock learned the hurdle-jumping response faster than controls that did not observe the demonstrators. It may be, however, that being in the presence of a cat being shocked was sufficient to increase the observers' fear (motivation) associated with the conditioning context. Under such conditions, the increase in motivation may account for the facilitated acquisition.

Perceptual Factors

When the observation of a demonstrator draws attention to the consequences of a response (e.g., a lever press), 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 might not react to a hole in the pen large enough for them to escape, unless they happen to be near another duck as it is escaping. Thus, the sight of a duck passing through the hole in the pen may merely draw attention to the hole. One could ask, for example, if observing a ball roll through the hole would produce a similar effect.

Local enhancement may also be involved in John et al.'s (1968, Exp. 1) finding of facilitated acquisition of an aversively motivated hurdle jump response. Attributing the matching behavior to local enhancement, in this case, may not be obvious, but observation of the demonstrator jumping over the hurdle may draw the observer's attention to the top of the hurdle. In other words, it might be sufficient to see a ball bounce over the hurdle to find facilitation of the hurdle-jumping response. Similarly, an attentional mechanism may be responsible for the rapid mastery of a V-shaped-fence detour problem when demonstrated by a human (Pongrácz et al., 2001). Seeing the demonstrator pass around the end of the fence may draw the observer's attention to the place where it can gain access to the goal on the other side. In general, whenever the

performance observed involves an object (e.g., a manipulandum, a hurdle, a barrier) to which the observer must later respond, local enhancement may play a role and appropriate control conditions should be included.

Although performance by the demonstrator may draw the attention of the observer to a location, the outcome of the demonstrator's behavior may also play a role in the observer's tendency to copy. For example, Lefebvre and Palameta (1988) found that pigeons that observed a model pierce the paper cover on a food well to obtain hidden grain later acquired that response on their own, whereas those that observed that same response, but with no grain in the well (the model performed in extinction), failed to acquire the response. In this case, the observed behaviors were quite similar for the two groups but the consequences of the observed behavior were quite different (see also Akins & Zentall, 1998). One might be inclined to interpret this result cognitively as the observer's understanding of the consequences of the demonstrator's behavior; however, a Pavlovian conditioning account, in terms of the pairing of attention to a location and the appearance of a reinforcer, may be sufficient to explain the more rapid acquisition of the target behavior by the observer when the demonstrator's behavior is reinforced. I will return to this point shortly.

Stimulus enhancement. In the case of local enhancement, the attention of an observer is drawn to a particular *place* by the activity of the demonstrator. The term stimulus enhancement is used when the activity of the demonstrator draws the attention of the observer to a particular *object* (e.g., a manipulandum). Quite often in the study of imitative learning, the object in question is at a fixed location, so local enhancement and stimulus enhancement are indistinguishable. In the duplicate-chamber procedure (see Warden & Jackson, 1935; Gardner & Engel, 1971), however, a manipulandum (e.g., a lever) is present in both the demonstration chamber and in the observation chamber. Under these conditions, drawing attention to the demonstrator's lever might not be expected to enhance the observer's lever. In fact, one could argue that it should retard acquisition of lever pressing by the observer because it should draw the observer's attention away from its own lever. However, the similarity between the demonstrator's lever and that of the observer may make it more likely that the observer would notice its own lever after having its attention drawn to the demonstrator's lever. Thus, stimulus enhancement can refer to the combination of a perceptual, attention-getting process resulting from the activity of the demonstrator in the presence of the lever and stimulus generalization between the demonstrator's and observer's levers. Because it subsumes the effects of local enhancement, the term stimulus enhancement may be more inclusive and thus is often preferred (Galef, 1988b).

Stimulus enhancement may also play a role in mate-choice copying by animals (Dugatkin, 1996; Galef, Lim, & Gilbert, 2008). For example, female guppies that see a demonstrator or model female in the presence of a courting male will prefer that male over an alternative male (Dugatkin, 1992; Dugatkin & Godin, 1992). In this case, it may not be possible to separate the observer's attention to the model female and, therefore, to the male nearby, from the putative attraction of the model to the adjacent male.

The facilitation of learning through perceptual factors presents a difficult problem for the study of imitation in animals. If the similarity between the demonstrator's location or the demonstra-

tor's manipulandum and that of the observer presents an interpretational problem because of perceptual factors, making the location or the nature of the manipulandum for the observer different from that of the demonstrator is likely to interfere with the observer's potential interpretation of the relation between the two tasks. This problem, which will be addressed later, requires a new approach to defining adequate control procedures.

Simple Social Learning

A number of cases of learning in a social context may be mediated by simple nonsocial learning mechanisms. Although social stimuli are present, and those social stimuli may play a role in facilitating acquisition of the target behavior (perhaps because, often, social stimuli are more salient than nonsocial alternatives), the processes by which the observer acquires the behavior may be more parsimoniously explained in terms of simpler individual (trial and error) learning processes.

Discriminated Following (or Matched Dependent) Behavior

Perhaps the clearest example of learning in a social context, for which the learning is likely to involve simple associative learning, is when the observer is reinforced for following the model. For example, rats can learn to follow a trained conspecific to food in a T maze in the absence of any other discriminative stimulus (Haruki & Tsuzuki, 1967). Although the leader rat in these experiments is clearly a social stimulus, the data are more parsimoniously interpreted in terms of simple discriminative learning. If, for example, the demonstrator were replaced with a block of wood pulled along by a string, or even an arrow at the choice point, directing the rat to turn left or right, it is clear that one would identify the cue (i.e., the demonstrator, the block of wood, or the arrow) as a simple discriminative stimulus. Even if following a demonstrator led to faster learning than following a passive signal, it might merely indicate that the social cue was more salient than either a static or moving, nonliving cue.

