

# Imitation: definitions, evidence, and mechanisms

Thomas R. Zentall

Received: 16 August 2005 / Revised: 3 July 2006 / Accepted: 5 July 2006 / Published online: 26 September 2006  
© Springer-Verlag 2006

**Abstract** Imitation can be defined as the copying of behavior. To a biologist, interest in imitation is focused on its adaptive value for the survival of the organism, but to a psychologist, the mechanisms responsible for imitation are the most interesting. For psychologists, the most important cases of imitation are those that involve demonstrated behavior that the imitator cannot see when it performs the behavior (e.g., scratching one's head). Such examples of imitation are sometimes referred to as opaque imitation because they are difficult to account for without positing cognitive mechanisms, such as perspective taking, that most animals have not been acknowledged to have. The present review first identifies various forms of social influence and social learning that do not qualify as opaque imitation, including species-typical mechanisms (e.g., mimicry and contagion), motivational mechanisms (e.g., social facilitation, incentive motivation, transfer of fear), attentional mechanisms (e.g., local enhancement, stimulus enhancement), imprinting, following, observational conditioning, and learning how the environment works (affordance learning). It then presents evidence for different forms of opaque imitation in animals, and identifies characteristics of human imitation that have been proposed to distinguish it from animal imitation. Finally, it examines the role played in opaque imitation by demonstrator reinforcement and observer motivation. Although accounts of imitation have been proposed that vary

in their level of analysis from neural to cognitive, at present no theory of imitation appears to be adequate to account for the varied results that have been found.

**Keywords** Imitation · Social facilitation · Stimulus enhancement · Affordance learning · Observational conditioning · Two-action procedure · Bidirectional control · Control procedure · Sequence imitation

## Introduction

This special issue of *Animal Cognition* (Watanabe and Huber 2006) devoted to research on the intelligent behavior of animals illustrates not only some of the remarkable abilities of animals but also serves to blur the line between humans and other animals. The present paper focuses on social learning, an ability that has received less attention than what its adaptive importance deserves. Perhaps one of the most underrated human learning abilities is learning from the observation of the behavior of another person. Children appear to be so predisposed to learn from the observation of others that Meltzoff (1988) has suggested that a more appropriate name for the human species would be *homo imitans*, man who imitates. The extent to which children learn by observation can be seen in the adage that pits adults' instructions to a child about how to behave against their own adult behavior, "Do as I say, not as I do."

## Biological approach to social learning

Biologists, who have long been interested in the adaptive value of behavior for the survival and reproductive success of the animal, have suggested that imitation may fill an important niche between species-typical, genetically predisposed behavior and individual (or trial and error) learning (Boyd

---

This contribution is part of the special issue "Animal Logics" (Watanabe and Huber 2006).

---

T. R. Zentall (✉)  
Department of Psychology, University of Kentucky,  
Lexington, KY, 40506-0044 USA  
e-mail: Zentall@uky.edu  
Tel.: + 606-257-4076  
Fax: + 606-323-1979

and Richerson 1988). The advantage of species-typical behavior is that it is reliable and does not depend on the vagaries of environmental reinforcement. Imagine how difficult they would be for a bird to have to learn to build a nest. It would first have to be motivated by the need to have some place to lay its eggs, it would probably have to lose many eggs before the appropriate shape and size were achieved.

However, species-typical behavior may not always be functional. Changes in the environment may force animals to learn by experiencing the consequences of their behavior. Hungry animals may have to learn to try new foods if their familiar foods are no longer available because of climate change or increased competition from other animals. But not all new foods are edible and some of them actually may be poisonous. Some animals have developed ways to reducing the potentially negative consequences of eating novel foods by testing small amounts that may not be sufficient to be fatal and by the very rapid association (one trial) of a novel taste with feeling ill (Garcia and Kolling 1966). Thus, individual learning has disadvantages as well.

Social learning may provide a functional compromise. Learning by observing others may provide more flexibility than is possible with species-typical behavior, but it may also avoid many negative consequences of making errors that often accompany individual learning (Boyd and Richerson 1988). In most cases, the behavior of others has already been shaped by consequences; therefore, doing what others do generally leads to favorable outcomes.

### Psychological approach to social learning

While biologists have tended to focus on the adaptive value of social learning, psychologists have been more interested in the mechanisms by which organisms learn from others. Rather than asking why animals learn from observing others, psychologists tend to be concerned with how they learn from others. If consequences are not experienced by the observer prior to performance, how do the observers know what to do?<sup>1</sup>

For certain forms of social learning (e.g., the repetition of a bird's song), one can propose a process similar to stimulus matching (Zentall and Hogan 1976) in which the listener attempts to match the song that it hears. A similar process may take place when the model's behavior has a clear effect on the environment (such as pushing open a door to obtain food). In this case, the social aspects of the observation may be incidental. Seeing the door open with food on the other

side may be sufficient to elicit door opening by the observer (Klein and Zentall 2003).

Social learning of this kind can be thought of as transparent (Heyes and Ray 2000) in the sense that the observer can see the similarity of the effect on the environment of the model's behavior and of its own behavior. More theoretically interesting is the ability to imitate opaque or invisible behavior; that is, a behavior that does not involve manipulation of objects in the environment and furthermore, that cannot be seen directly by the observer when the observer is performing it. Consider a child imitating an adult who is scratching his own head. How does the child know when she has imitated appropriately?

According to Piaget (1962), imitation can be a product of the sensory–motor stage of development. During this period, children learn to coordinate visual inputs with motor outputs such that they can efficiently reach for objects that they can see. One can perhaps account for cases of transparent imitation (e.g., imitating a model scratching his arm) by way of stimulus and response generalization (the observer would engage in motor behavior until her response matches that of the demonstrator), but opaque imitation requires additional processes. To invoke such a process to account for the imitation of head scratching, one must posit that one can visualize the appearance of one's own head and it is not clear how one would show that such visualization can take place.

Alternatively, one could account for opaque imitation by positing the ability to take the perspective of a third person. To accomplish this, in a sense, the child must ask herself, what I should do such that a third person would say that my behavior matches the behavior of the model. In many cultures, one could perhaps learn such correspondence from extended exposure to mirrors because mirrors would allow the individual to learn the correlation between proprioceptive sensations and visual appearance, but the ability to recognize oneself in a mirror appears to be unique to humans and other great apes (Gallup 1970). Thus, if perspective taking were necessary for opaque imitation, one should not be able to find evidence for opaque imitation in other animals.

Although there is some evidence from imitation research with 3-year-old children (Gleissner et al. 2000) that they make a similar number of errors when they cannot visually monitor their own response (e.g., ear-lob tug) than when they can (e.g., knee touch), the absence of an effect of invisible-versus opaque-response in these children may reflect either their experience with imitation games or their higher cognitive functioning rather than an inherent absence of difference between these two classes of behavior. It would be of interest to know whether younger or less experienced children would show the same ability to imitate opaque behavior.

Several reviews of social learning in animals have attempted to categorize the different classes of social

<sup>1</sup> There is a growing trend toward an integration of the biological and psychological approaches (see, e.g., Bjorklund and Bering 2003; Caldwell and Whiten 2002; Hare and Tomasello 2005).

learning and distinguish them from imitation (Whiten and Ham 1992; Heyes 1994; Whiten et al. 2004). Imitation, like many processes for which cognitive mechanisms are implied, is typically defined very generally and then qualified by specifying processes that are to be excluded. The view that imitation, especially imitation that would be considered opaque, requires mechanisms that are as cognitive as perspective taking means that if one studies imitation in animals, one must develop designs that control for the possibility that other, perhaps simpler, mechanisms are involved. For example, animals may be predisposed to engage in certain behaviors (e.g., eating) when others are seen engaging in those behaviors (species-typical behaviors). Alternatively, being in the presence of conspecifics (other animals of the same species) may result in an increase in general arousal, which may make certain behaviors more probable (motivational effects). Also, the behavior of others may draw attention to a place or object independently of the behavior itself, and that attention may facilitate learning (perceptual enhancement effects). Finally, observers may learn the relation between the effect of the observed behavior on the environment, and that may facilitate performance by the observer (observational conditioning or affordance learning).

To better define imitation, I will first describe these alternative processes and explain why they must be experimentally separated from imitation if one wants to claim that a particular species is capable of imitation. I will then describe several designs that have been used to assess imitation. I will also examine several variables that have been thought to be important in imitation by humans to determine if they have a similar effect on animals. Finally, I will present several hypotheses that have been proposed to account for imitation and show that they may not be adequate to account for the effects found.

### Species-typical factors

#### *Mimicry*

Perhaps the simplest case of copying is when one species physically appears like another. This form of copying is often referred to as mimicry. When a relatively defenseless animal takes on the appearance of or acts like an animal that has better defenses, it is known as *Batesian* (or *Mertensian*) mimicry. A well-known case of Batesian mimicry is that of the palatable viceroy moth mimicking the appearance of the unpalatable monarch butterfly (Turner 1984). Such mimicry results from natural selection of the increased fitness incurred by those moths that cannot easily be discriminated by predators from the bad-tasting butterfly, and it is an example of convergent evolution that does not involve behavior.

A special case of mimicry-involving behavior is the broken-wing display of certain ground-nesting birds, such as the killdeer or the avocet (Sordahl 1981). When the female bird is near the nest and a predator approaches, the bird flies away from the nest while mimicking the erratic flight pattern that might be shown by a bird with a broken wing. Although one can speculate about the origins of this behavior, it appears to be genetically based (i.e., the predator serves as a *releaser*) and it does not require learning.

#### *Contagion*

When two or more animals engage in similar behavior and that behavior is species-typical, the coordinated behavior is often attributed to *contagion* (Thorpe 1963; also called *mimesis*, Armstrong 1951, or *response facilitation*, Byrne 1994). Contagion can be used to describe certain courtship displays when they involve coordinated movements between the male and female that can sometimes appear to be virtual mirror images (Tinbergen 1960). Also, antipredatory behavior can be considered contagious when it involves the coordinated movement of a group of animals for defensive purposes. Such behavior occurs in certain mammalian species (e.g., herding) and avian species (e.g., flocking). When this coordinated behavior is aggressive (i.e., is directed toward rather than away from danger), it is known as *mobbing* (Hoogland and Sherman 1976). Contagion can also be shown in an appetitive context. For example, a satiated animal in the presence of food will often resume eating upon the introduction of a hungry animal that begins eating (Tolman 1964). In the case of contagion, the behavior of one animal appears to serve as a releaser for the unlearned behavior of others (Thorpe 1963).

