Dolphin Imitation: Who, What, When, and Why?

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Abstract

The imitative ability of nonhuman animals has intrigued a number of scholars and, in doing so, has generated a considerable amount of controversy. Although it is clear that many species can learn via observational learning, there is a lack of consensus concerning both what sorts of things can be learned by watching others and what types of observational learning should count as imitation. These disputes have led to disagreements about the extent to which various nonhuman species engage in imitation, based in large part on different definitions of imitation. An animal's imitative success also depends on the context. For example, dolphins can be taught to imitate on demand, and studies using such elicited imitation tasks have yielded mixed results. Dolphins can imitate behaviors produced by other dolphins and other animals (including humans) and are capable of deferred imitation. When dolphins are asked to imitate, it seems easier for them to reproduce familiar behaviors than novel ones. Adult dolphins appear to be more successful than juveniles at imitating on demand; however, young dolphins appear more likely than adults to spontaneously imitate behaviors. Young dolphins frequently spontaneously imitate the play behaviors of their peers, and sometimes acquire novel play behaviors in the process. Following Kuczaj et al. (2005), we suggest that the distinction between elicited and spontaneous imitation is important, and that understanding both types of imitation is essential. In addition to learning more about the factors that are influential when animals imitate, it is also imperative to understand the types of models and behaviors that are most likely to be imitated, the types of animals that are most likely to imitate others, and ontogenetic changes that occur in imitation.

Key Words: imitation, observational learning, context, bottlenose dolphin, *Tursiops truncatus*, mental representation, mimicry

Introduction

Early theorists tended to believe that imitation in nonhumans reflected relatively primitive mental abilities, but nonetheless recognized the significance of imitation in the ontogeny of an individual's behavioral repertoire (Wallace, 1870; Darwin, 1871; Romanes, 1883; Baldwin, 1895; Thorndike, 1898; Morgan, 1900; Washburn, 1936). Most believed that the role of imitation in ontogeny was to facilitate an individual's acquisition of behaviors already in the group's repertoire rather than the creation of new behaviors. In this sense, imitation was thought to facilitate group conformity and group traditions (the transmission of known behaviors among individuals) more than individual innovation.

Imitation, Behavioral Traditions, and Innovation

The human capacity for imitation is well-known (Piaget, 1962; Bandura, 1997; Meltzoff & Prinz, 2002), and the capacity for imitation has been argued to be one of the hallmarks of human cognition and culture (Meltzoff & Gopnik, 1993; Tomasello, 1999). Imitation clearly facilitates the transmission of known behaviors from one individual to another (and so from one generation to the next), and may also be involved in the discovery and incorporation of innovative behaviors into a group's behavioral repertoire (see Galef, 2003; Kuczaj et al., in press). If imitation plays some role in the acquisition of novel behaviors, then imitation may facilitate behavioral flexibility—the ability of members of a group to adapt to changing circumstances.

The capacity for flexibility is another of the hallmarks of humans, and it is reflected in our behavior, thought, and communication systems. The capacity for flexibility has resulted in many diverse human cultures, for flexibility makes change possible (and inevitable). The human capacity for flexibility emerges relatively early in ontogeny (Piaget, 1952; Gopnik et al., 1999), but the factors that influenced its phylogeny are a bit murky. Reynolds (1976) proposed that the evolution of the human capacity for flexibility rested on four phenomena: (1) increasing delays in maturation, (2) increasing interest in manipulating objects, (3) increasing significance of play for social development, and (4) increasing reliance on observational learning. Although we agree with Reynolds that each of these factors undoubtedly influenced the evolutionary path of our capacity for flexibility, observational learning is the focus of this paper.

Observational learning, behavioral flexibility, and culture are closely intertwined. Culture is acquired through various forms of social learning (Boyd & Richerson, 1996, 2000; Rendell & Whitehead, 2001), one of which is observational learning, which may help maintain behavioral traditions by facilitating the transmission of behaviors from one animal to another. Innovation is necessary to add new behaviors to a group's repertoire, however, and Poirier & Fitton (2001) noted that innovators, the agents of cultural change, have been relatively little studied. Morgan (1900) suggested that more "interesting" models would be imitated more than mundane models, and one might expect innovative behaviors to be more interesting than familiar ones. Consistent with this view, bottlenose dolphin calves are more likely than adults to produce innovative play behaviors. Dolphin calves are also most likely to imitate the novel play behaviors produced by their peers (Kuczaj et al., 2005, in press).