Observational Conditioning

As noted in the section on local enhancement, the observation of a performing demonstrator may not merely draw attention to the object being manipulated (e.g., the lever), but because the observer's interaction with the object is often followed immediately by presentation of food to the demonstrator, a Pavlovian association may be established. This form of conditioning has been called observational conditioning (Whiten & Ham, 1992) or valence transformation (Hogan, 1988), and it occurs when the observer learns the relation between some event in the environment and the reinforcer (e.g., a rat approaches a lever that has appeared shortly before the demonstrator—that has pressed the lever—has been fed). Although such conditioning would have to take the form of higher order conditioning (because the observer would not actually experience the unconditional stimulus), there is evidence that such higher order conditioning can occur even in the absence of a demonstrator. If, for example, pigeons are presented with a localized light, followed shortly by the presentation of inaccessible grain, it is sufficient to initiate pecking to the light (Zentall &

Hogan, 1975). The presence of a demonstrator drawing additional attention to the light (by pecking at it) and to the reinforcer (by eating) may further enhance associative processes in the absence of imitative learning.

With regard to the nature of the conditioning process, it is of interest that when reinforcement of the demonstrator's response cannot be observed (or the response-reinforcer association is difficult to make), acquisition may be impaired (Akins & Zentall, 1998; Heyes, Jaldow, & Dawson, 1994). Furthermore, rats appear to acquire a lever-pressing response faster following observation of a lever-pressing demonstrator if they are fed at the same time as the performing demonstrator (Del Russo, 1971). Although that result was mentioned earlier in the context of increased motivation on the part of the observer, it is also possible that feeding the observer following the demonstrator's response may result in simple Pavlovian conditioning (i.e., the pairing of movement of the lever with food).

Socially transmitted food preferences (e.g., Galef, 1988a; Strupp & Levitsky, 1984) represent a special case of observational conditioning. Although food preference may appear to fall into the category of unlearned behavior, subject to elicitation through contagion, consuming food with a *novel* taste should be thought of as an acquired behavior. The mechanisms responsible for socially acquired food preferences appear to have strong simple associative learning components (e.g., learned safety or the habituation of neophobia to the novel taste), for which the presence of a conspecific may serve as a catalyst. Furthermore, these specialized mechanisms may be unique to foraging and feeding systems.

One of the best examples of observational conditioning is in the acquisition of fear of snakes by laboratory-reared monkeys exposed to a wild-born conspecific in the presence of a snake (Mineka & Cook, 1988). Presumably, the fearful conspecific serves as the unconditioned stimulus and the snake serves as the conditioned stimulus. Exposure to a fearful conspecific or to a snake alone is insufficient to produce fear of snakes in the observer. Interestingly, not all stimuli are as easily associated with a fear response. For example, a fearful wild-born conspecific in the presence of a flower is not sufficient for observational conditioning. For an excellent discussion of the various forms of observational conditioning, see Heyes (1994).

Goal Emulation, Object-Movement Reenactment, and Emulation via Affordance Learning

When subjects learn about their environment and use this information to achieve their own goals, it may not require demonstration by another organism. Instead, the learning can be defined in terms of the occurrence of events in the environment that typically lead to reinforcement or the products of the behavior of a demonstrator. Although the terms emulation, end-state emulation, goal emulation, object-movement reenactment, and emulation via affordance learning cannot always be clearly differentiated, they have been used in somewhat different contexts (Hopper, 2010; Huang & Charman, 2005).

End-state or outcome emulation is used when the presence of an outcome motivates an observer to replicate the result. An observer may see a demonstrator obtain food by making a response and thus may be induced to explore because it is motivated to obtain food itself. Goal emulation, or, more properly, outcome emulation, has

been used to describe, for example, an observer's understanding that a tool can be used to obtain a reward but not exactly how that tool should be used (Tomasello, 1990). Object-movement reenactment refers to copying what an object does (e.g., a door moves toward the animal or away from the animal to gain access to reinforcement), without regard to the specific actions of the demonstrator (Whiten et al., 2004). Emulation or emulation via affordance learning refers to learning how the environment works (Byrne, 1998).

For purposes of the present review, the term emulation will be used to indicate learning about those changes in the environment, independent of the actions of a demonstrator, that are necessary to obtain a goal. When observation of a demonstrator allows an animal to learn how the environment functions, a sophisticated form of learning may be involved. For example, if a pigeon observes a screen (that is capable of moving to the left or to the right) move to the left to allow access to food, when the pigeon is given access to the screen, it is more likely to move the screen in the same direction (Campbell, Heyes, & Goldsmith, 1999; Klein & Zentall, 2003). However, because learning how the environment works may occur in the absence of the behavior of another animal, one would not want to view such learning as social learning. Emulation resembles observational conditioning in the sense that both involve the relation between environmental events and an outcome, and the two may not be easy to disentangle (Byrne, 1998). The difference is that, in observational conditioning, the response to be accounted for is closely related to the unconditioned response to the reinforcer; for example, a pigeon pecking a light that has been followed by reinforcement or a rat approaching a lever, the appearance of which has been closely followed by the delivery of food. Emulation, on the other hand, could involve a more arbitrary, means-end, instrumental relation, such as learning that a swinging door swings out (rather than in) to obtain food on the other side (Bugnyar & Huber, 1997).

Emulation may be involved in a procedure used with chimpanzees in which they learn to open a box to obtain a reward (Whiten & Custance, 1996). Some demonstrator chimpanzees were trained to poke a bolt to open the box, whereas other demonstrators were trained to twist and pull the bolt to achieve the same result. Observers given access to the box tended to remove the bolt the same way that they had seen it removed. However, because the bolt moved differently in the two cases, it is possible that the observers learned how the bolt moved (by emulation) rather than to copy the actions of their demonstrators (by imitation).

Emulation may also have played a role in an experiment in which observation of experienced demonstrators facilitates the opening of hickory nuts by red squirrels, relative to trial-and-error learning (Weigle & Hanson, 1980). In this case, differential local enhancement can be ruled out because animals in both groups quickly approached and handled the nuts, and the observers actually handled the nuts less than control animals (perhaps because observers were more efficient at opening them). However, those animals that observed demonstrators opening nuts were able to see the open nuts (end-state emulation), and they had the opportunity to associate open nuts with eating by the demonstrator (Heyes & Ray, 2000).

Chimpanzees that observed a demonstrator spit water into a cylinder to raise a floating peanut learned to do the same (Tennie, Call, & Tomasello, 2010). But emulation may be involved in this

case as well because observers that watched a human experimenter pour water into the cylinder were just as likely to spit water into the cylinder as those in the other group. Thus, the observers in the second group learned that water inserted into the cylinder would raise the level of the peanut. That is, they learned to emulate via the affordances of the task.