#### Motivational factors

The typical procedure for assessing social learning is to assess the probability that an observer will perform a demonstrated behavior following observation. But performance of a behavior may occur spontaneously and if it does, the consequences of the behavior will influence the likelihood that the behavior will be performed again. Thus, it is important to compare the probability that the behavior will occur relative to an appropriate control. As we will see, determination of the appropriate control is an evolving process determined by what alternative processes one thinks might facilitate performance of the behavior. For example, the most obvious control would be a group of animals that acquires the response on its own (i.e., individual-learning control); however, this is clearly not sufficient. It is possible, for example, that the mere presence of another animal may influence the probability of certain behaviors.

### *Social facilitation*

It has been hypothesized that the mere presence of a conspecific can affect the motivational level (or level of arousal) of an animal (Zajonc 1965). The effect of such an increase in arousal, which Zajonc called social facilitation, may depend on the context in which the animal finds itself. Consider an experiment involving the acquisition of bar pressing by a rat. Increased arousal produced by the mere presence of a conspecific may increase the rat's general level of activity, and an increase in general activity is likely to bring the rat into contact with the bar that is to be pressed (Gardner and Engle 1971).

Alternatively, an isolated animal in a novel environment may be fearful, and fear in an enclosed environment may reduce exploratory behavior. If the presence of a conspecific reduces fear and increases exploratory behavior, it may lead to a higher probability (by chance) that the target behavior will be performed (Davitz and Mason 1955; Morrison and Hill 1967). Thus, experiments concerned with imitation must include a control for the possibility that the presence of another animal might result in an increase (or decrease) in motivation that could lead to facilitated performance of the target behavior (Zentall and Levine 1972; Levine and Zentall 1974).

One further potential source of demonstrator-provided motivation should be mentioned. Although the mere presence of a conspecific may contribute to the motivational state of an observer, the general (nonspecific) activity of the demonstrator may make an additional contribution. Being in the presence of an *active* conspecific (e.g., one that is working for food but is not responding in a way that is relevant to the target response) might generate even more activity in an observer.

### *Incentive motivation*

Reinforcement provided to the observer during the demonstration of a target response may also play a role in the rate at which the response is acquired (i.e., it may provide incentive motivation – the knowledge that food can be acquired in this context). Del Russo (1971) found significant facilitation of bar pressing by a group of observers that got fed whenever their bar-pressing demonstrators got fed (relative to an individual-learning control). This facilitation may have involved a general increase in arousal on the part of the reinforced observer or a more specific association of the apparatus context with reinforcement. In either case, observers that receive reinforcement when demonstrators make the appropriate response would likely be more active following observation than nonreinforced comparison groups, and a more active animal would be more likely to learn on its own through incidental contact with the bar.

### *Transfer of fear*

Observation of a novel response being acquired (or being performed) by a demonstrator that is motivated by the avoidance of painful stimulation (e.g., electric shock) may be a particularly good procedure to use in searching for evidence of social learning because of the great evolutionary value that such social learning should have (i.e., in the natural world aversive events are often fatal). However, if one is interested in imitation, the observation of a demonstrator in distress presents the need for a special kind of control. Emotional cues provided by a conspecific either escaping from or avoiding shock may provide emotional cues of pain or fear of pain that could instill fear in an observer. For example, John et al. (1968) found that cats that had observed a demonstrator being trained to jump over a hurdle to avoid foot shock 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, and the difference in initial fear experienced by cats that observed the demonstrator and those that did not observe the fearful demonstrator may have been sufficient to facilitate acquisition.

To make interpretation of the results of experiments involving observation of aversive conditioning even more difficult, under different conditions, induced fear of this kind can actually impair learning by an observer. For example, Sanavio and Savardi (1980) found that rats that observed a trained demonstrator that had acquired a discriminated shuttle avoidance response acquired that response faster than rats that observed a merely present demonstrator; however, rats merely exposed to the empty shuttle box acquired the shuttle response fastest. Thus, trying to identify mere presence and emotional/motivational effects and isolate them from the effects of social learning may be quite difficult. One approach is to use well-trained demonstrators to reduce the likelihood that pain-produced cues might be transmitted to the observers (Del Russo 1975); however, it may not be possible to avoid the effects of demonstrator-provided, fear-produced cues.

One way to reduce problems associated with differential motivational cues encountered with observation of aversively motivated conditioning is to include a control group that is exposed to performing demonstrators but with the observer's view of a critical component of the demonstrator's response blocked. Such a control was included in an experiment by Bunch and Zentall (1980) who used a candle-flame-avoidance task originally developed by Lore et al. (1971). Laboratory rats that have had no prior experience with a flame show a natural curiosity when presented with a candle flame. They cautiously approach the flame and withdraw quickly on contact (when the flame

singes their nose or their whiskers). Even so, repeated contacts are made until they learn to avoid contact with the flame.

Bunch and Zentall (1980) found that rats learned the candle-flame-avoidance task faster after having seen a demonstrator acquire the task, as compared with (1) a group for which a small barrier was placed in front of the candle such that the observer's view of the rat's contact with the candle was blocked and (2) a social facilitation control group that made no contacts with the flame. Thus, although a variety of auditory cues (a potential by-product of the demonstrator's pain), olfactory cues (e.g., potentially produced by singed whiskers, defecation, and urination), and visual cues (e.g., seeing the demonstrator approach and then rapidly withdraw from something directly behind the barrier) associated with the task should have provided comparable motivational cues for these control observers, task acquisition was not facilitated as much as for observers that could also observe the demonstrator's contact with the candle.

What is interesting about this flame-contact-blocked control group is that it differs from the typical control group, which would attempt to remove the fear-inducing cues provided by the demonstrator and ask if there were still facilitated learning. Instead, this control group should have provided all of the demonstrator's fear-inducing cues but eliminated the important cause of those cues, the contact with the flame.

Another means of controlling for potential motivational cues provided by the demonstrator performing a pain- or fear-motivated task is to expose the observers to demonstrators performing a discrimination (Kohn 1976; Kohn and Dennis 1972). In this research, rats that observed a demonstrator performing a relevant shock-avoidance discrimination acquired that task faster than controls for which the demonstrator's discrimination was the reverse of the observer's (i.e., the cue that signaled shock for the demonstrator signaled safety for the observer and vice versa).

#### Perceptual factors

When the observation of a demonstrator draws attention to the location of an action or the object of an action (e.g., a lever), it may alter the salience of the lever (stimulus enhancement) or the place in the environment where the lever is located (local enhancement). Thus, whenever the behavior being demonstrated is directed toward an object, that object may attract the observer's attention independently of what the demonstrator does to that object (i.e., the behavior to be imitated). In fact, animals may learn much about the functional significance of objects in nature by having their attention drawn to those objects when manipulated by conspecifics. But learning facilitated by such attention-getting would not qualify as imitation.

#### Local enhancement

Local enhancement refers to drawing attention to a locale or place (Roberts 1941). This attentional response may lead to observation that would not otherwise have been as readily seen (Thorpe 1963). For example, Lorenz (1935) noted that ducks enclosed in a pen may not pass through 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 draw attention to the hole and allow the observer to notice it.

Local enhancement has also been implicated in the finding that puncturing the top of milk bottles by great tits in Great Britain spread in a systematic way from one neighborhood to another (Fisher and Hinde 1949). Although the technique of pecking through the top of the bottle may be learned through observation, it is also likely that attention was drawn to the bottles by the presence of the feeding birds, and once at the bottles, the observers found the reward and consumed it. Then, learning to identify milk bottles as a source of food can readily generalize to other open bottles, and drinking from opened bottles can readily generalize to an attempt to drink from a sealed bottle, which in turn can lead to puncturing of the top.

As Denny et al. (1988) have shown, local enhancement can be studied in its own right. Exposing rats to the movement and sound of a bar being activated (by the experimenter from outside the chamber) followed by the presentation of food, can facilitate the acquisition of the bar-pressing response by the observers, relative to various control procedures.

Local enhancement may also account for John et al.'s (1968, Experiment 2) finding of socially facilitated acquisition of lever pressing by cats. Cats in an experimental group that observed another cat lever pressing for food, learned to press that lever faster than cats in a control group that observed another cat that was fed periodically without lever pressing. But observation of lever pressing may draw attention to the lever rather than to the cat pressing the lever. Local enhancement is especially likely in this context, in which observation of the moving lever might encourage lever approach upon removal of the demonstrator (especially by cats, a species known for its motivation to explore).

Similarly, local enhancement may play a role in the faster acquisition of lever pressing by kittens that observed their mothers as demonstrators, than by kittens that observed an unfamiliar female demonstrator (Chesler 1969), because orientation toward the mother may be more likely than orientation toward an unfamiliar cat.

Local enhancement may also be involved in John et al.'s (1968, Experiment 1) finding of facilitated acquisition of an aversively motivated hurdle-jump response. The distinction between imitation and local enhancement may be a subtle one in this case, but observation of the jumping demonstrator

may draw the observer's attention to the top of the hurdle. In other words, seeing an object move over the hurdle, or even placing a flashing light at the top of the hurdle might be enough to facilitate the hurdle-jumping response. In general, whenever the behavior observed involves an object to which the observer must later respond, local enhancement may play a role (Corson 1967; Jacoby and Dawson 1969; Oldfield-Box 1970; Denny et al. 1988; Herbert and Harsh 1944).

In other cases, it may be possible to control for local enhancement effects by including proper controls. Lefebvre and Palameta (1988), for example, found that pigeons that observed a model pierce the paper cover of 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.

### *Stimulus enhancement*

The term stimulus enhancement is often used when the activity of the demonstrator draws the attention of the observer to a particular *object* (Spence 1937). Because Spence defined a stimulus in terms of a class of events sharing common attributes, the notion of stimulus enhancement is much broader than that of local enhancement. 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 (Warden and Jackson 1935; Gardner and Engel 1971), however, there are two manipulanda (e.g., levers), one in the demonstration chamber and the other in the observation chamber. Under these conditions, drawing attention to the demonstrator's lever should not facilitate acquisition of lever pressing by the observer. In fact, one could argue that it should retard acquisition of lever pressing by an 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 notices its own lever after having its attention drawn to the demonstrator's lever because of stimulus generalization (Henning and Zentall 1981; Levine and Zentall 1974; Zentall and Levine 1972). Thus, stimulus enhancement refers 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 lever and the observer's lever. Because it subsumes local enhancement, the term stimulus enhancement may be more inclusive and thus, may be preferable (Galef 1988b).