Types of Observational Learning

Observational learning and imitation are not synonyms. Tomasello (1999) described various ways, such as the following, in which observational learning could occur yet not involve imitation.

Exposure—Individuals learn about their environment by virtue of maintaining close physical proximity to individuals that have more experience. For example, a young dolphin might learn the location of an underwater mount teeming with fish simply by staying in close proximity to its mother.

Stimulus Enhancement—Individuals become interested in an object as the result of observing others interacting with the object (first described by Spence, 1937). Increased interest in an object may result in object manipulation, thereby facilitating the acquisition of new object-related behaviors via trial and error learning. For example, a young killer whale (*Orcinus orca*) might become intrigued about playing with a sea lion pup after watching other whales toss the pup about. Playing with the pup might then result in the killer whale's acquisition of foraging behaviors appropriate to such prey. In such a case, the killer whale did not learn to prey on sea lions by observing other whales do so. Instead, interest in the sea lion was piqued by observing other whales play with the pup, and the observing whale's subsequent interactions with the sea lion resulted in behaviors that might benefit its future foraging efforts.

Goal Emulation—Individuals are enticed by the end result of an observed behavior. Consequently, they attempt to achieve the same result but not necessarily with the same behaviors that the model used. For example, Haggerty (1909) devised a task in which a monkey had to climb up the side of a cage, stick its arm into a wooden chute, and pull a rope in the chute to release food. After watching a monkey go through this process on four separate occasions, another monkey was provided an opportunity to obtain the food. The monkey did not reproduce the behaviors it had observed, but instead, attempted to obtain the food in various other ways, finally succeeding via trial and error. More recently, Call et al. (2005) reported that chimpanzees (*Pan troglodytes*) were more likely to reproduce the outcomes of observed actions than the actual actions themselves, while human children (Homo sapiens) were more likely to produce the actions. Thus, there appear to be species differences in terms of what is learned from observing others.

Herman (2002) suggested that bottlenose dolphins (*Tursiops truncatus*) may sometimes focus on the functional aspect of a modeled behavior rather than the actual form of the behavior and thus produce goal-emulated behaviors rather than imitative ones. For example, a dolphin that watches a model place a ball in a basket might also place a ball in the basket when asked to mimic the behavior, but it may do so in a different way than the model. The extent to which dolphins engage in goal emulation rather than actual imitation is not clear, but we suspect that they are capable of various forms of observational learning, including imitation.

As the above examples illustrate, there are ways in which animals can learn via observation that do not involve the imitation of observed behaviors. Heyes (1993) distinguished imitation and non-imitative social learning in the following way: imitation occurs when animals learn about behavior from observing conspecifics, whereas non-imitative social learning occurs when animals learn about the environment from observing others. Both types of observational learning are important, but imitation has proven much more controversial.

What Should Count as Imitation?

The extent to which a model behavior must be preserved in a reproduction for the reproduction to count as imitation is a matter of some debate. Thorpe (1963) proposed stringent criteria for imitation, suggesting that imitation occurs only when the behavior is both exactly reproduced and novel. Whiten & Ham (1992) did not believe that imitation must involve an exact reproduction of the model and argued that imitation occurred when an animal has learned something about the form of an act from observing another perform the act. We concur with this view and believe that imitations rarely, if ever, perfectly replicate a model's behavior. Thus, requiring exact reproductions of model behaviors for imitation is far too exclusive.

The notion that imitated behaviors must be novel is also stringent, but it is a requirement that allows humans to more reliably conclude that imitative social learning has occurred (see also Zentall, 1996; Byrne & Russon, 1998). Of course, determining if a behavior that one witnessed an animal perform for the first time is actually novel is a daunting task unless one knows the animal's complete behavioral repertoire and history. For example, Kinnaman (1902) reported that one rhesus monkey (Macacus rhesus, previously known as Macaca mulatta) learned to pull a plug from a box with its teeth to obtain food only after watching another monkey succeed at this task. Although this is an example of observational learning, it is unclear if the behavior was truly novel or an application of a known behavior (pulling something out with one's teeth) to a novel context.