Although emulation typically takes place in a social context, it may not be considered social learning because it does not require learning the *actions* of a demonstrator. To help make this distinction, learning involving the actions of a demonstrator is often compared with a "ghost" control, which does not involve a social stimulus. However, emulation is a phenomenon of interest in its own right. Learning about things and how they work by observation has important implications for cognitive learning. There is evidence not only that chimpanzees can emulate the movement of a tool (Nagell, Olguin, & Tomasello, 1993), as well as increasing the level of water in a cylinder to gain access to a reward (Tennie et al., 2010), but also that pigeons (Klein & Zentall, 2003) and dogs (Miller, Rayburn-Reeves, & Zentall, 2009) can emulate the direction of movement of a screen permitting access to food.

Birdsong

A special case of matching behavior by animals is the acquisition of birdsong (Hinde, 1969; Marler, 1970; Nottebohm, 1970; Thorpe, 1961; see also vocal mimicry, e.g., Pepperberg, 1986, 2002; Thorpe, 1967). Although, for a few species of songbird, to a large extent, the development of species-typical song is regulated by maturation and the seasonally fluctuating release of hormones, for others, social interaction plays a large role (Saar, Mitra, Derégnaucourt, & Tchernichovski, 2008; White, Gros-Louis, King, Papakhian, & West, 2007). Notably, regional variations in birdsong appear to depend on the bird's early experience with conspecifics (Baptista & Petrinovich, 1984). Thus, young songbirds learn their regional dialect by copying the song of more mature conspecifics.

But acquisition of birdsong dialect is a special case of social learning. First, although it is learned and acquisition of other species' songs is possible (see Pepperberg, 1988, for a review), birdsong is a variation on a species-typical behavior and thus is relatively constrained. Second, and most importantly, birdsong takes place in the auditory modality, and a characteristic of animal-produced auditory events is that the stimulus produced by the demonstrator and that produced by the "observer" can be a close match, not only to a third party (i.e., the experimenter) but also to the observer itself (Thorpe, 1961). Thus, verbal behavior, for which comparisons between one's own behavior and that of others may be relatively easy to acquire, because one can hear one's own utterances with relative fidelity, may be a special "prepared" case of generalized stimulus identity learning (e.g., animals that have been trained to match shape stimuli can now use the principle of stimulus matching to match novel hue stimuli; see Zentall, Edwards, & Hogan, 1983). Byrne (2002) suggests that matching a vocalization is likely to be mediated by copying the final result and thus could be considered an example of outcome emulation.

This analysis of the copying of verbal behavior can also be applied to certain examples of visual behavior copying. Any behavior that produces a clear change in the environment, such that, *from the perspective of the observer*, there is a match between the

stimulus produced by the demonstrator and that produced by the observer, may be a case of stimulus matching (e.g., observing someone turning up the volume of a radio—when the knob turns to the right, the volume increases). Such cases of visual-stimulus matching can be distinguished from the perhaps more abstract and interesting case in which no visual stimulus match is possible (e.g., the imitation of hands clasped behind the back when observing a person who has his hands clasped behind his back), which Piaget (1962) called imitation of invisible actions.

Traditions

A tradition is a behavior that may be acquired socially but is then passed on to other individuals, presumably by social means (Laland & Galef, 2009). Traditions can be thought of as the building blocks of cumulative culture that is characteristic of human populations. When traditions can be modified and improved by learning, it permits the accumulation of knowledge in a population, which has been referred to by Tomasello (1994) as a "ratchet effect" (see Tennie, Call, & Tomasello, 2009).

Supposedly, if one population of animals engages in a particular behavior that other nearby populations do not, one might conclude that a tradition is involved. The problem with this interpretation is that the evidence for traditions in natural settings requires that one distinguish the social transmission of behavior from other differences between the populations that might be responsible for the behavioral differences, such as genetic and environmental differences, and it is virtually impossible to isolate social transmission from nonsocial means by which behavior can spread throughout a population (Langergraber et al., 2010; van Schaik et al., 2003).

An alternative approach has been to study traditions experimentally (i.e., by introducing a new behavior and studying its spread or diffusion through a population; Tomasello et al., 1997). Although considerable laboratory research on the diffusion of behavior has been conducted with human groups (see Mesoudi & Whiten, 2008), only a few studies of this kind have been done with nonhuman animals. For example, evidence for the diffusion of either of two techniques for extracting trapped food has been demonstrated in chimpanzees (see Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009), meerkats (Thornton & Malapert, 2009), and mongooses (Müller & Cant, 2010). There is even evidence for the diffusion of an acquired taste preference in rats (Galef & Allen, 1995). But Claidière and Sperber (2010) have argued that the diffusion of behavior that has been demonstrated (e.g., Whiten et al., 2009) is insufficiently stable to qualify as a tradition.

Although traditions may involve the kinds of complex social learning that will be discussed in the next section, I have chosen to include a brief discussion of traditions here, rather than in the next section, because there are likely to be a variety of mechanisms involved in the spread of traditions including stimulus enhancement, observational conditioning, and emulation.

The Social Learning of Behavior

To researchers interested in the possibility that, under certain conditions, there may be cognitive processes involved in social learning, the most interesting forms of social learning are those that cannot be easily explained by any of the previously described mechanisms. Such complex social learning is generally referred to as imitation or true imitation.

Imitation

The term imitation is used to indicate behavior of an observer that matches the behavior of a demonstrator but that cannot be accounted for with any of the motivational, attentional, or simple learning processes described earlier. Under appropriate conditions, the bidirectional control and two-action procedures are accepted methods for demonstrating imitation.