Stimulus enhancement may also be involved in the facilitated acquisition by an observer of a demonstrator performing a discrimination (e.g., responding in the presence of an S + stimulus but not in the presence of an S – stimulus). If

the demonstrator is required to make contact with the positive stimulus, but not the negative stimulus, the positive stimulus is likely to attract the observer's attention and responding to it may be facilitated (Kohn and Dennis 1972; Kohn 1976; Edwards et al. 1980; Vanayan et al. 1985; Fiorito and Scotto 1992).

Stimulus enhancement may also play an important role in mate-choice copying by guppies (Dugatkin 1996). Female guppies that see a model female in the presence of a courting male will tend to prefer that male over an alternative male (Dugatkin 1992; Dugatkin and Godin 1992). But the courting behavior itself may draw attention to the male, and the observing female may be more attracted to the familiar male than to the unfamiliar one.

The facilitation of learning through perceptual factors presents a most difficult problem for the study of imitation in animals. If the similarity between the demonstrator's manipulandum and that of the observer allows for stimulus enhancement, how is one to study imitation in the absence of stimulus enhancement? This problem, which will be addressed later, will require a new approach to the design of experiments and to the defining of adequate control procedures.

### Nonimitational learning factors

There are a number of cases of social learning that may be mediated by nonsocial learning mechanisms. Although social stimuli are present and they may play a role in facilitating acquisition of the target behavior (perhaps because the social stimuli are more salient than nonsocial alternatives), the mechanisms by which the observer acquires the behavior may be more parsimoniously explained in terms of individual learning processes sometimes mediated by species-typical behavior.

### *Imprinting*

The first example of social learning that should be distinguished from imitation is imprinting. Imprinting is a process that occurs primarily in species that do not have the luxury of a nest or den in which to protect their young. In such species (e.g., fowl and grazing mammals), the young are hatched (or born) in a precocious state that allows them to move about following a very brief period of inactivity. To compensate for their mobility (which could also put them at a great risk of predation) these species have evolved the predisposition to follow the first moving object they see. Although this object is generally their mother, laboratory experiments show that almost any moving object can function as the object of imprinting (Hess 1973).

Imprinting is a curious process that combines a strongly predisposed behavior (following) with considerable

flexibility (learning) in the nature of the object that is followed. Although one could say, in a very general sense, that the imprinted young are imitating the mother, the act of following (or approach), is more parsimoniously interpreted as a simple conditioning process, with fear reduction serving as the reinforcer (Kovach and Hess 1963).

#### *Discriminated following (matched dependent) behavior*

Rats can learn to follow a trained conspecific to food in a “T” maze (if following is rewarded) in the absence of any other discriminative stimulus (Bayroff and Lard 1944; Church 1957; Haruki and Tsuzuki 1967). This kind of learning is sometimes referred to as discriminated following or matched dependent behavior. 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 or leader 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, one would refer to the cue (i.e., the demonstrator, the block of wood, and 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 a moving nonliving cue (Stimbert 1970).

#### *Observational conditioning*

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 orientation to 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 and Ham 1992) or valence transformation (Hogan 1988). Similarly, in the case of aversive consequences, the pairing of an object with the demonstrator’s fear response can lead to observational conditioning (Mineka and Cook 1988; Whiten and Ham 1992).

Although observational 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 in the absence of a demonstrator. If, for example, the onset of a localizable light is followed soon after by the presentation of inaccessible grain, it is sufficient to produce pecking to the light by pigeons (Zentall and Hogan 1975). The presence of a demonstrator drawing additional attention to the object to be manipulated (by pecking) and to the reinforcer (by eating) may further enhance associative processes in the absence of imitative learning.

If such a conditioning process is involved, it would suggest that observation of reinforcement of the demonstrator’s response should play an important role in such learning. In fact, if the demonstrator’s response is not reinforced, or if it cannot be observed, there is evidence that acquisition is impaired (Akins and Zentall 1998; Groesbeck and Duerfeldt 1971; Heyes et al. 1994). Furthermore, rats appear to acquire a bar-pressing response faster following observation of a bar-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 direct Pavlovian conditioning (i.e., the pairing of bar movement with food).

Observational conditioning may also play a role in an experiment in which observation of experienced demonstrators facilitated the opening of hickory nuts by red squirrels, relative to trial-and-error learning (Weigle and Hanson 1980). Differential local enhancement can be ruled out, in this case, because animals in both groups quickly approached and handled the nuts, and the observers actually handled the nuts less than controls (perhaps because observers were more efficient at opening them). However, observers alone got to see the open nuts and they had the opportunity to associate open nuts with eating by the demonstrator.

Similarly, in an experiment already described, Palameta and Lefebvre (1985) showed that a majority of pigeons in three experimental groups that observed a demonstrator piercing a paper cover to obtain grain were able to show similar paper-piercing behavior after a single period of observation, whereas pigeons that observed the demonstrator eating without having to pierce paper and those that observed paper piercing with no food to eat, in general did not learn. Although this experiment involved several important control conditions, the observers in the experimental groups were the only ones that observed both paper piercing and food. Thus, these groups were the only ones that observed food that was initially hidden underneath the paper, and such learning may confound imitation with observational conditioning.

Socially transmitted food preferences (e.g., Galef 1988a; Strupp and Levitsky 1984) may represent a special case of observational conditioning. Although food preference would appear to fall into the category of unlearned behavior subject to elicitation through contagion, consuming a food with a *novel* taste can be thought of as an acquired behavior. The mechanisms responsible for socially acquired food preferences have been posited to have 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 (Galef 1996). On the other hand, there is also evidence that learning phenomena (e.g., blocking, overshadowing, and latent inhibition) readily found in

conditioning experiments with more typical stimuli and outcomes, are not easily found in experiments involving the social enhancement of food preferences (Galef and Durlach 1993). Thus, different mechanisms may be involved.

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 and Cook 1988). Presumably, the fearful conspecific serves as the unconditioned stimulus, and the snake serves as the conditioned stimulus. In support of this hypothesis, it appears that exposure to a fearful conspecific alone or to a snake alone is insufficient to produce fear of snakes in the observer.

#### *Affordance learning (or object movement reenactment)*

Affordance learning is similar to observational conditioning; however, in the case of affordance learning it is not necessary to specify the reinforcer. Affordance learning can be described as learning how the environment works. For example, one can learn how a door works by watching someone turn the knob and push the door away. One may infer the reward to be leaving the room, and evidence for learning may require that the observer be motivated to leave the room but it is possible for learning to occur without having such motivation (latent learning).

Affordance learning also implies that the response to be acquired is more complex than a simple approach response suggested by observational conditioning. For this reason, if learning involves observation of the movement of an object in a particular direction, in the absence of a demonstrator, it is usually referred to as affordance learning or object movement reenactment. For example, Klein and Zentall (2003) allowed pigeons to observe a screen that was placed in front of a feeder opening. For some of the pigeons the screen moved away from the opening to the left whereas for others it moved away from the opening to the right. When the pigeons were later allowed access to the screen, which was placed in front of the feeder opening, there was a significant tendency for them to push the screen away in the direction that they saw it moved.

#### *Bird song*

A special case of matching behavior by animals is the acquisition of bird song (Hinde 1969; Marler 1970; Nottebohm 1970; Thorpe 1961; see also vocal mimicry; e.g., Pepperberg 1986; Thorpe 1967). Although for many species of song bird the development of species-typical song is regulated to a large extent by maturation and the seasonally fluctuating release of hormones, regional variations in the song appear to depend on the bird's early experience with conspecifics (Baptista and Petrinovitch 1984). Thus, one could

say that young song birds learn their regional dialect by imitating the song of more mature conspecifics.

Acquisition of the bird-song dialect is a special case of imitation for three reasons. First, although it is learned, bird song is a variation on a species-typical behavior and thus, is relatively constrained. Second, according to Heyes (1994), in the acquisition of bird song, components of the matching behavior occur by chance, and these components increase in frequency because they are intrinsically rewarding. Heyes refers to such behavior as copying rather than imitation. But finally, and most importantly, bird song takes place in the auditory modality. A characteristic of 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. Thus, verbal behavior, for which comparisons between one's own behavior and that of others is relatively easy because one can hear one's own utterances with relative fidelity, may be a special "prepared" case of generalized, stimulus identity learning (in which animals that have been trained to match shapes can now use the principle of matching to match novel hue stimuli; see Zentall et al. 1983). Although one might argue that no two birds sound exactly alike and moreover, a bird's song is not likely to sound the same to itself as it does to another bird so true stimulus matching cannot take place, it is very likely that great similarity can be detected between the song of the model and that of the social learner.

This analysis of the imitation of verbal behavior can also be applied to certain examples of visual imitation. 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). When visual matching is involved, it is generally classified as affordance learning. Such cases of visual stimulus matching can be distinguished from the more abstract and interesting case in which no visual stimulus match is possible (e.g., the imitation of a person who has his hands clasped behind his back).

#### *Imitation*

The previous discussion of social and nonsocial factors that must be distinguished from imitation may place prohibitively difficult constraints on evidence for imitation in animals.

Some researchers have even argued that true imitation requires that the observer recognize the intentional structure of the actions of the demonstrator (Tomasello et al. 1993). However, if this level of evidence is required, then imitation is not likely to be found in any nonverbal animal, and many examples of imitation in young humans with limited



language ability would have to be rejected as well. Alternatively, we can use a functional approach that attempts to control for the presence of all of the nonimitative factors described, and considers any matching behavior that is left as evidence for imitation.

With the problems of control in mind, one approach to the study of imitation in animals has been to define the control condition somewhat differently. Instead of using the typical experimental paradigm in which all variables are held constant across groups except the one being tested (see e.g., Zentall and Levine 1972), we can consider the imitation of an alternative response as the potential control group. That is, if manipulation of an object can be accomplished in one of two different ways, one can compare the performance of observers that watched a demonstrator manipulate the object in one way with that of observers that watched a demonstrator manipulate the object in a different way. In fact, both the groups can then serve as experimental groups with each serving as the control group for the other.