The lack of consensus concerning what types of observational learning should count as imitation led to disputes about the extent to which nonhuman species engage in imitation (e.g., Visalberghi & Fragaszy, 1990; Byrne & Russon, 1998; Kuczaj et al., 1998; Bard & Russell, 1999; Tomasello, 1999; Fritz & Kotrschal, 2002; Herman, 2002; Whiten, 2002; Kuczaj et al., 2005). These disputes are important because they rest on the belief that all imitation is not the same, a notion that is common throughout the history of the comparative study of imitation.

For example, Morgan (1900) distinguished instinctive imitation, intelligent imitation. intentional imitation, and reflective imitation. Instinctive imitation occurs when an animal produces a model behavior (e.g., a hen pecks at the ground), which signals another animal to reproduce the behavior (e.g., a chick pecks at the ground after observing its mother do so). Morgan believed that instinctive imitation results in young animals learning behavior already "familiar to its species" and so facilitates group conformity and group identity. Intelligent imitation occurs when an animal attempts to perfect behaviors first learned via instinctive imitation. For example, a dolphin calf that first mimics a whistle it has heard as the result of instinctive imitation perfects its

production of this whistle during intelligent imitation. Intentional imitation involves a decision to imitate, and so it is more purposeful than instinctive imitation. The environment is still of utmost importance, however, since intentional imitation depends on the observation of interesting events. For example, a dolphin calf that witnesses another dolphin playing with bubbles might then try to produce and bite bubbles, but only if the calf had found the modeled behavior to be interesting. Reflective imitation is also intentional, but it is guided more by the mental representation of the imitative behavior than by a recently observed modeled behavior. This is similar to Piaget's (1952) deferred imitation, and it involves the imitation of an absent model. For example, a child that watches another child throw a temper tantrum and the next day produces her first such tantrum represents Morgan's (1900) reflective imitation and Piaget's deferred imitation. Morgan believed that instinctive imitation is found in many animal species, intelligent imitation in fewer species, and that evidence for intentional and reflective imitation is non-existent outside of humans.

The distinction between different forms of imitation remains important in contemporary theorizing about imitation in animals and humans. For example, Kuczaj et al. (2005) focused on three types of imitation: (1) kinesthetic, (2) symbolic, and (3) mindful.

Kinesthetic imitation occurs when the imitator matches its bodily movements and postures to those of the model. This type of imitation may be automatic or intentional. Possible examples of automatic kinesthetic imitation include the imitation of adult facial behaviors by young infants (Meltzoff & Moore, 1977; Meltzoff & Prinz, 2002) and the synchronous behavior exhibited by many dolphin species (Connor et al., 2000; Bauer & Harley, 2001). Kinesthetic imitation also may be intentional as when a child crouches like a lion that it has seen at the zoo or a dolphin spontaneously turns in a circle after watching a human do so. This form of imitation is similar to Tomasello's (1999) mimicry and Morgan's (1900) instinctive imitation.

Gopnik (1993) suggested that kinesthetic imitation rests on a cross-modal representational system that encodes information about one's own behaviors in the same way that it encodes information about others' behaviors. Thus, the child that watches another stick its tongue out is thought to represent that event in the same manner that she would represent her own tongue protrusion. As a result, the system allows representations of others' behaviors and representations of one's own kinesthetic sensations to be mapped onto one another. Gopnik's notion of a cross-modal representational system fits well with the discovery of mirror neurons in rhesus monkeys (Rizzolatti et al., 1996). Rhesus monkeys have individual neurons that respond when an action is performed and when it is witnessed, and such neurons have been suggested to be the neurological basis of imitation.

It is not clear if humans possess individual neurons that react in the same way as macaque monkey mirror neurons, but we seem to have some sort of "mirror neural systems." These areas of the human brain react similarly whether performing or observing an action and increase in activity if an individual is observing a behavior that he or she intends to imitate (Grezes et al., 1999). These mirror neural systems have been suggested to play key roles in imitation, empathy, language acquisition, and creativity (Arbib, 2005; Iacoboni, 2005), and so they may be involved in forms of imitation outside of the kinesthetic realm as well as a host of other sophisticated cognitive skills.