One issue that often comes up when imitation is considered is whether the behavior that is observed and later performed must be novel to the observer. In principle, one would think that novelty of the behavior would be a prerequisite (see Thorpe, 1961). But, in practice, novelty is a difficult requirement to assess. Birds may have a number of different behaviors available to them, but which of these has never been performed before? A bird may peck at a red light that one may presume it has never seen before, but it has surely pecked at objects before. Even in the case of a sequence of responses, it can be argued that each component of the sequence is likely to have been performed earlier. In fact, one could argue that it would be very difficult for an animal to perform a response sequence if the individual components of the sequence had never been performed before. Thus, a requirement that is more tractable than novelty is that the behavior should be novel or otherwise improbable (Thorpe, 1961). That is, if the response is unlikely to occur in the absence of its demonstration, one can consider it improbable, and thus, if it should occur following conditions of observation, and it cannot be explained easily by any of the previously described mechanisms, it can be attributed to the behavior demonstrated. To be considered imitation, it is important that there be evidence of behavior transmission.

The bidirectional control procedure. When an overhead pole can be pushed to the left or to the right, observer rats tend to push the pole in the same direction that they saw a demonstrator push it (Heyes & Dawson, 1990; see also Klein & Zentall, 2003, for similar results with pigeons, and Miller et al., 2009, with dogs). To distinguish this learning from emulation, a control condition (sometimes referred to as a "ghost" control), in which the manipulandum appears to move by itself without a demonstrator pushing it, is needed (see Hopper, 2010; Hopper, Lambeth, Schapiro, & Whiten, 2008). Although the ghost control provides a necessary comparison condition, it can be argued that it does not control for social facilitation (the mere presence of a conspecific, see Klein & Zentall, 2003) nor does it control adequately for observation of the outcome or goal (the observed "demonstrator" should be provided with reinforcement to control for the motivation induced by seeing an conspecific eating as well as potential associations between the moving manipulandum and the sight a conspecific eating—what Hopper et al., 2008, call an enhanced ghost control). But if one controls for social facilitation by including the presence of an inactive conspecific (Hopper, 2010), the conspecific may be distracting or imitation of the conspecific could result in the absence of emulation but for the wrong reason. Thus, if one uses the bidirectional control procedure, there may not be an ideal control procedure.

The two-action procedure. If the demonstrator produces the same effect on a manipulandum in one of two different ways (e.g., by stepping on or by pecking at a manipulandum; see Figure 1) it
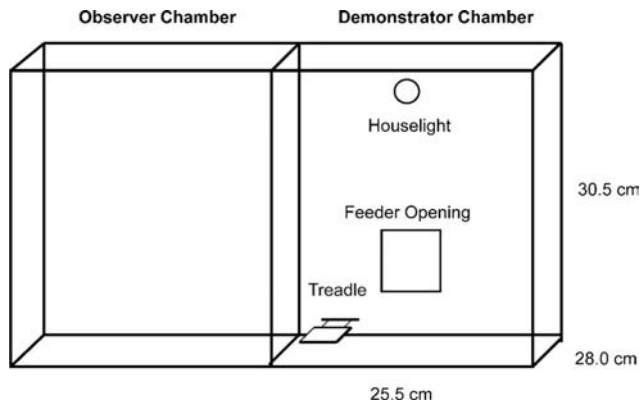
Observer Chamber   **Demonstrator Chamber**

Figure 1. The two-action apparatus: Observer birds could see a demonstrator bird either stepping on the treadle or pecking at the treadle. Observer birds could then step or peck for food.

is known as the two-action procedure. It should be noted that in some cases in which the bidirectional control has been used, it has been referred to as the two-action procedure (e.g., Bugnyar, & Huber, 1997; Whiten, 1998). However, the two-action procedure differs from the bidirectional control in that the movement of the manipulandum is the same with either action. In the bidirectional control, the manipulandum moves differently (e.g., in the case of Heyes & Dawson, 1990, either to the left or to the right). With the two-action procedure, because the two responses have the same effect on the manipulandum, the two-action procedure controls for emulation as well as local and stimulus enhancement. It also controls for social facilitation because a conspecific is present in both conditions.

Akins and Zentall (1996) trained Japanese quail to activate a treadle (a small metal plate near the floor of the chamber; see Figure 1) for food, either by pecking at the treadle or by stepping on it. When later given access to the treadle, observers used the same part of their body as their respective demonstrator had used to make the responses (see also Zentall, Sutton, & Sherburne, 1996, for similar results with pigeons). Of course, one could argue that pecking and stepping are responses that are predisposed and thus are neither novel nor of low probability; however, selectively directing those responses to a never-before-seen treadle, following the observation of those specific responses made by a demonstrator, would not normally be considered already-acquired responses. Furthermore, Kaiser, Zentall, and Galef (1997) have found that in the absence of a treadle pecking or stepping demonstrator (no demonstrator or a merely present demonstrator), the probability of the occurrence of either response is very low.

It is important to note, first, that the environmental consequences of stepping and pecking were the same (i.e., everything was the same except the actions or response topographies of the demonstrators). Second, there was little, if any, similarity between the visual stimulus the observer saw during observation and the visual stimulus it saw during its own performance of either response. That is, the appearance of the demonstrator's beak on the treadle must have appeared quite different to the observer from the sight of its own beak on the treadle. Similarly, although perhaps not so obviously, when the quail stepped on the treadle (located near the corner of the chamber between the feeder and the ob-

server), it pulled its head back and thrust its chest forward and, for this reason, 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. For these reasons, in such an experiment, the imitated response can be thought of as opaque to the observer, and any account of imitation based on visual-visual stimulus matching is implausible.

A similar example of imitation involving two actions was reported in marmosets by Voelkl and Huber (2000). Demonstrators opened a plastic (photographic film) canister either by using their hands or by using their teeth. All of the observers that watched the canister being opened with the teeth did the same, whereas almost half of the observers that watched the canister being opened with the hand did so as well.

The two-action procedure allows one to assess a special case of social learning—called imitation of invisible actions or opaque imitation—that directly controls for emulation because, from the perspective of the observer, the observer's behavior does not match that of the demonstrator. Opaque imitation is of particular interest to comparative psychologists because the mechanisms responsible for the transmission of information from the demonstrator to the observer are not well understood (see Whiten, 2005), and when it occurs in children, traditionally, it has been attributed to the ability to take the perspective of a third person (Piaget, 1962). However, it seems unlikely that perspective-taking is the mechanism responsible for imitation (see Ray & Heyes, 2011) because perspective-taking does not appear in children before the age of 3 years (Selman, 1980, says it occurs between the ages of 3 and 6 years)—yet other animals (e.g., Japanese quail, pigeons, and marmosets) show evidence of imitation.