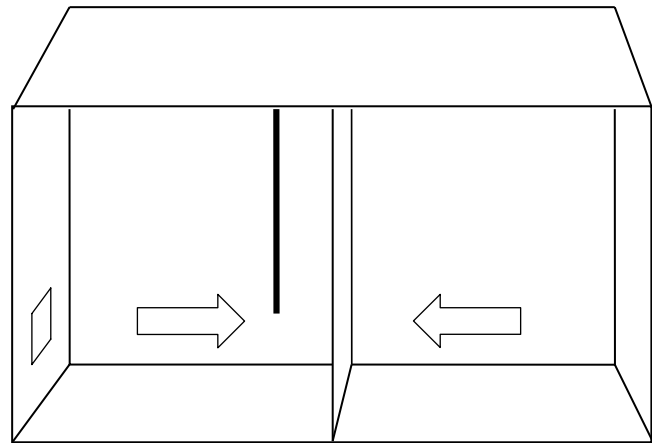
#### *Bidirectional control procedure*

Custance et al. (1999) used “artificial fruit” to simulate the shell of fruit that must be removed by a monkey to gain access to the edible portion inside. In fact, demonstrators opened a latched clear plastic box, and they could do so in one of two distinctively different ways. Observer monkeys permitted to observe the box opened in one of those ways showed a significant tendency to open the box in the same way that they had observed.

Similarly, Dawson and Foss (1965) found that budgerigars acquired a lid-removal task (by individual learning) in one of three different ways: Pushing the lid off with the beak, twisting it off with the beak, or grasping it with the foot and pulling it off. Observers were then exposed to the performing birds, and when the observers were given the opportunity to perform themselves, each observer removed the lid in same way as its demonstrator (see also, Galef et al. 1986 for similar but more modest results with this procedure).

Will et al. (1974), noted a related effect in a study in which rats observed either a trained demonstrator performing a successive discrimination or an experimentally naive demonstrator. They found that the trained demonstrators typically responded with one of three distinctive patterns when the discriminative stimulus was available, and that the observers learned not only to respond in the presence of one stimulus and not in the presence of the other, but they also learned the *pattern* of responding of their demonstrator (e.g., alternating a bar press with eating, or making a burst of bar presses followed by eating the accumulated pellets).

Heyes and Dawson (1990) have reported similar results for rats that observed demonstrators expressly trained to respond in one of two different ways. After observing demon-



**Fig. 1** Schematic of the bidirectional control apparatus (Heyes and Dawson 1990)

strators push an overhead bar either to the left or to the right, Heyes and Dawson found that observers given access to the bar tended to push the bar in the same direction as their demonstrator. Remarkably, the observers matched the demonstrators’ behavior in spite of the fact that, because the observers faced the demonstrators during the period of observation, the direction of bar motion (relative to the observer’s body) during observation was opposite that of the bar’s motion when the observers performed (Fig. 1).

In principle, the bidirectional control procedure provides the best control for all of the nonimitational factors mentioned earlier. In practice, however, in much of the research that has used this procedure, in addition to the differences in response topography between the observation conditions there have been differences in the consequences of those topographies. For example, in the budgerigar lid-removal experiment, one of the demonstrators learned to push the lid back whereas another demonstrator learned to grasp the lid in its beak and twist it off (as if it were hinged at one side edge). Thus, each of the different response topographies found by Dawson and Foss (1965) had a different effect on the lid. To what extent did the distinctive movement of the lid (lids slide off to the back versus lids twist off to the right), rather than the demonstrator’s response topography, produce the strong correlation between observer and demonstrator lid-removal technique? The birds may have learned how the lids worked, or what was referred to earlier as affordance learning or object movement reenactment (Gibson 1979; Tomasello 1996; Whiten 1998a) rather than the appropriate response for a bird to remove the lid. Similarly, in the artificial fruit experiment (Whiten et al. 1996), seeing the way in which the latch worked (independent of the response topography used by the demonstrator) may have contributed to the matching behavior (see also Voelkl and Huber 2000).

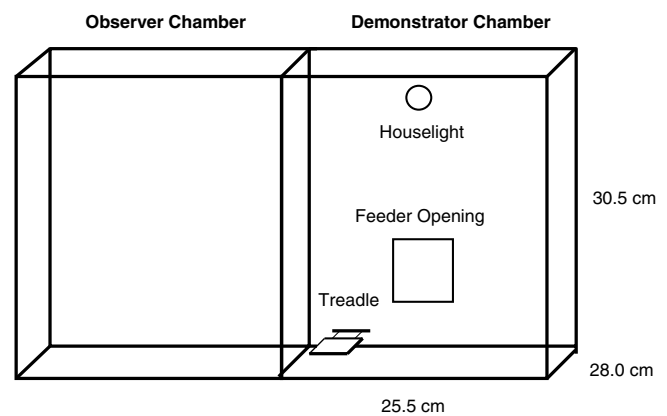
In the Heyes and Dawson (1990) experiment, too, the overhead bar moved in different directions (toward different

walls of the demonstrator's chamber) for the two observation groups. Heyes et al. (1994, Experiment 2) attempted to control for the fact that in the two cases, the movement of the bar was toward two different walls. In that experiment, between the time of observation and observer performance, the location of the bar was shifted from the common wall between the two chambers to one of the sidewalls (i.e., a 90° shift in the direction of possible movement of the bar). Thus, during observation, the bar moved either to the left or the right, whereas during observer performance, the bar moved toward the front or the back of the chamber. Once again, from the perspective of the bar-pushing animal, a significant match was found between the direction of bar push for demonstrators and observers. Later research suggested, however, that olfactory cues, specific to the side of the bar against which the demonstrators pushed, were likely to have been responsible for this imitation-like effect (Heyes and Ray 2000; Mitchell et al. 1999). The observers could detect the place on the bar that the demonstrators pushed, and in exploring those places, they too tended to push on the bar.

One means of controlling for learned affordances is to include control groups that observe a demonstrator and observe the environmental manipulation but it is not the demonstrator that is responsible for the manipulation. Akins et al. (2002) used such a control in an experiment in which Japanese quail observed a demonstrator pushing a screen either to the left or to the right, away from a feeder opening. The control group observed a demonstrator trained to refrain from pushing the screen, while the screen was pushed to the left or to the right unobtrusively by the experimenter. Quail in the experimental groups showed a significant tendency to match the screen push that they observe whereas those in the control groups did not (see also Klein and Zentall 2003).

#### *Two-action procedure*

In a variation of the bidirectional control procedure known as the two-action procedure, Akins and Zentall (1996) tried to overcome the problem of differential environmental consequences produced by the two different responses. They accomplished this by training Japanese quail to respond to a treadle (a small metal plate located about 1.3 cm from the floor of the chamber) for food, either by pecking at the treadle with their beak or by stepping on the treadle with their foot (Fig. 2). With a common manipulandum and the common movement of the manipulandum, the effect of the two response topographies on the environment should be common as well. Akins and Zentall found that observers showed a significant tendency to respond to the treadle with the same part of the body (beak or foot) as their respective demonstrator (see also Zentall et al. 1996, for similar results with pigeons). Kaiser et al. (1997) proposed that the two-action procedure, together with a control for individual learning, provides the



**Fig. 2** Schematic of the two-action procedure apparatus (Akins and Zentall 1996)

most convincing evidence yet for imitative learning in animals.

In the Introduction, I noted that from the viewpoint of cognitive processes, a particularly interesting form of response matching involved opaque responses that appeared different to the observer when performed by itself and when observed in others. With this in mind, in the present case, it is very unlikely that there was any similarity between the visual stimulus seen by the observer during observation and that seen by the observer during its own performance of the same response. Specifically, the demonstrator's beak as it pecked the treadle must have appeared quite different to the observer from the observer's own beak as it pecked the treadle. Similarly, though perhaps not so obviously, when the quail stepped on the treadle (located near the corner of the chamber; Fig. 2) they pulled back their head and thrust their body forward. Thus, they could not see their foot making contact with the treadle. Therefore, any account of the imitation found in these experiments in terms of stimulus matching would be quite implausible.

#### *Gestural imitation*

A form of imitative learning conceptually related to the two-action procedure occurs when the gestures of a model are copied (in the absence of object manipulation). Imitation of gestures has been found in a number of species (e.g., chimpanzees, Custance et al. 1995; Hayes and Hayes 1952; orangutans, Russon and Galdikas 1993; and a parrot, Moore 1992). Remarkably, in the case of the parrot, the models were human rather than a conspecific. Thus, there was little similarity between corresponding body parts of the observer and the demonstrator. Because objects were not involved, local and stimulus enhancement should be irrelevant. Furthermore, each imitated gesture serves as a control for the others because it is the topography of the response that is important. In addition, the fact that a

broad range of gestures have been shown to be imitated within a few seconds of demonstration suggests that no account based on differential motivation is likely to play a role.

The remarkable ability of some animals to learn from observing an entirely different species is perhaps best exemplified by the work of Pepperberg (1988) with a parrot using the model/rival technique (first reported by Todt 1975). In the model/rival technique, two human experimenters demonstrate the training of a particular behavior to the parrot, with one human taking the role of the teacher and other the role of the student. Analysis of the various mechanisms that contribute to learning under these model/rival conditions clearly is not possible. Certainly, vocal mimicking of the type already discussed in the section on the acquisition of bird song plays a role and observational conditioning may play a role as well, but the examples of gestural imitation already cited (Moore 1992) together with the remarkable cognitive capacity of these birds (Pepperberg 1990) suggests that this species may be capable of considerable learning through imitation.

### Sequence imitation

Recently, Byrne (2005) has suggested that the imitation of actions such as those described here may be produced by a form of predisposed reflexive response that he calls social mirroring resulting from a process he refers to as response facilitation. Of course, such reflexes would have to (1) be predisposed for each response (pecking or stepping) individually, (2) be directed toward a particular object (the treadle or the screen), and (3) be capable of being deferred following observation (see section on deferred imitation). It is possible that so-called mirror neurons in the premotor cortex could serve that purpose (Gallese et al. 1996), but to date, they have been shown only for transparent behavior. Furthermore, Byrne (2005) suggests that social mirroring can be explained in terms of conventional associative learning; however, the mechanism responsible for the imitation of opaque responses, in particular, would seem to require more than associative learning processes.