Symbolic imitation occurs when the imitator must create a lasting representation that stands for the original event. For example, deferred imitation involves the reproduction of behavior that was observed in the past and for which no model is presently available, so it requires that the imitator have a mental representation of model behavior to produce an imitation (Piaget, 1952, 1962). Thus, a dolphin that watches another attempt to balance itself on the edge of a dock and sometime later attempts to balance itself on the edge of the dock is engaging in symbolic imitation. The mental representation of the original event stands for, or symbolizes, the original event. Symbolic imitation also occurs when the representation of the model behavior requires more than a simple "mirror image" of the original observed event such as when the observer must represent two different perspectives in order to reproduce the model's behavior (Whiten, 1996, 2002; Mitchell, 2002a, 2002b).

Mindful imitation requires that the imitator recognize and encode the model's intentions as well as the model's behaviors. Consequently, individuals reproduce the behavior of a model to achieve the same goal as the model. This has also been called true imitation (Tomasello et al., 1993; Tomasello, 1996). For example, a child that watches another child build a wall of pillows to hide behind engages in mindful imitation only if she reproduces the model's behavior and understands that the model's behavior was based on the intent to hide behind the pillows.

Why Study Dolphin Imitation?

Bottlenose dolphins sometimes spontaneously synchronize their behaviors, a capacity that may have provided an evolutionary foundation for the emergence of imitative abilities (Bauer & Harley, 2001). Support for the notion that synchrony involves imitation comes from a study of elicited synchronous behaviors reported in Herman (2002). Two bottlenose dolphins proved capable of performing both known and novel behaviors synchronously when asked to do so. Video analysis revealed that one dolphin typically led the other as they performed synchronous behaviors, suggesting that the trailing dolphin was imitating the behavior of the lead dolphin. These results, coupled with dolphins' sophisticated cognitive abilities (Herman, 1980; Schusterman et al., 1986; Marino, 2002; Kuczaj & Walker, 2006) and social nature (Shane et al., 1986; Pryor & Norris, 1998; Mann et al., 2000), make it likely that dolphins benefit from various forms of observational learning, including imitation.

Studies in which dolphins are asked to imitate behaviors they have seen a model perform have met with mixed results (Kuczaj et al., 2005). Dolphins can imitate each other's behavior on demand once they have been trained to do so, but they are more likely to succeed if the modeled behaviors are familiar (Xitco, 1988; Herman et al., 1989; Bauer & Johnson, 1994). Dolphins are also capable of imitating the behavior of humans when asked to do so (Harley et al., 1998), and sometimes they are able to imitate human behaviors that they have not seen humans produce before. For example, a dolphin that watched a human push a kickboard on the surface of the water with his head subsequently pushed the kickboard with its rostrum.

In an interesting twist on the elicited imitation method, Mercado et al. (1998) asked the bottlenose dolphins used in the Harley et al. (1998) study to imitate their own behavior. An example of self-imitation in the Mercado et al. (1998) study might begin with a dolphin being asked to touch a ball with its pectoral fin. After it had done so, the dolphin was then asked to "repeat" what it had just done. One dolphin proved quite capable of imitating her preceding behaviors, but the other dolphin fared much worse, demonstrating the range of individual differences that can occur when animals are asked to imitate.

Mercado et al. (1999) replicated the above selfimitation study, but with three objects in the tank rather than a single object (as had been the case in Mercado et al., 1998). Placing multiple objects in the tank required the dolphin to remember the object as well as the action. The dolphins were more likely to repeat an action correctly than to select the correct object. This suggests that dolphin representations of their own behaviors may be more action-based than object-based, and that actions may be more important than objects in the dolphin representations of their world (see Kuczaj & Walker, 2006, for further discussion of action-based and object-based representations in dolphins).