Variables That May Influence Opaque Imitation

Several variables have been found to influence whether imitation will be found or not, and those variables may be of interest not only because of their practical implications but also because they may help to identify the nature of the cognitive processes that are involved.

Demonstrator reinforcement. A cognitive account of imitation implies that the observer understands what the demonstrator is doing and, perhaps, even why it is doing it. If such an interpretation is correct, whether evidence of imitation is found may depend on the consequences of the demonstrated response for the demonstrator. Alternatively, animals may have a species-typical tendency to imitate regardless of the consequence of the behavior for the demonstrator. However, it should be clear that even if the tendency to imitate is predisposed and independent of demonstrator reinforcement, it does not explain how the observer understands what it should do to replicate the behavior of the demonstrator.

Interestingly, Akins and Zentall (1998) found that quail imitated when they observed demonstrators receiving a reward after they pecked or stepped on a treadle but not in the absence of demonstrator reinforcement (see also Palameta & Lefebvre, 1985; but see McGregor, Saggerson, Pearce, & Heyes, 2006). Although the effects of the presence versus the absence of demonstrator reinforcement suggest a cognitive account (i.e., there is no reason to imitate if reinforcement does not follow the response), it is possi-

ble to explain the effect of demonstrator reward on observer imitation by appealing to observational conditioning (the simpler form of learning described earlier). In observational conditioning, an observer's attention may be drawn to a stimulus (in this case, the demonstrator quail depressing the treadle) because this action precedes demonstrator reinforcement (for the observer, a secondary reinforcer). Although observational conditioning might account for the effect of reinforcement on observation, observational conditioning cannot account for the *correspondence* between observer's and demonstrator's response topographies. Thus, the effect of demonstrator reinforcement may be to act as a catalyst to bring out imitative learning in an observer.

The effect of the outcome for the demonstrator may play an even more important role when responses are demonstrated that are more complex than pressing a treadle. For example, in one experiment, in the presence of a chimpanzee, humans performed a task in which first one response (poking a stick in a hole in the top of a box) did not lead to obtaining food but another response (poking the stick in a hole in the side of the box) did (Horner & Whiten, 2005). Next, subjects were given access to the box and the stick. Interestingly, when the box was opaque, so that subjects could not see that the top hole did not provide access to food, the subjects often started by poking the stick into the top hole. However, when the box was transparent and subjects could see that the top hole did not provide access to food, the subjects generally avoided poking the stick in the top hole and instead poked the stick directly into the side hole that had produced the food. Horner and Whiten (2005) proposed that when the box was transparent, subjects recognized the causal structure of the task and avoided the response that did not lead to reward; however, when the box was opaque, it was not clear that inserting the stick in the top hole was not a necessary prerequisite to inserting the stick in the side hole. Thus, the chimpanzees could acquire the entire sequence of responses through observation, but they omitted part of the sequence when it was apparent that one of the demonstrated responses was not necessary to achieve the goal. It has been argued that this stick-poking behavior may not actually involve imitation because the chimpanzees were adept at stick poking and only needed to learn where to poke the stick (Tennie, Call, & Tomasello, 2006). Furthermore, in the case of the transparent box, it may have been that causal information (the result of the first stick-poke) overrode learning where to poke (local enhancement).

Surprisingly, although the chimpanzees omitted the initial unnecessary response when the box was transparent, the children in the Horner and Whiten (2005) study did not. This result suggests that children are more prone to "blind" copying, that is, copying that is intrinsically reinforcing and has no other goal, than are chimpanzees. For example, children will often imitate the posture of an adult when there is no extrinsic reinforcement, that is, without social reinforcement or even if they are not visible to the adult or to others. Blind imitation or overimitation may be the major distinction between the copying behavior of humans (especially children) and other animals. On the other hand, there is evidence that children do not always blindly imitate (see Gergely, Bekkering, & Király, 2002; Meltzoff, 1995; Nielsen, 2008; Uzgiris, 1981; Whiten et al., 2009). The conditions under which blind imitation and selective imitation will be found are likely to depend on contextual factors, such as whether imitation is reinforcing in its own right and whether causal information is judged to be impor-

tant. Thus, there is evidence that older children are more prone to overimitate than younger children (Huang, Heyes, & Charman, 2006), perhaps because the older children see imitation as a game or an end in itself rather than as a means to an end. With regard to the acquired tendency to imitate observed behavior by children, it would be interesting to know if this ability varies across cultures depending on the importance that the culture places on learning by imitation.

Observer motivation. If, at the time of observation, observers are not motivated to obtain the reinforcers for which the demonstrators are working, will they acquire the response for use later when they are motivated? Such learning might be expected if animals are predisposed to learn from a demonstrator and blindly imitate. Alternatively, it could imply a higher level of cognitive functioning. For example, it could indicate the ability of the observer to retrieve an earlier representation of an observed behavior or even the ability of the observer to plan for the future (Piaget, 1936; Tulving, 2004), if the observer recognized that although the information was not useful at the time of observation, it may be useful at a later time.

The hypothesis that observer motivation affects imitation was tested in quail by comparing imitative learning by quail that were either hungry or sated at the time of observation (Dorrance & Zentall, 2001). It was found that hungry quail matched the demonstrator's reinforced behavior, whereas sated quail, when later tested hungry, did not. Animals that are not hungry may not be motivated to learn from a conspecific or they may not attend as well to the behavior of the conspecific. Thus, differential motivation or differential attention during the time of observation could account for differential learning by the two groups. One might also propose that a representation of the observed behavior does not survive the delay between observation and performance required by the need to test the animal when sufficiently hungry. That possibility will be addressed in the next section.

Deferred imitation. As noted earlier, Bandura (1969) proposed that there is an important cognitive difference between immediate imitation (which Bandura called imitation) and deferred imitation (which he called observational learning), in which some time passes between the time of observation and performance by the observer (see also Piaget, 1936, for an earlier version of this theory). For Bandura (1969), immediate imitation may be a reflexive response akin to contagious behavior, whereas deferred imitation indicates a more cognitive process in which an observer has to *represent* the response at the time of observation for later retrieval when performance is assessed.