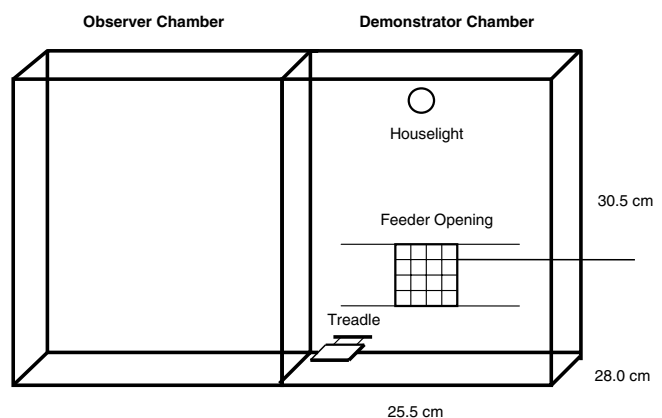
Alternatively, Byrne (2002) suggested that learning by copying involves skill acquisition involving a hierarchical set of responses. If an animal could imitate a sequence of responses it would suggest a more cognitive integrative process. Byrne has referred to the imitation of hierarchical sequences as *program-level* imitation because observation of the behavioral sequence may result in a program of behavior that the observer can produce. According to Byrne, to qualify as program-level imitation not only must a sequence of behavior be imitated but also the sequence must have a logical hierarchical structure (Byrne 1994, p. 242). Although few examples of such program-level imitation have

been provided by Byrne, he does suggest one, leaf eating performed by gorillas in natural environments in which it is difficult to distinguish imitation from individual learning because the similarity in behavioral sequence used among the animals may be attributed to the fact that the sequence recorded may just have been the best way to accomplish the goal.

Whiten (1998b) provided a more readily interpreted demonstration of sequence imitation by chimpanzees. Using the demonstration of a sequence of behavior to open an “artificial fruit,” which varied among observers, Whiten found that observers showed a strong tendency to match the sequence demonstrated.

Recently, we have investigated sequence imitation in pigeons (Nguyen et al. 2005). In a  $2 \times 2$  design, demonstrator pigeons were trained to either peck at a treadle or step on the treadle and then push a screen, either to the left or to the right, away from a feeder opening (Fig. 3). To obtain food, the observer pigeons could step or peck and then push the screen to the left or to the right with any of the four possible sequences. (Actually, the pigeons could have pushed the screen prior to responding to the treadle, so in fact, there were eight possible sequences of the two responses.) We found that the sequence produced by the observers was significantly correlated with the sequence demonstrated. Furthermore, there was a significant conditional probability of matching treadle response given a matching screen-push response. Thus, it was not the case that some pigeons had imitated one of the responses and others had imitated the other response.

Further research on sequence imitation by animals, especially birds, needs to be examined before a strong conclusion can be drawn. However, the fact that animals other than the great apes are capable of imitating behavioral sequences suggests that program-level imitation in the form of the imitation of a sequence of behaviors is not conceptually different from the imitation of a single action.



**Fig. 3** Schematic of the sequence imitation apparatus (Nguyen et al. 2005)

### *Deferred imitation*

A distinction made between imitation that occurs at the same time as demonstration (or immediately thereafter) and observational learning that occurs some time after demonstration of the target behavior (Bandura 1969). Those who make this distinction consider immediate response matching to be of a simpler kind (e.g., a form of contagious or reflexive behavior). According to this view, deferred imitation is not reflexive but must represent the internalization of the demonstrator's behavior because the stimulus complex associated with demonstration is no longer present. Thus, according to this view, deferred imitation exemplifies a higher level of cognitive behavior.

If deferred imitation is qualitatively different from immediate imitation, it is appropriate to ask at what point that transition occurs. When the duplicate-chamber procedure is used (e.g., Zentall and Levine 1972), the observer can perform in the presence of the performing demonstrator, so it is reasonable to refer to the matching behavior found as immediate imitation. In the case of the two-action procedure, however, the demonstrator is typically removed and the observer is placed in the demonstrator's chamber where it is allowed to perform. In this case, some time elapses (typically about 1 min) between the demonstrator performance and the observer performance. The duration of 1 min should be sufficiently long to exclude the kind of reflexive response thought to be responsible for immediate imitation and to warrant calling the correlation between the demonstrator and the observer behavior deferred imitation.

As it turns out, however, we have even stronger evidence that quail are capable of showing deferred imitation. Dorrance and Zentall (2001), in their study of the effects of observer motivation on imitation, included a group of quail that observed the demonstration of treadle pecking or treadle stepping, and were given the opportunity to perform 30 min later. These quail showed response matching that was comparable to a standard imitation group that was tested immediately after observation. Thus, Japanese quail show deferred imitation for up to half an hour. 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 an explanation of the response matching found in these studies.

### *Generalized imitation*

Imitation of a particular response can be thought of as one example of a broad class or concept of imitative behavior. Consider the fact that children can learn to imitate on command. Can an animal learn the general concept of imitation and then apply it when asked to do so in a "do-as-I-do" test?

Hayes and Hayes (1952) found that a chimpanzee (Viki) learned to respond correctly to the command "Do this!" over a broad class of behavior. More recently, Custance et al. (1995) have replicated this result under more highly controlled conditions. Furthermore, Custance and Bard (1994) using the "do-as-I-do" procedure, have found that actions on parts of the body that cannot be seen by the performer were just as readily copied as those that could be seen. As noted earlier, the importance of behavior that cannot be seen by the performer (e.g., touching the back of one's head) is that it rules out the possibility that some form of visual stimulus matching might account for the behavioral match. As evidence of the generality of this effect, results very similar to those found by Custance et al. have been reported by Call (2001) in an orangutan.

The establishment of a "do-as-I-do" concept not only verifies that chimpanzees can imitate, but it also demonstrates that they are capable of forming a generalized behavior-matching concept (i.e., the chimpanzees have acquired the concept of imitation). It is quite likely that this advanced level of imitation is limited to humans and the great apes (Miles et al. 1996; Tanner and Byrne 1999).

### *Goal emulation*

Under certain conditions an observer may attempt to reproduce the *results* that the model's behavior has achieved by a method other than that used by the demonstrator. Whiten and Ham (1992) have used the term goal emulation to describe this nonmatching form of imitation in which an observer may "understand" that a particular observed behavior has certain consequences, but it may also recognize that the goal could be achieved by any one of a larger class of behaviors. (Goal emulation should not be confused with what Tomasello has called emulation, a process similar to affordance in which learning about the *results* of behavior is sufficient to facilitate acquisition.)

Goal emulation is a kind of imitation that is similar to what Mitchell (1987) calls fourth-level imitation. At this level, "the organism is not bound to reproduce the model, but reorganizes the relationship between model and copy to its own ends" (p. 207). If an adult human were to see someone who was carrying packages push a door open by backing into it, would likely use a hand to accomplish the same goal. Imitation at this level is produced extensively by humans (e.g., children engaged in make-believe play), but Mitchell suggests that it also can be found in animals (see section on intentionality).

But how does one distinguish between a failure to imitate and goal emulation (understanding how a demonstrator is achieving a goal and choosing a different, perhaps more efficient way to achieve the same goal)? Recent evidence with young children (14 months) suggests how such a distinction

could be made (Gergely et al. 2002). When these children were shown a means of turning on a light by depressing it with the head, whether they imitated the head push or not depended on whether the demonstrator's hands were free. If the demonstrator had her hands on the table (implying the hands could have been used to depress the light) the children were quite likely to imitate her response (using their head). However, if the demonstrator was wrapped in a blanket with hands not free, the children were not likely to imitate her response and instead used their hands. The authors proposed that the children had reasoned that with hands free the demonstrator chose to use her head for a reason, so they too used their head, but with hands occupied the demonstrator did not have a choice and had to use her head. In this case, the children reasoned that they did not have the same constraint as the demonstrator and they could use their hand to turn on the light. But it is not always possible to make such an inference especially in research with animals.

The possibility that true imitation could be present in the absence of a match between the behavior of the demonstrator and the observer raises problems for the assessment of imitative learning beyond those already mentioned. The procedure used by Dawson and Foss (1965) provides a useful example. If a budgerigar observes another removing the lid of a food container with its foot but “decides” that it could accomplish the same result (perhaps more easily) with its beak, the observer's behavior would be scored as nonimitative. Thus, the possibility of goal emulation raises potential problems even when the two-action procedure is used. On the other hand, the possible ambiguity in the interpretation of findings resulting from the use of the two-action procedure would be a problem only if one *failed* to find evidence for behavioral matching. Furthermore, alternatives to the two-action procedure are even less appealing because they tend to err on the side of failing to rule out simpler mechanisms. Thus, the two-action procedure remains a useful, albeit perhaps relatively conservative, test of imitative learning.

### *Intentionality*

Interest in imitation research can be traced, at least in part, to the assumption that true imitation involves some degree of intentionality or goal directedness. This is certainly the case with many of the higher order forms of imitation, such as the human dancer who repeats the movements of the teacher. Unfortunately, intentionality, because of its indirect nature, can only be inferred, and evidence for it appears most often in the form of anecdote rather than experiment. Ball (1938), for example, noted the case of a young rhesus monkey that, while kept with a kitten, was observed to lap its water in the same way as a cat. Ball noted further that lapping is extremely rare in rhesus monkeys. Thus, given that monkeys

do not usually drink this way, the suggestion is that the young rhesus monkey was attempting to imitate the cat.

Similarly, Mitchell (1987), in an analysis of various levels of imitation, provides a number of examples of imitation at these higher levels. For example, he describes the young female rhesus monkey who seeing her mother carrying a sibling, walks around carrying a coconut shell at a same location on her own body (Breuggeman 1973). Again, the implication is that the young female was attempting to imitate her mother.

Such anecdotes, by their very nature, are selected and are difficult to verify. If there were some way to bring these examples of intentional imitation under experimental control, it would greatly increase their credibility. Furthermore, intentionality is sometimes used to indicate not just goal-directed behavior but a mental state involving belief or desire. Although there is no way that such mental processes can be verified (even indirectly), such speculation can lead to more carefully controlled experiments that may provide stronger evidence.

### *Symbolic imitation*

At the highest level of imitative behavior, what Mitchell (1987) refers to as fifth-level imitation, not only does the behavior of the observer not match that of the demonstrator, but the differences are explicit and they are produced for the purpose of drawing attention to certain characteristics of the model. Examples of such symbolic imitation can be found in the human use of parody and caricature. Such forms of imitation are mentioned primarily for completeness and to note the degree of subtlety that can be involved in imitation.