Of course, dolphins are not limited to reproducing behavior when humans ask. Dolphins spontaneously imitate their own behavior and that of others as a number of interesting anecdotes in the literature attest. For example, Taylor & Saayman (1973) reported the case of an Indian Ocean bottlenose dolphin calf (*Tursiops aduncus*) looking through an underwater window and watching a human smoking a cigarette. The calf swam away, nursed from its mother, returned to the window, and released the milk from its mouth in an apparent attempt to imitate the human's behavior.

Another case was equally impressive.

The dolphin, after repeatedly observing a diver removing algae growth from the glass underwater viewing port, was seen cleaning the window with a seagull feather while emitting sounds almost identical to that of the diver's air-demand valve and releasing a stream of bubbles from the blowhole in a manner similar to that of exhaust air escaping from the diving apparatus.... Subsequently (the dolphin) used food-fish, sea slugs, stones and paper to perform similar cleaning movements at the window. (Taylor & Saayman, 1973)

Bottlenose dolphin calves (*Tursiops truncatus*) often spontaneously imitate behaviors, including some they have never produced before (Kuczaj et al., 2005, in press). For example, one of the calves we observed was rolling his head at the surface of the water and creating waves, a behavior we had not witnessed before. While the calf was producing this behavior, another calf joined him and began to mimic the first calf's behavior. In some cases, imitation was deferred, with the imitations occurring some time after the model behavior had been observed (ranging from 15 min to 3 d). For example, a young calf watched its mother blow individual bubbles, after which the mother bit each of the bubbles. The calf had not produced this behavior before, but approximately 45 min after watching its mother do so, the calf blew some small bubbles and bit a few of them.

An interesting observation of calf imitation was provided by K. Sexton (pers. comm., 2005). He observed two bottlenose dolphins (that he believed to be *Tursiops gilli*) bow riding, one of which was a juvenile. The adult dolphin performed a barrel roll and then turned its head toward the juvenile. The adult repeated this behavior several times, after which the juvenile attempted a barrel roll, but lost its position on the pressure wave while doing so. The adult immediately left, but both animals returned within a few minutes. The adult then performed two barrel rolls, looking toward the juvenile after each roll was completed. The juvenile again attempted a roll, and once again fell off the wave. The adult followed, and both animals quickly returned to the wave. The adult produced one roll following their return, after which the juvenile attempted a roll, once again losing its position in the wave. The adult did not follow the juvenile this time, and the juvenile soon returned. At this point, the juvenile completed a roll and managed to stay on the wave, after which it looked toward the adult. It then produced several successive rolls in a row.

The Significance of Context

Some animals other than humans spontaneously imitate actions produced by others and may learn novel behaviors in this manner. When asked to imitate, animals appear more likely to succeed when the modeled behavior is familiar, however. The difference between spontaneous imitations and those produced in response to a request reflects the different demands inherent in the two situations (Kuczaj et al., 2005). Some beings, particularly young children and animals, are more likely to imitate a novel behavior if they spontaneously elect to do so rather than if being asked to do so. This disparity may reflect the fragility of young children's and animals' representational abilities and/or differing motivations to imitate different models.

The nature of the model is significant for humans, dolphins, monkeys, and apes (Galef, 1992; Mitchell, 1994; Russon & Galdikas, 1995; Bandura, 1997; Kuczaj et al., 2005, in press). For example, Werner & Kaplan (1963) reported that human infants mimic the movements of people before they imitate the movements of inanimate objects (such as the swaying motion of a clock pendulum). This developmental pattern suggests that infants are more intrigued by the actions of other humans than those of objects. Not all behavior is equally likely to be imitated, however. For example, social interaction increases the likelihood of imitation for both humans and nonhuman primates (Killen & Uzgiris, 1981; Meltzoff, 1996; Bard & Russell, 1999).

Human models are more likely to be imitated if they are perceived to be competent or possess high status (Bandura, 1986). Imitation also increases prosocial behavior among adult humans (van Baaren et al., 2004). Specifically, adults who are imitated tend to be more helpful and generous. This increase in prosocial behaviors extends beyond the imitator to others in general. If one of the functions of imitation is to increase positive social behaviors, a bias to imitate those one knows may have evolved to enhance existing social bonds. For example, orangutans (*Pongo pygmaeus*) are more likely to imitate models (other orangutans and humans) if the animals had previous experience with the models (Russon & Galdikas, 1995).