To determine if animals are capable of deferred imitation, as part of a study already cited (Dorrance & Zentall, 2001), hungry quail observed either a treadle-pecking or treadle-stepping conspecific. When one group of quail was tested 30 minutes later, they imitated as frequently as observers tested immediately following observation. If, as Bandura (1969) proposed, deferred imitation is evidence of a more cognitive process, then quail show good evidence of the cognitive representation of the earlier observed behavior.

Enculturation. One of the variables that may play a role in imitative learning by primates appears to be the degree to which the animals have had extensive interactions with humans—what Tomasello (1990) refers to as enculturation. Enculturated chimpanzees and orangutans readily show signs of imitative learning

(Tomasello, Gust, & Frost, 1989; Tomasello, Savage-Rumbaugh, & Kruger, 1993; Russon & Galdikas, 1993, 1995), whereas lab-housed and reared chimpanzees often do not (Whiten & Custance, 1996, but see Tomasello & Call, 2004). Furthermore, Tomasello et al. (1993) have suggested that enculturated apes may develop an understanding of intentionality (see Searle, 1983).

Enculturation may produce its effect in a number of ways. First, it may reduce the apes' anxiety (response to novelty) during testing. Second, it could increase their attentiveness to social cues (see, e.g., Bering, 2004). Third, it could give them prior reinforced experience with imitating (i.e., it could allow them to experience a form of learning to learn). Fourth, there could be a general kind of learning to learn (i.e., learning that a task will be presented in which reinforcement can be obtained). Fifth, enculturation may actually improve the general cognitive ability of the animal.

Although Whiten (1993) suggested the failure to observe imitation in nonenculturated apes may be related to the fact that human demonstrators have been used, the use of conspecifics in such experiments does not guarantee success (Tennie et al., 2006, 2010; Tomasello et al., 1997). A better understanding of the various components of enculturation might provide important insights into the mechanisms involved in imitation by apes.

Gestural single-response imitation.   The two-action procedure provides the best control for nonimitative learning; however, if the to-be-demonstrated behavior is a gesture, and it is sufficiently unlikely to occur by chance, it may not be necessary to have a control group. Instead, one can use a within-subject design and observe the behavior of the observing animal for some time before it observes the gesture of the demonstrator (Tomasello et al., 1997).

More Complex Forms of Imitation

Program level imitation.   Byrne (1994) has distinguished action-level imitation, involving a single response, for example, pressing a lever or poking at a bolt, from program-level imitation that involves learning a coordinated sequence of actions leading to reward. Byrne and Russon (1998) describe the sequence of behaviors needed by gorillas to consume leaves that have stinging nettles on one side. They have argued that the sequence of actions was socially acquired, but the results of an experiment by Tennie, Hedwig, Call, and Tomasello (2008) suggest that gorilla nettle-feeding derives mostly from genetic predispositions and individual learning of plant affordances.

Nonetheless, one can ask if it is possible for animals to acquire a sequence of actions through observation. Evidence for the imitation of a response sequence by chimpanzees has been demonstrated by Whiten and Custance (1996) using the artificial fruit task in which a box containing a treat can be opened only by performing a sequence of actions on the box's "defenses," and observers appear to learn how to do this through observation.

There is also evidence that pigeons will imitate a sequence of two quite different response alternatives. Nguyen, Klein, and Zentall (2005) trained demonstrators to either step on a treadle or peck at the treadle to present a feeder, access to which was blocked by a screen. The demonstrator then had to push the screen in the assigned direction (left or right). Observers could then step on or peck at the treadle and then push the screen in either direction. Results indicated that there was a significant correlation between

the response sequence performed by the demonstrator and the response sequence performed by the observer. Thus, although program-level imitation likely involves a greater memory load, contrary to Byrne's (1994) distinction, program-level imitation does not appear to be conceptually different from imitation of a single response. Instead, the difference appears to be quantitative.

Generalized gestural imitation.   A form of imitative learning that is conceptually related to the two-action procedure involves copying the gestures of a model on command (e.g., "Do this!"). Successful do-as-I-do performance has been reported in chimpanzees (Custance, Whiten, & Bard, 1995; Myowa-Yamakoshi & Matsuzawa, 1999), orangutans (Call, 2001; Miles, Mitchell, & Harper, 1996), dolphins (Herman, Matus, Herman, Ivancic, & Pack, 2001), dogs (Huber et al., 2009; Topal, Byrne, Miklosi, & Csanyi, 2006), and parrots (Pepperberg, 1988), but only to a limited extent in monkeys (Fragaszy, Deputte, Cooper, Colbert-White, & Hémery, 2011). Remarkably, because the imitated models were humans, in the case of dolphins and parrots, there would be little similarity between the corresponding body parts of observer and the human demonstrators.

Custance, Whiten, and Bard (1995) found that chimpanzees learned to respond to the command "Do this!" by imitating a broad class of behaviors demonstrated by humans, including touching the back of the head and other actions that could not be seen as they were performed. Thus, such imitated opaque actions cannot be explained as some form of visual- stimulus matching. Furthermore, because objects are not involved in this kind of imitation, local and stimulus enhancement are irrelevant. Finally, each imitated gesture serves as a control for other imitated gestures, and the broad range of gestures that have been imitated within a few seconds of demonstration suggests that differential motivation does not play a role. Success in such do-as-I-do experiments shows not only that (enculturated) chimpanzees can imitate but also that they are capable of forming a generalized *concept* of imitation because they selectively imitate any of a broad class of gestures when cued to do so.

Byrne and Tanner (2006) have offered a different interpretation of the positive results of do-as-I-do studies. They propose that the behaviors imitated were not novel, that is, they were already in the animals' repertoire and the sight of the demonstration merely evoked a similar response (response enhancement). But as noted earlier, truly novel responses are very difficult to define, especially if one considers that the presumed novel behavior is likely to be similar to some past behavior by the observer. Thus it is more reasonable to require that the response have a very low probability of occurrence in the absence of observation of its demonstration by the model and that it cannot be explained by an alternative account. Furthermore, the notion of response enhancement fails to deal with the most perplexing question of the correspondence problem—how it is that the seen response of another comes to match the felt response of the observer. In Byrne and Tanner's (2006) view, those responses are "prewired" and reflexive. The possibility that an observed response will be reproduced automatically, perhaps by means of the mirror system (Rizzolatti, Fadiga, Fogassi, & Gallese, 2002), will be addressed shortly.