### *Cultural variation*

One more factor that has implications for imitation is cultural variation or tradition (Huffman 1996). When one sees a particular pattern of behavior in one community of humans but not in others, it is generally attributed to culture. When similar variance occurs in chimpanzees and one cannot attribute that variance to environmental peculiarities (e.g., the presence of a particular predator), one can also consider it cultural in nature. Presumably, if many members of a community have acquired a particular behavior that is rarely seen in other communities, the within-community spread of the behavior can be attributed to social learning (Whiten and Ham 1992), and when this pattern of tradition occurs often in different communities it is easy to draw an analogy to human social groups (Whiten et al. 1999).

As these behaviors are transmitted from one member of the community to others under natural conditions it is likely that a combination of individual learning and social learning (including imitation) is involved. But the contribution of

this line of research is not in isolating the mechanisms responsible for the spread of a novel behavior, but in drawing parallels between nonhuman primate and human communities (Tomasello 1996).

#### Converging evidence for a cognitive component in opaque imitation

The demonstration of opaque imitation in birds provides evidence that the phenomenon does not occur only in higher primates (great apes) and is more general than has been thought. However, if imitation involves cognitive processes suggesting that the observer “understands” the events that it is observing (Piaget 1962), it may be instructive to examine the effect on behavioral matching by animals of the manipulation of variables that might be expected to have an effect on the probability of finding imitation.

#### *Reinforcement of the demonstrated response*

If an observer sees a demonstrator make a response, does observing the demonstrator being rewarded for making the response affect the likelihood that the observer will imitate the response? On the one hand, the tendency to imitate may be genetically predisposed and imitation may not depend on the observed consequences of the demonstrator’s behavior. Of course, to say that the tendency to imitate may be predisposed does not explain how the observer understands what to do, so some form of cognition is still likely to be involved. On the other hand, if imitation is as cognitive a process as it is sometimes hypothesized to be (Piaget 1962) the likelihood of response matching may depend on the expected outcome for the observer. A human observer might reason, “If I would perform that response, I might expect to receive a similar reward.”

Akins and Zentall (1998) tested this hypothesis by exposing quail to either a treadle-pecking or treadle-stepping demonstrator. For half of the quail in each group, responses by the demonstrator were reinforced. For the remaining quail, responses by the demonstrator were not reinforced. Akins and Zentall found that only observers that had seen their demonstrator rewarded for responding showed significant evidence of imitation.

A cognitive interpretation of this finding assumes that the lack of correspondence between the observer and the demonstrator response topography for observers that do not observe the demonstrator being rewarded for responding results from a performance decrement rather than from a learning decrement (i.e., a lack of motivation). A simpler account of this finding suggests that with this procedure, an association between the demonstrator’s behavior and reinforcement (observational conditioning) is necessary for imitation to occur. Thus, a cognitive understanding of the relation between the

treadle response and reward may not be required to account for these results. However, the observational conditioning account does not provide an alternative to imitative learning because it cannot explain the correspondence between the observer’s and demonstrator’s response topographies. Instead, it may be that reinforcement acts as an incentive or catalyst to bring out imitative learning.

#### *Observer motivation*

Observers appear to require an incentive to imitate. Is it also important for them to be motivated to observe? To answer this question, we allowed prefed (sated) Japanese quail to observe demonstrators either stepping on a treadle or pecking at the treadle for food. When later tested under moderate levels of food deprivation, these quail showed no evidence of imitative learning. However, quail that observed while deprived of food and were later tested under moderate levels of food deprivation (similar to that of the quail that observed while sated) showed excellent imitative learning (Dorrance and Zentall 2001). It thus appears that the relevance of the outcome of the observed behavior to the observer’s motivation also plays a role in imitative learning.

#### Possible mechanisms involved in imitation

Piaget (1962) suggested that opaque imitation requires that the observer be able to take the perspective of the demonstrator. Although perspective taking may be within the capacity of animals as genetically close to humans as the great apes (see, e.g., Hare et al. 2000), it seems unlikely that pigeons and Japanese quail are capable of such a level of cognitive inference. Several alternative mechanisms have been proposed that vary in the level of analysis from neural to cognitive, and although each may play some role for animals, none appears to capture the important aspects of the results of the experiments reported here.

#### *Mirror neurons*

Recently, it has been found that there are neurons in the ventral premotor area of the frontal lobes of rhesus macaque monkeys that are active when the monkeys perform certain responses (e.g., picking up a grape), and those neurons also fire when the monkeys watch someone else (a human) perform the same response (Gallese et al. 1996). This finding has been heralded as the mechanism responsible for imitation. As exciting as this finding is, it fails to provide an adequate account of imitation.

First, virtually all behavior involves neural activity in the brain. Locating representative neurons does not tell us how they came to be mirror neurons. It is possible, for example, that they are the end product of a complex cognitive

process. On the other hand, they may also represent genetically predisposed hard wiring of the nervous system.

Second, the kind of imitation represented by mirror neurons has not yet been shown for an instance of opaque response correspondence that is the focus of psychological interest. Mirror neurons are active whenever there is a visual match between the demonstrator's performance and the monkey's own performance, and as noted earlier, such response matching potentially can be explained as a special case of generalized, stimulus identity learning (Zentall et al. 1983).

#### *Genetically predisposed matching behavior*

Alternatively, it is possible that evolution has provided animals with a natural tendency to match the behavior of conspecifics. If viewed as an example of species-typical behavior, such a mechanism would fall into the category of contagious behavior or what Byrne refers to as response enhancement. As noted earlier, a sated chicken will begin eating again if placed in the company of another chicken that is eating. But such a mechanism requires that there be a number of very specific, well-defined behaviors for each imitated behavior that is found, and that each of these contagious behaviors should have evolved independently. Also, contagious behavior generally occurs in unison, whereas in most of the examples of imitation described in this review, the period of observation is separate from the period of observer performance—sometimes by as much as 30 min (Dorrance and Zentall 2001). Such a latency is far longer than any known reflexive response. Finally, the relatively arbitrary nature of the demonstrated behavior (pecking or stepping on a treadle, and pushing a screen in one direction or the other) would seem unlikely to have evolved in a natural environment.

#### *Inference based on transparent similarity*

Mitchell (2002) has proposed that animals may infer examples of opaque imitation from the physical similarity between demonstrator behavior and observer performance available under conditions of transparent imitation. For example, for humans, one can see the similarity between one's arm and the arm of another, and one can learn how the sight of one's arm corresponds to the feel of one's arm. Similarly, one can see the similarity between one's shoulder and the shoulder of another, and one can learn how the sight of one's shoulder corresponds to the feel of one's shoulder. Now, although one can see the head of another, one cannot see one's own head but one can feel one's own head and from that one can infer though a process of generalization that one has a head. Thus, if one wants to imitate someone who scratches his head, one should be able to infer the presence of one's own head and make the appropriate response.

This hypothesis is a very clever alternative to Piaget's perspective-taking hypothesis, but it is not clear that it is any less cognitive, nor is there any evidence that animals such as pigeons or quail are capable of making such inferences.

#### Directions for future research

##### *Generality of imitation*

Birds appear to be particularly predisposed to imitate others and that predisposition may be especially prevalent in social, precocious birds such as fowl (e.g., Japanese quail). On the other hand, aside from rats that are not known to be a particularly visual species, there has not been much published research with mammalian species other than primates, and that research suggests that among primates only the great apes show a predisposition to imitate comparable to that of birds. If this generalization is accurate, it has important implications for the study of comparative cognitive abilities. Specifically, imitative learning may not have the same adaptive value for most mammals that it has for birds. Alternatively, investigators may not have found the appropriate tasks and contexts required to demonstrate imitative learning by other mammals.

##### *Nature of the response*

As already noted, with the exception of the great apes, the best evidence for imitative learning has been found in birds. Yet, because birds use their "arms" to fly, the response repertoire of birds is much more limited than that of many mammalian species such as monkeys or even rats. The elegance of the two-action procedure depends on being able to study two responses (such as pecking at and stepping on a treadle) that can be clearly differentiated by their topography yet produce essentially the same effect on the environment. Furthermore, these responses have a very low probability of occurrence in the absence of observation (Kaiser et al. 1997). However, the generality of the imitation effect would be greatly enhanced if there were a larger repertoire of responses for which imitation could be found. This might be a fruitful direction for future research.

##### *Specificity of observer motivation*

Dorrance and Zentall (2001) found that if the observers were not hungry at the time they observed the demonstrator responding for food, they were not likely to perform the observed behavior later when hungry. In this case, the observers were presumed to be in an unmotivated state. Would the same results obtain, however, if the observers were motivated but the motivation of the observers was different from that of the demonstrators? For example, would imitation be found if the

observers were water-deprived and the demonstrators were working for food?

#### *Deferred imitation*

The separation of the period of observation from the period of performance, as is the case with the two-action procedure, should distinguish between a reflexive response such as Byrne's (2002) notion of response enhancement and deferred imitation. For those who feel that such brief separation (approximately 60 s) is not sufficient to rule out response enhancement (Akins and Zentall 1996), our demonstration that two-action imitation can be found in Japanese quail when 30 min has elapsed between observation and performance should be more convincing (Dorrance and Zentall 2001). The extent to which birds can bridge still longer intervals between observation and performance is not known and is worthy of further investigation.

#### *Sequence imitation*

Together with the evidence for deferred imitation reported by Dorrance and Zentall (2001), evidence for sequence imitation by pigeons (Nguyen et al. 2005) strengthens the argument that this kind of response matching is not just some form of response enhancement or reflexive responding. Further results showing that sequences of responses can be imitated would suggest that this is a more general finding. It would be useful to know not only if other response sequences could be acquired in this way but also if imitation could be extended to sequences of three or even four responses.

#### *Learned affordances or object movement reenactment*

As mentioned earlier, Akins et al. (2002) and Klein and Zentall (2003) found that observers that watched the screen move either to the left or the right (unobtrusively by the experimenter) in the presence of a nonperforming demonstrator did not imitate. However, interestingly, observers that watched the screen move in the absence of another bird did show a significant tendency to match the movement of the screen. Although this would be considered affordance learning or object movement reenactment rather than imitation, it should be of interest in its own right. To what extent can animals acquire a response to a stimulus by merely observing the pairing of the stimulus with a consequence? Certainly, there is evidence that responding will often occur to a stimulus when it is merely paired with food (autoshaping, Brown and Jenkins 1968) but when that response is more than a simple peck to the conditioned stimulus, as in the push of a screen in a specific direction, it is likely that a more sophisticated explanatory mechanism is needed.