Bottlenose dolphin calves (Tursiops truncatus) prefer certain types of models (Kuczaj et al. 2005, in press). They occasionally imitate their mothers and other adults. Calves are much more likely to imitate other calves, although prowess influences the likelihood that the model will be imitated. Young dolphins are more likely to imitate older (and more competent) peers than the behaviors of younger less competent peers. Similarly, capuchin monkeys (Cebus paella) are more likely to watch skilled nutcrackers than unskilled ones (Ottoni et al., 2005). These results fit well with Morgan's (1900) suggestion that more "active, intelligent and mischievous" animals provide models for others to imitate. Morgan also suggested that the absence of such models resulted in reduced curiosity and initiative in a group of animals, a notion that has implications for both cultural innovation and the well-being of social animals maintained in captive facilities.

In addition, the opportunity to choose a model and to select from the behaviors may explain why animals exhibit more superior imitative abilities in spontaneous imitation than in elicited imitation tasks. In addition, brain activity in adult humans increases if they watch someone with the intention to imitate the observed behavior later (Grezes et al., 1999). Perhaps this neurological system is more likely to be activated if young human children and animals choose to imitate a behavior rather than being asked to do so.

Where Do We Go From Here?

Ontogeny-In his seminal work on the ontogeny of imitation in human children, Piaget (1952, 1962) distinguished self-imitation, imitation of known behaviors produced by others, and imitation of novel behaviors produced by others. He believed that during ontogeny, self-imitation emerged prior to the imitation of others, and that imitation of known behaviors emerged earlier than imitation of novel behaviors. Thus, a child's capacity for imitation changes during the course of development. Species also differ in terms of their abilities to produce the forms of imitations described by Piaget, but little is known about the ontogeny of imitative abilities in nonhuman species. For example, bottlenose dolphin calves engage in imitative behaviors (Kuczaj et al., 2005, in press), but the developmental trajectory of their imitative abilities has not been determined. Information concerning the ontogeny of imitative skills in nonhuman species (including cetaceans and pinnipeds) is sorely needed.

Context: The Nature of the Model and the Task Influence Imitation—Additional information concerning the characteristics of imitated models would benefit both in the understanding of the imitative process and the ability to design elicited imitation tasks that more accurately assess imitative skills. For example, we know little about how the context influences the likelihood that an animal's behavior will be imitated, particularly for cetaceans. Dolphin calves are more likely to imitate peers in a play context, but they might be more likely to imitate their mothers in a foraging context. We also need to learn more about the social consequences of imitating or being imitated. If imitation is in fact the sincerest form of flattery, then subordinate animals may sometimes imitate dominant animals as a form of appeasement. If so, subordinate animals should engage in imitation more often than dominant animals.

Approximately 50 years ago, von Uexküll (1957) used the term Umvelt to refer to the sensory world of each species, noting that species have unique ways of perceiving and interpreting their environment. Individuals within a species also vary in terms of the information they process from given experiences. Bandura (1997) proposed that three types of environments need to be distinguished when considering the effect of context on observational learning: (1) imposed, (2) selected, and (3) created. An imposed environment is one that is presented to an organism and is what elicited imitation tasks create. The selected environment refers to the part of the environment that the organism actually experiences (von Uexküll's Umvelt), while the created environment is constructed by the organism's own behavior. Regardless of whether imitation is elicited or spontaneous, the imitator must select the aspects of the model's behavior to mimic and then create the reproduction. Unfortunately, the processes involved in the selection and creation of imitated behaviors are far from clear.

It is important to compare spontaneous and elicited imitation because elicited imitation tasks alone may underestimate an organism's imitative abilities (Kuczaj et al., 2005). It is also dangerous to rely solely on observations of spontaneous imitations. Spontaneous behavior is typically more open to multiple interpretations than is behavior that occurs in more controlled studies. Some of these interpretations might overestimate an animal's cognitive abilities. Morgan's (1903) famous admonition to avoid attributing "higher mental processes" to animals unless absolutely necessary is as valid today as it was 100 years ago. But, care also should be taken not to arbitrarily restrict higher mental processes to particular types of tasks. In such cases, we run the risk of underestimating an organism's cognitive repertoire.