Intentionality.   Interest in imitation research can be traced, at least in part, to the possibility that imitation involves some degree of purposiveness or goal directedness. When an animal imitates the behavior of another animal, it is not clear that the goal is to obtain

the same outcome as the demonstrator. In the case of blind imitation, the goal of the observer is generally not the same as the goal of the demonstrator. When behavioral copying depends on the outcome of the demonstrator's behavior, it suggests that the observer's intention is responsible (but see Akins & Zentall, 1998). Intentionality (Searle, 1983) is surely involved in many higher order forms of imitation by humans, such as the student dancer who repeats the movements of a teacher. Interestingly, when it comes to the precise movements involved in dance or in sports, we humans are not particularly good at repeating them from demonstration. Instead, it is typically necessary to practice the movements many times and to learn from their consequences. In fact, the use of mirrors by dancers to perfect their movements suggests that trial-and-error stimulus matching plays an important role in the learning process (a process that Galef, 2010, refers to as *performance emulation*).

Intentionality is difficult enough to study in humans because, although they generally have language, they may not always be aware of their intentions, especially their intention to copy the behavior of others (see, e.g., Chartrand & Bargh, 1999). It is even more difficult to study in animals, and evidence for intentionality appears most often in the literature in the form of anecdote rather than experiment.

Mitchell (1987), for example, provides a number of examples of imitation in animals at these higher levels that imply intentionality. For example, the author discusses observations of a young female rhesus monkey who, after seeing her mother carrying a sibling, walked around carrying a coconut shell at the same location on her own body. If there were some way to conduct experiments involving the manipulation of intentionality, the credibility of these anecdotes would be greatly increased.

Understanding the intentions of others.   Evidence suggests that 14-month-old children are able to understand the intentions of another person and use this understanding to mediate their imitative behavior (Gergely, Nadasdy, Csibra, & Biro, 1995). When young children watched a demonstrator, whose hands were occupied, turn on a light by touching it with her forehead, they subsequently turned on the light more efficiently by using their hands. However, when the demonstrator's hands were not occupied, so that observing children might assume that it was necessary to use their forehead to turn on the light, children showed a greater tendency to copy the demonstrator by using the forehead.

Curiously, as children get older, they may engage in more acts of blind imitation. Thus Huang et al. (2006) reported that when 41-month-old children were shown a failed attempt to complete a response, they were more likely to copy the failed attempt than 31-month-olds. That is, in this case, younger children appeared to understand the intentions of the adult better than the older children. It may be, however, that the older children were more likely to have social copying (repeating the actions of the model, a kind of "follow the leader") as a goal rather than merely obtaining the outcome.

Results similar to those reported by Gergely et al. (1995) have also been found with enculturated chimpanzees (Buttelmann, Carpenter, Call, & Tomasello, 2007). More surprising, there is evidence that dogs may be able to make similar inferences (Range, Viranyi, & Huber, 2007). When dogs watched a dog demonstrator with a ball in its mouth pull a rod with its paw to obtain a treat, the observer dogs pulled the rod more efficiently with the mouth.

However, if the demonstrator's mouth was not occupied and it pulled the rod with its paw, the observers also pulled the rod with the paw, suggesting that dogs, like human children, cannot only imitate but also understand the intentions of the demonstrator (but see Kaminski et al., 2011, for an alternative explanation).

Symbolic imitation.   At the highest level of imitative behavior, what Mitchell (1987) refers to as fifth-level imitation, the behavior of the observer does not actually match the behavior of the demonstrator. In fact, the differences between the actions of the demonstrator and those of the observer are explicit, and they are produced for the purpose of drawing attention to specific characteristics of the demonstrator. Examples of such symbolic imitation can be found in the human use of parody and caricature— exaggerating someone's limp or their facial expression. Such forms of imitation are mentioned primarily for completeness and to note the degree of subtlety that can be involved in imitation.

Possible Behavioral and Biological Mechanisms

Recently, there have been several attempts to account for imitation using simpler behavioral and biological mechanisms. These are addressed here because they purport to provide simpler accounts of imitative processes.

An Associative Learning Account of Imitation

Ray and Heyes (2011; see also Heyes & Ray, 2000) have proposed an associative learning account of imitation based on Pavlovian and instrumental conditioning processes. According to their associative sequence learning model, in the case of humans, imitation is learned through prior experience with (a) direct self-observation (the correspondence of one's body parts, e.g., fingers with those of others), (b) mirror self-observation (the correspondence of felt actions with the image of those actions in a mirror), (c) synchronous action (two individuals happen to be making the same response), (d) acquired equivalence experience (experiencing a similar reaction when one is making a response, e.g., someone saying, "You look angry," and when someone else is making the same response, someone saying, "He looks angry"), and (e) being imitated (mothers imitate their babies and they reinforce imitation by their babies).

In the case of imitation by animals, for example, the two-action procedure with Japanese quail (Akins & Zentall, 1996) stepping and pecking have been reinforced in the past when they have occurred in the presence of other animals engaged in similar behavior. According to this theory, it is assumed that before participating in any experiment, observers ate at the same time as others and consequently learned to peck when others were pecking, and they fed from a similar feeder and consequently learned to step toward the feeder when others were doing so. As a result, seeing others pecking or stepping in the context of an experiment would become a discriminative stimulus for engaging in the same behavior.

However, there are several problems with this account. First, it is highly speculative and is not supported by data. For example, in our laboratory, birds are typically not fed at the same time, so pecking and stepping at the same time as other birds would not have been reinforced. Second, the theory requires that the home-cage context will generalize to the experimental context despite the

fact that the two contexts are quite different. Third, in the two-action procedure, the treadle is usually not actually located in front of the feeder. In our apparatus it is located in the front corner nearest to the observer and in a direction away from the feeder (see Figure 1). Finally, it is not clear how associative sequence learning can account for results of bidirectional control experiments in which a screen encountered for the first time is pushed in the same direction as a demonstrator pushed it. As Whiten (2005) suggests, if the processes responsible for imitation involve basic learning processes that are present in many animal species, why is it that only humans, certain great apes, dolphins, and birds show clear evidence of imitation learning?