## Conclusions

Procedures have been developed that are capable of separating opaque imitation from other forms of social influences and social learning. Results with several species indicate that opaque imitation can be found reliably under a number of conditions, and the pattern of variables that appear to influence opaque imitation are consistent with similar findings with humans. Thus, there is convergent evidence for imitation in animals. Such results should not be surprising because social learning, by imitation and otherwise, provides clear benefits to many organisms over genetically based behavior and individual learning. However, the mechanism by which animals are able to match their behavior to that of a demonstrator, when the observer cannot see both, is not easily accounted for and remains somewhat of a mystery.

**Acknowledgement** Preparation of the manuscript was facilitated by Grant MH 63726 from the National Institute of Mental Health.

## References

- Akins CK, Klein ED, Zentall TR (2002) Imitative learning in Japanese quail (*Coturnix japonica*) using the bidirectional control procedure. *Anim Learn Behav* 30:275–281
- Akins CK, Zentall TR (1996) Imitative learning in male Japanese quail (*Coturnix japonica*) using the two-action method. *J Comp Psychol* 110:316–320
- Akins CK, Zentall TR (1998) Imitation in Japanese quail: The role of reinforcement of the demonstrator's response. *Psychon Bull Rev* 5:694–697
- Armstrong EA (1951) The nature and function of animal mimesis. *Bull Anim Behav* 9:46–49
- Ball J (1938) A case of apparent imitation in a monkey. *J Genet Psychol* 52:439–442
- Bandura A (1969) Social learning theory of identificatory processes. In: Goslin DA (ed) *Handbook of socialization theory and research*. Rand-McNally, Chicago, pp 213–262
- Baptista LF, Petrinovich L (1984) Social interaction, sensitive phases, and the song template hypothesis in the white-crowned sparrow. *Anim Behav* 32:172–181
- Bayroff AG, Lard KE (1944) Experimental social behavior of animals. III. Imitational learning of white rats. *J Comp Physiol Psychol* 37:165–171
- Bjorklund DF, Bering JM (2003) A note on the development of deferred imitation in enculturated juvenile chimpanzees (*Pan troglodytes*). *Develop Rev* 23:389–412
- Boyd R, Richerson PJ (1988) An evolutionary model of social learning: The effect of spatial and temporal variation. In: Zentall TR, Galef BG Jr (eds) *Social learning: Psychological and biological perspectives*. Erlbaum, Hillsdale, NJ, pp 29–48
- Breuggeman JA (1973) Parental care in a group of free-ranging rhesus monkeys. *Folia Primatol* 20:178–210
- Brown PL, Jenkins HM (1968) Auto-shaping the pigeon's key peck. *J Exp Anal Behav* 11:1–8
- Bunch GB, Zentall TR (1980) Imitation of a passive avoidance response in the rat. *Bull Psychon Soc* 15:73–75
- Byrne RW (1994) The evolution of intelligence. In: Slater PJB, Halliday TR (eds) *Behavior and evolution*. Cambridge University Press, Cambridge, UK, pp 223–265



- Byrne RW (2002) Imitation of novel complex actions: What does the evidence from animals mean? *Adv Stud Behav* 31:77–105
- Byrne RW (2005) Social cognition: Imitation, imitation, imitation. *Curr Biol* 15:498–500
- Caldwell CA, Whiten A (2002) Evolutionary perspectives on imitation: Is a comparative psychology of social learning possible? *Anim Cogn* 5:193–208
- Call J (2001) Body imitation in an enculturated orangutan (*Pongo pygmaeus*). *Cybernet Syst* 32:97–119
- Chesler P (1969) Maternal influence in learning by observation in kittens. *Science* 166:901–903
- Church RM (1957) Two procedures for the establishment of imitative behavior. *J Comp Physiol Psychol* 50:315–318
- Corson JA (1967) Observational learning of a lever pressing response. *Psychon Sci* 7:197–198
- Custance DM, Bard KA (1994) The comparative and developmental study of self-recognition and imitation: The importance of social factors. In: Parker ST, Mitchell RW, Boccia ML (eds) *Self-awareness in humans and animals: Developmental perspective*. Cambridge University Press, Cambridge, UK, pp 207–226
- Custance DM, Whiten A, Bard KA (1995) Can young chimpanzees imitate arbitrary actions? Hayes and Hayes revisited. *Behaviour* 132:839–858
- Custance DM, Whiten A, Fredman T (1999) Social learning of artificial fruit capuchin monkeys (*Cebus apella*). *J Comp Psychol* 113:13–23
- Davitz JR, Mason DJ (1955) Socially facilitated reduction of a fear response in rats. *J Comp Physiol Psychol* 48:149–151
- Dawson BV, Foss BM (1965) Observational learning in budgerigars. *Anim Behav* 13:470–474
- Del Russo JE (1971) Observational learning in hooded rats. *Psychon Sci* 24:37–45
- Del Russo JE (1975) Observational learning of discriminative avoidance in hooded rats. *Anim Learn Behav* 3:76–80
- Denny MR, Clos CF, Bell RC (1988) Learning in the rat of a choice response by observation of S-S contingencies. In: Zentall TR, Galef BG Jr (eds) *Social learning: Psychological and biological perspectives*. Erlbaum, Hillsdale, NJ, pp 207–223
- Dorrance BR, Zentall TR (2001) Imitative learning in Japanese quail depends on the motivational state of the observer at the time of observation. *J Comp Psychol* 115:62–67
- Dugatkin LA (1992) Sexual selection and imitation: Females copy the mate choice of others. *Am Nat* 139:1384–1389
- Dugatkin LA (1996) Copying and mate choice. In: Heyes CM, Galef BG (eds) *Social learning in animals: The roots of culture*. Academic, San Diego, CA, pp 85–105
- Dugatkin LA, Godin JGJ (1992) Reversal of female mate choice by copying. *Proc R Soc Lond B* 249:179–184
- Edwards CA, Hogan DE, Zentall TR (1980) Imitation of an appetitive discriminatory task by pigeons. *Bird Behav* 2:87–91
- Fiorito G, Scotto P (1992) Observational learning in *Octopus vulgaris*. *Science* 256:545–546
- Fisher J, Hinde RA (1949) Further observations on the opening of milk bottles by birds. *Br Birds* 42:347–357
- Galef BG Jr (1988a) Communication of information concerning distant diets in a social, central-place foraging species: *Rattus norvegicus*. In: Zentall TR, Galef BG Jr (eds) *Social learning: Psychological and biological perspectives*. Erlbaum, Hillsdale, NJ, pp 119–139
- Galef BG Jr (1988b) Imitation in animals: History, definition, and interpretation of data from the psychological laboratory. In: Zentall TR, Galef BG Jr (eds) *Social learning: Psychological and biological perspectives*. Erlbaum, Hillsdale, NJ, pp 3–28
- Galef BG Jr (1996) Social enhancement of food preferences in Norway rats: A brief review. In: Heyes CM, Galef BG (eds) *Social learning in animals: The roots of culture*. Academic, San Diego, CA, pp 49–64
- Galef BG Jr, Durlach PJ (1993) Absence of blocking, overshadowing and latent inhibition in social enhancement of food preferences. *Anim Learn Behav* 21:214–220
- Galef BG Jr, Manzig LA, Field RM (1986) Imitation learning in budgerigars: Dawson and Foss (1965) revisited. *Behav Processes* 13:191–202
- Gallese V, Fadiga L, Fogassi L, Rizzolatti G (1996) Action recognition in the premotor cortex. *Brain* 119:593–609
- Gallup GG Jr (1970) Chimpanzees: Self recognition. *Science* 167:86–87
- Garcia J, Koelling RA (1966) Relation of cue to consequence in avoidance learning. *Psychon Sci* 4:123–124
- Gardner EL, Engel DR (1971) Imitational and social facilitatory aspects of observational learning in the laboratory rat. *Psychon Sci* 25:5–6
- Gergely G, Bekkering H, Király I (2002) Rational imitation in preverbal infants. *Nature* 415:755
- Gleissner B, Meltzoff AN, Bekkering H (2000) Children's coding of human action: Cognitive factors influencing imitation in 3-year-olds. *Dev Sci* 3:405–414
- Gibson J (1979) *The ecological approach to visual perception*. Houghton Mifflin, Boston
- Groesbeck RW, Duerfeldt PH (1971) Some relevant variables in observational learning of the rat. *Psychon Sci* 22:41–43
- Hare B, Call J, Agnetta B, Tomasello M (2000) Chimpanzees know what conspecifics do and do not see. *Anim Behav* 59:771–785
- Hare B, Tomasello M (2005) Response: The emotional reactivity hypothesis and cognitive evolution. *Trends Cogn Sci* 9:464–465
- Haruki Y, Tsuzuki T (1967) Learning of imitation and learning through imitation in the white rat. *Annu Anim Psychol* 17:57–63
- Hayes KJ, Hayes C (1952) Imitation in a home-reared chimpanzee. *J Comp Physiol Psychol* 45:450–459
- Henning JM, Zentall TR (1981) Imitation, social facilitation, and the effects of ACTH 4–10 on rats' barpress behavior. *Am J Psychol* 94:125–134
- Herbert MJ, Harsh CM (1944) Observational learning by cats. *J Comp Psychol* 37:81–95
- Hess EH (1973) *Imprinting*. Van Nostrand/Reinhold, New York
- Heyes CM (1994) Reflections on self-recognition in primates. *Anim Behav* 47:909–919
- Heyes CM, Dawson GR (1990) A demonstration of observational learning in rats using a bidirectional control. *Q J Exp Psychol B* 42:59–71
- Heyes CM, Jaldow E, Dawson GR (1994) Imitation in rats: Conditions of occurrence in a bidirectional control procedure. *Learn Motiv* 25:276–287
- Heyes CM, Ray ED (2000) What is the significance of imitation in animals. *Adv Stud Behav* 29:215–245
- Hinde RA (ed) (1969) *Bird vocalizations*. Cambridge University Press, Cambridge, UK
- Hogan DE (1988) Learned imitation by pigeons. In: Zentall TR, Galef BG Jr (eds) *Social learning: Psychological and biological perspectives*. Erlbaum, Hillsdale, NJ, pp 225–238
- Hoogland JL, Sherman PW (1976) Advantages and disadvantages of bank swallow (*Riparia riparia*) coloniality. *Ecol Monogr* 46:33–58
- Huffman MA (1996) The study of nonhuman primate culture in Japan. In: Heyes CM, Galef BG (eds) *Social learning in animals: The roots of culture*. Academic, San Diego, CA, pp 267–289
- Jacoby KE, Dawson ME (1969) Observation and shaping learning: A comparison using Long-Evans rats. *Psychon Sci* 16:257–258
- John ER, Chesler P, Bartlett F, Victor I (1968) Observational learning in cats. *Science* 159:1489–1491
- Kaiser DH, Zentall TR, Galef BG Jr (1997) Can imitation in pigeons be explained by local enhancement together with trial-and-error learning? *Psychol Sci* 8:459–465