Comparing performance across different tasks and different situations is essential for valid diagnoses of cognitive abilities, and imitation is well-suited for such comparisons.

Individual Differences—The comparative study of imitation focuses on species differences, which is essential for a complete understanding of imitation. It is also important to investigate individual differences within a species. Bandura (1997) noted that imitation involved attention, retention, motivation, and production, all of which could vary among individuals and across situations. Bandura suggested that self-efficacy was an important factor in children's selection and creation of their environments. He defined selfefficacy as an individual's perception of his or her competence in dealing with the environment and suggested that high self-efficacy was an essential aspect of persistent behavior. Thus, animals with high self-efficacy should be more likely to imitate novel behaviors than animals with low self-efficacy. One obvious problem with this hypothesis is that it is difficult to reliably assess self-efficacy in animals; however, efforts to assess consistent individual differences in animals ("personality") may provide diagnostic tools that make it possible to test predictions about the relationship between self-efficacy and imitation (Gosling, 2001; Highfill & Kuczaj, 2006).

Self-Recognition and Imitation-A number of theorists have suggested that a capacity for kinesthetic-visual matching provides the basis for both imitation and self-recognition (Parker, 1991; Gopnik, 1993; Mitchell, 1995, 2002c). Given that dolphins have the capacity to imitate, it should come as no surprise that dolphins have also been found capable of self-recognition (Marten & Psarakos, 1994; Delfour & Marten, 2001; Reiss & Marino, 2001). The best evidence for dolphin self-recognition comes from two disparate sources. Reiss & Marino (2001) demonstrated that bottlenose dolphins can use a mirror image to examine parts of their bodies, an ability that is typically assumed to be reflective (no pun intended) of some form of self-recognition. Herman et al. (2001) reported that a bottlenose dolphin was able to comprehend gestural symbols that referred to nine of its body parts, an ability that suggests that dolphins are aware of their bodies. The dolphin in Herman et al. (2001) was also adept at imitating other dolphins and humans (Herman, 2002). These results are consistent with the notion that self-recognition and imitation are related, but the precise nature of this relationship is far from clear. We suspect that there is more than one such relationship. For example, the type of self-awareness reported by Reiss & Marino (2001) is different from that reported by Herman and his colleagues (2001). We have seen

that not all forms of imitation are the same, and determining the precise relationships between various forms of imitation and self-awareness is crucial for a better understanding of these two important cognitive phenomena.

Conclusions

Different forms of imitation involve different types of mental representation. The ability to delay imitation requires a capacity to mentally represent and remember the model behavior (Piaget, 1962). Even the capacity to imitate one's own behaviors has representational implications. Self-imitations have been proposed as precursors of pretend play and, as such, might be important indices of symbolic functioning (Preyer, 1890; Piaget, 1962; Bretherton, 1984; Mitchell, 2002a). Determining the precise nature of the relationship between imitation and mental representation is difficult, however (Whiten, 1996; Suddendorf & Whiten, 2001; Kuczaj et al., 2005). The extent to which young children's and animals' imitations reflect representational capacity and perhaps even facilitate the ontogeny of more advanced representational skills is a matter of considerable importance, and it is one reason why the study of imitation by dolphins and other animals is significant.

Available evidence suggests that animals can imitate and that dolphins may be one of the most proficient nonhuman species in this regard. We have seen that dolphins can imitate themselves and others. They can imitate both familiar and novel actions produced by other dolphins and other animals (including humans), and they are capable of deferred imitation. When dolphins are asked to imitate, it seems easier for them to reproduce familiar behaviors than novel ones. Moreover, adult dolphins appear to be more successful than juveniles at imitating on demand. Young dolphins appear more likely to spontaneously imitate behaviors in which they are interested, however (Kuczaj et al., 2005), a phenomenon that might influence cultural change.

Although it seems clear that some species other than humans can imitate, we do not know how dolphins or other animals imitate (Zentall, 2005). Learning how, why, when, and who animals imitate will increase our understanding of the minds of other species and, in turn, place our own abilities into evolutionary perspective.

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