Kinesthetic-Visual Matching

Another solution to the correspondence problem was proposed by Guillaume (1926/1971) and expanded on by Mitchell (1997b). The idea is that in addition to visual-visual matching (the ability to have a generalized concept of sameness—the concept that two things look the same) and kinesthetic-kinesthetic matching, some animals also are able to match across modalities and recognize the similarity between something they can see and something that they can feel. It is presumed that this ability is acquired through experience with objects and parts of one's body that can be both seen and felt. Given considerable experience seeing and feeling objects, and parts of one's body that can be seen, one should then be able to generalize to parts of one's body that cannot be seen. To accomplish this, one would have to be able to form an image or representation of the parts of one's body that one cannot see. For older children and adult humans from cultures with mirrors, it would not seem unreasonable to learn the correspondence between how an object looks and how it feels. And there is evidence that chimpanzees and several other species that have had some exposure to a mirror may show evidence that they can recognize themselves in a mirror. However, there is little evidence (except in human children) that generalized bodily imitation and self-recognition occur in the same individual (Mitchell, 1997a).

Possible Biological Mechanisms

Response Facilitation

Byrne and Russon (1998) have proposed that response facilitation can account for reports of imitation found in animals. As noted earlier, response facilitation implies that observation of a response elicits a similar response in an observer. By this account, the observed behavior is already in the repertoire of the observer and observation of it automatically primes the representation of the behavior in the brain, increasing the probability that the behavior will occur. Although this view provides a noncognitive mechanism for the kinds of response imitation most frequently studied in animals, it does not provide a particularly convincing account of imitation of behaviors that an animal encounters for the first time in an experimental setting, for example, pushing a screen to left or right to access food (when accompanied by the appropriate controls for emulation). Furthermore, it is not clear how the observed behavior became connected to the observer's motor response. Of course one could propose that it evolved as an adaptation to an unpredictable environment by means of something like the mirror

system (see next section). However, if this were the case, one would have to posit the evolution of predisposed connections for each behavior that has been found to be imitated—an unlikely and unparsimonious account, given the range of behavior and contexts in which it has been found. In addition, as we will see, the mirror system is constrained in the kinds of imitation that it is able to explain.

The Mirror System

There is evidence that neurons found in the premotor cortex of monkeys are activated not only when the monkey picks up an object but also when it sees either a human or another monkey pick up an object (Rizzolatti et al., 2002). These so called *mirror* neurons have been proposed to be responsible for imitation, and their presence in the premotor cortex rather than the visual cortex suggests that they may have a preparatory cognitive function. However, it is important to know whether these mirror neurons belong to "prewired" neural pathways that evolved to facilitate imitation or they have to be trained to behave the way they do. If learning is required, mirror neurons may result from imitation rather than be its cause (Csibra, 2007; Heyes, 2010). Furthermore, although mirror neurons may be involved in stimulus matching, it is not clear that they can account for perceptually opaque imitation in which there is little similarity between the visual input animals receive from watching the behavior of another and what they can see of their own behavior. But perhaps most important, although evidence for mirror neurons was originally reported in monkeys, with the exception of the study by Voelkl and Huber (2000) with marmosets, there is surprisingly little evidence that monkeys imitate (Fragaszy & Visalberghi, 2004; Visalberghi & Fragaszy, 1990).

Ferrari, Bonini, and Fogassi (2009) have described an innovative solution to this paradox. They suggest that there are two pathways that are involved in copying the behavior of others. The first is a direct parieto-premotor pathway that exerts a direct influence on the motor output during action observation. This pathway is involved in simple motor acts such as grasping (Rizzolatti et al., 2002) and does not require learning. It is responsible for neonatal imitation, such as described by Meltzoff and Moore (1977) and Lepage and Théoret (2007) in humans, and by Ferrari et al. (2006) in monkeys. However, Heyes, Bird, Johnson, and Haggard (2005) showed that nonmatching, or incompatible sensorimotor training—in which the participant repeatedly performs one action while observing another—can abolish and even reverse both imitative behavior and the action matching properties of the mirror neuron system.

The second pathway is indirect, linking parietal and premotor areas with ventro-lateral prefrontal cortex (see Tanji & Hoshi, 2008). This pathway could exploit the sensory-motor representations provided by the direct pathway for more complex cognitive and behavioral functions, such as those required for delayed imitative behaviors and opaque imitation. But it is precisely those processes that presumably take place in the prefrontal context that are of greatest interest to those who are interested in the processes responsible for complex imitative processes.

Others have argued that the behavioral aspect of mirror neurons are a by-product of the simulation theory of emotion recognition (Goldman & Sripada, 2005), which allows humans to have empa-

thy and also prepares them to act similarly to the behavior of others (Gallese, 2001). Humans then learn when to engage in similar behavior (imitate) and when to inhibit that behavior. Furthermore, they can also learn to engage in quite arbitrary behavior when presented with the behavior of another person (Catmur, Walsh, & Heyes, 2007). This simulation model can account not only for perspective taking but also for opaque imitation by humans. However, it is not clear that it can account for the opaque imitation shown by Japanese quail (Akins & Zentall, 1996) and pigeons (Zentall et al., 1996). And at this time, possible avian correlates of mirror neurons have been found only in the song system of vocal-learning birds (Prather, Peters, Nowicki, & Mooney, 2008).

Conclusions

Procedures have recently been developed that separate imitation from other forms of social influence and social learning, and the results of initial studies indicate that species from chimpanzees to quail can imitate. Such findings should not be surprising because social learning, whether by imitation or some other process, often provides greater benefits than genetically predisposed behavior or trial-and-error learning (Boyd & Richerson, 1988). However, the processes involved that enable animals to match their behavior to that of a demonstrator are poorly understood. Imitation may involve some form of coordination of visual and tactile sensory modalities, perspective taking, or response facilitation. However, the role of such processes in opaque imitation is still unknown. A reasonable strategy to better understand the mechanisms involved in imitation would be to determine the necessary and sufficient conditions for opaque imitation to occur and to explore the range of behaviors that animals can imitate.

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