- Klein ED, Zentall TR (2003) Imitation and affordance learning by pigeons (*Columba livia*). *J Comp Psychol* 117:414–419
- Kohn B (1976) Observation and discrimination learning in the rat: Effects of stimulus substitution. *Learn Motiv* 7:303–312
- Kohn B, Dennis M (1972) Observation and discrimination learning in the rat: Specific and nonspecific effects. *J Comp Physiol Psychol* 78:292–296
- Kovach JK, Hess EH (1963) Imprinting: Effects of painful stimulation upon the following response. *J Comp Physiol Psychol* 56:461–464
- Lefebvre L, Palameta B (1988) Mechanisms, ecology, and population diffusion of socially learned food-finding behavior in feral pigeons. In: Zentall TR, Galef BG Jr (eds) *Social learning: Psychological and biological perspectives*. Erlbaum, Hillsdale, NJ, pp 141–164
- Levine JM, Zentall TR (1974) Effect of conspecific's presence on deprived rats performance: Social facilitation vs distraction/imitation. *Anim Learn Behav* 2:119–122
- Lore R, Blanc A, Suedfeld P (1971) Empathic learning of a passive avoidance response in domesticated *Rattus norvegicus*. *Anim Behav* 19:112–114
- Lorenz K (1935) Der Kumpan in der Umwelt des Vogels: der Artgenosse als auslösendes Moment sozialer Verhaltensweisen. *J Fur Ornithol* 83:137–213, 289–413
- Marler P (1970) A comparative approach to vocal learning: Song development in white-crowned sparrows. *J Comp Physiol Psychol* 71:1–25
- Meltzoff AN (1988) The human infant as *homo imitans*. In: Zentall TR, Galef BG Jr (eds) *Social learning: Psychological and biological perspectives*. Erlbaum, Hillsdale, NJ, pp 319–341
- Miles HL, Mitchell RW, Harper SE (1996) Simon says: The development of imitation in an enculturated orangutan. In: Russon AE, Bard KE, Parker ST (eds) *Reaching into thought: The minds of the great apes*. Cambridge University Press, Cambridge, UK, pp 278–299
- Minaka S, Cook M (1988) Social learning and the acquisition of snake fear in monkeys. In: Zentall TR, Galef BG Jr (eds) *Social learning: Psychological and biological perspectives*. Erlbaum, Hillsdale, NJ, pp 51–75
- Mitchell CJ, Heyes CM, Dawson GR (1999) Limitations of a bidirectional control procedure for the investigation of imitation in rats: Odour cues on the manipulandum. *Q J Exp Psychol* 52:193–202
- Mitchell RW (1987) A comparative-developmental approach to understanding imitation. In: Bateson PPG, Klopfer PH (eds) *Perspectives in ethology*, vol 7. Plenum, New York, pp 183–215
- Mitchell RW (2002) Imitation as a perceptual process. In: Nehaniv CL, Dautenhahn K (eds) *Imitation in animals and artifacts*. MIT, Cambridge, MA, pp 441–469
- Moore BR (1992) Avian movement imitation and a new form of mimicry: Tracing the evolution of a complex form of learning. *Behaviour* 122:231–263
- Morrison BJ, Hill WF (1967) Socially facilitated reduction of the fear response in rats raised in groups or in isolation. *J Comp Physiol Psychol* 63:71–76
- Nguyen NH, Klein ED, Zentall TR (2005) Imitation of two-action sequences by pigeons. *Psychon Bull Rev* 12:514–518
- Nottebohm F (1970) Ontogeny of bird song. *Science* 167:950–956
- Oldfield-Box H (1970) Comments on two preliminary studies of “observation” learning in the rat. *J Genet Psychol* 116:45–51
- Palameta B, Lefebvre L (1985) The social transmission of a food-finding technique in pigeons: What is learned? *Anim Behav* 33:892–896
- Pepperberg IM (1986) Acquisition of anomalous communicatory systems: Implications for studies on interspecies communication. In: Schusterman R, Thomas J, Wood F (eds) *Dolphin behavior and cognition: Comparative and ethological aspects*. Erlbaum, Hillsdale, NJ, pp 289–302
- Pepperberg IM (1988) The importance of social interaction and observation in the acquisition of communicative competence: Possible parallels between avian and human learning. In: Zentall TR, Galef BG Jr (eds) *Social learning: Psychological and biological perspectives*. Erlbaum, Hillsdale, NJ, pp 279–299
- Pepperberg IM (1990) Referential mapping. *Appl Psycholinguist* 11:23–44
- Piaget J (1962) *Play, dreams, and imitation in childhood*. Horton, New York
- Roberts D (1941) Imitation and suggestion in animals. *Bull Anim Behav* 1:11–19
- Russon AE, Galdikas BMF (1993) Imitation in ex-captive orangutans (*Pongo pygmaeus*). *J Comp Psychol* 107:147–161
- Sanavio E, Savardi U (1980) Observational learning of a discriminative shuttlebox avoidance by rats. *Psychol Rep* 44:1151–1154
- Sordahl TA (1981) Slight of wing. *Nat Hist* 90:42–49
- Spence KW (1937) The differential response in animals to stimuli varying within a single dimension. *Psychol Rev* 44:430–444
- Stimbert VE (1970) A comparison of learning based on social and nonsocial discriminative stimuli. *Psychon Sci* 20:185–186
- Strupp BJ, Levitsky DA (1984) Social transmission of food preferences in adult hooded rats (*Rattus norvegicus*). *J Comp Psychol* 98:257–266
- Tanner J, Byrne RW (1999) Imitation in a captive lowland gorilla: A spontaneous experiment. University of St. Andrews, Fife, Scotland, unpublished manuscript
- Thorpe WH (1961) *Bird song: The biology of vocal communication and expression in birds*. Harvard University Press, Cambridge, MA
- Thorpe WH (1963) *Learning and instinct in animals*, 2nd edn. Harvard University Press, Cambridge, MA
- Thorpe WH (1967) Vocal imitation and antiphonal song and its implications. In: Snow DW (ed) *Proceedings of the XVI International Ornithological Congress*. Blackwell, Oxford, UK, pp 245–263
- Tinbergen N (1960) *The herring gull's world*. Doubleday, Garden City, New York
- Todt D (1975) Social learning of vocal patterns and modes of their applications in Grey parrots. *Zeitschrift für Tierpsychologie* 39:178–188
- Tolman CW (1964) Social facilitation of feeding behaviour in the domestic chick. *Anim Behav* 12:245–251
- Tomasello M (1996) Do apes ape? In: Heyes CM, Galef BG (eds) *Social learning in animals: The roots of culture*. Academic, San Diego, CA, pp 319–346
- Tomasello M, Kruger AC, Ratner HH (1993) Cultural learning. *Behav Brain Sci* 16:495–552
- Turner GJR (1984) Mimicry: The palatability spectrum and its consequences. In: Vane-Wright RI, Ackery PR (eds) *The biology of butterflies*. Academic, New York, pp 141–161
- Vanayan M, Robertson H, Biederman GB (1985) Observational learning in pigeons: The effects of model proficiency on observer performance. *J Gen Psychol* 112:349–357
- Voelkl B, Huber L (2000) True imitation in marmosets. *Anim Behav* 60:195–202
- Warden CJ, Jackson TA (1935) Imitative behavior in the rhesus monkey. *J Genet Psychol* 46:103–125
- Watanabe S, Huber L (2006) Animal logics: Decisions in the absence of human language. *Anim Cogn* DOI 10.1007/s10071-006-0043-6
- Weigle PD, Hanson EV (1980) Observation learning and the feeding behavior of the red squirrel (*Tamiasciurus hudsonicus*): The ontogeny of optimization. *Ecology* 61:213–218
- Whiten A (1998a) Evolutionary and developmental origins of the mindreading system. In: Langer J, Killen M (eds) *Piaget, evolution, and development*. Erlbaum, Hillsdale, NJ, pp 73–99
- Whiten A (1998b) Imitation of the sequential structure of actions by chimpanzees (*Pan troglodytes*). *J Comp Psychol* 112:270–281

- Whiten A, Custance DM, Gomez J-C, Teixidor P, Bard KA (1996) Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). *J Comp Psychol* 110:3–14
- Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, Boesch C (1999) Cultures in chimpanzees. *Nature* 399:682–685
- Whiten A, Ham R (1992) On the nature and evolution of imitation in the animal kingdom: Reappraisal of a century of research. In: Slater PJB, Rosenblatt JS, Beer C, Milinski M (eds) *Advances in the study of behavior*, vol 21. Academic, New York, pp 239–283
- Whiten A, Horner V, Marshall-Pescini S (2004) Selective imitation in child and chimpanzee: A window on the construal of others' actions. In: Hurley S, Chater N (eds) *Perspectives on imitation: From mirror neurons to memes: vol 1. Mechanisms of imitation and imitation in animals*. MIT, Cambridge, MA, pp 263–283
- Will B, Pallaud B, Soczka M, Manikowski S (1974) Imitation of lever pressing “strategies” during the operant conditioning of albino rats. *Anim Behav* 22:664–671
- Zajonc RB (1965) Social facilitation. *Science* 149:269–274
- Zentall TR, Edwards CA, Hogan DE (1983) Pigeons' use of identity. In: Commons ML, Herrnstein RJ, Wagner A (eds) *The quantitative analyses of behavior: Discrimination processes*, vol 4. Ballinger, Cambridge, MA, pp 273–293
- Zentall TR, Hogan DE (1975) Key pecking in pigeons produced by pairing key light with inaccessible grain. *J Exp Anal Behav* 23:199–206
- Zentall TR, Hogan DE (1976) Imitation and social facilitation in the pigeon. *Anim Learn Behav* 4:427–430
- Zentall TR, Levine JM (1972) Observational learning and social facilitation in the rat. *Science* 178:1220–1221
- Zentall TR, Sutton J, Sherburne LM (1996) True imitative learning in pigeons. *Psychol Sci* 7:343–346