Social Cognition

Social cognition refers to the processes unique to learning about and interacting with other individuals. Most often these are members of one's own species (*conspecifics*), but interactions with members of other species may involve the same mechanisms. Just because a situation is social it need not engage specifically social cognition. For example, many territorial male songbirds associate the songs of their neighbors with the location from which they are usually sung, and they attack if they hear a neighbor singing elsewhere. A change in location is a cue that the neighbor may be trying to take over new territory, so the behavior functions to defend the attacker's territorial boundaries. The mechanism is associative learning together with habituation (here, of aggressive behavior) to familiar configurations (Dong & Clayton, 2009), a social *use* of basic cognitive mechanisms rather than specifically social cognition.

This chapter has three main sections. First, the basics: what do animals know about their social companions and how do they come to know it? A central issue here is whether any animals have theory of mind. That is, do animals know anything about others' knowledge, beliefs, or other mental states, or do they respond to behavioral cues alone? Do species differ in this respect and how are any differences related to phylogeny, social system, and/or brain size? Next we address social learning. What and how do animals learn from each other? Do any animals imitate, and if so how is imitation possible? Can any animals be said to teach? Does social learning result in anything that could be called culture, or is culture unique to humans? Finally we look at the intrinsically social activity of communicating. Does emitting communicative signals

imply understanding others' need for information, that is, theory of mind? What does animal communication have in common with human language?

Most of the questions in the preceding paragraph do not yet have clear answers. The study of social cognition is perhaps the fastest growing and most contentious area discussed in this book. The tension between explanations in terms of basic processes and those invoking mentalistic understanding, or folk psychology, is nowhere stronger than here. Many of the theoretical ideas reflect a traditional primatocentric approach, but this is gradually being overturned by increasing evidence that social behaviors of nonprimate mammals, some birds, and even fish may equal in complexity those of apes and monkeys.

Social Behavior: The Basics

Social Complexity and Social Knowledge

The relatively large brains of primates and their exceptional performance in laboratory tests of cognition have long been thought to reflect adaptations to the complex cognitive demands of social life (Byrne & Bates, 2010; Humphrey, 1976; Jolly, 1966). This *social theory of intellect* (or *social brain theory*) has considerable support, but there is also much to debate. For example, what measure of sociality should be correlated with what aspect of brain size? Sheer group size does not insure high demands on cognition. In herds or flocks, anonymous individuals may just follow rules about how to move relative to near neighbors (Couzin, 2009). The social brain hypothesis seems to assume general rather than modular intelligence, but unlike with hippocampus size and spatial memory in food-storing birds (Chapter 2), we know very little about the neural underpinnings of social cognition (Healy & Rowe, 2007; but see Lefebvre & Sol, 2008). Here, further comparative analysis of social behavior can develop hand in hand with neurobiology (Dunbar & Shultz, 2007).

The most interesting social cognition appears in species that form stable groups in which the members recognize each other as individuals with differentiated social roles such as dominant-subordinate, pair-bonded, mother-offspring. Here the number of relationships that might be learned increases exponentially with group size, if nothing else increasing demands on memory. Each kind of relationship, perhaps simultaneously with other relationships, predicts different behaviors. For instance, a baboon approaching an infant needs to know not only who its mother

is but that mother's kinship and/or dominance relationships to itself. The mother's response may be modulated by recent events such as a fight between her relatives and those of the approaching baboon (Cheney & Seyfarth, 2007). But arguably some problems in the physical world equal social problems in complexity. One confronting some primates is tracking the availability of fruits in a tropical forest with hundreds of species ripening on different schedules, and indeed there is some evidence that the nature of species-typical foraging problems is correlated with brain measures (Byrne & Bates, 2010; Dunbar & Shultz, 2007). Nevertheless, there is a fundamental difference between the social and physical worlds, as reflected in the models in behavioral ecology. Optimality models are used in foraging theory (Chapter 3) because the environment can be assumed to change only as a result of the actor's behavior, but game theory is used to model social behavior, including social foraging, because here the best thing to do depends on what others are doing.

Much of what we know about animal social organization comes from studies in the field or with reasonably sized captive groups. Long-term observations can yield enough data to support causal inferences, for example, as to whether sheer spatial proximity or relationship best predicts mutual aid against aggressors (e.g., Silk, 1999), but experiments are most revealing. In one approach, hidden loudspeakers present sequences of vocalizations representing either familiar or unexpected social interactions between the subject's social companions (see Cheney & Seyfarth, 2007). Differences in the responses evoked, for example, looking longer toward a speaker playing an incongruous sequence such as a dominant animal vocalizing submissively toward a subordinate, reveal sensitivity to the social information involved.

Studies like those just sketched have revealed much about the social knowledge of primates and many other species (de Waal & Tyack, 2003; Emery, Clayton, & Frith, 2007), but experiments on captive animals are usually necessary to learn how such knowledge is acquired and what it consists of. The challenge here is controlling the behavioral events to be learned about. One way to address it is illustrated by the studies of social transitive inference described in Chapter 3 in which jays and fish watched staged interactions between live conspecifics. An approach permitting better control over characteristics of the stimulus animals is to splice audio (cf. McGregor, 2005) or video recordings to create artificial interactions. In one such study, rhesus macaques were trained to indicate the dominant one of two individuals in each of several short video clips. For instance, one monkey might be threatening and the other jumping away. They then

generalized to scenes showing different individuals (Paxton et al., 2010), suggesting these monkeys have a social concept of dominance.

Elements of Social Cognition

A key ingredient of social cognition is implicit in the preceding discussion: animals know other individuals' relationships to each other, and they may learn about these *third-party relationships* by observing, or *eavesdropping* (cf. McGregor, 2005). At one time it appeared (Tomasello & Call, 1997) that sensitivity to third-party relationships set primates apart from other species, but it is now clear that this sensitivity is shared not only by nonprimate mammals (e.g., hyenas; Holekamp, Sakai, & Lundrigan, 2007) but also—as indicated by the transitive inference studies mentioned earlier—by some birds and fish. Exactly what knowledge of a third-party relationship consists of is a largely unanswered question. For example, primate kinship may be expressed by frequent mutual grooming, sitting close together, cooperating in aggressive interactions, among other ways. Are such multiple behaviors encoded in a unitary way, similar to the behavioral abstractions discussed later in this chapter in the context of theory of mind? What would representing sets of behavioral interactions as relationships have in common with representing physical categories (Chapter 2)? Are relationships encoded hierarchically, for example, as dominance relationships within families that themselves have dominance relationships (Bergman, Beehner, Cheney, & Seyfarth, 2003)?

Two very basic ingredients set social apart from physical cognition. First, living beings are distinctive in being animate, that is, moving on their own, and goal directed. Much evidence from human infants and some from other species indicates that simple cues to animacy engage a set of expectations peculiar to living beings. Even a cartoon of moving colored balls may be seen as a social interaction: if Red moves toward Green, which moves away as Red approaches, Red is perceived as chasing Green (Scholl & Tremoulet, 2000). Young children encode motion like that at the top of Figure 4.1 as that of something animate, looking longer at a test display inconsistent with goal directedness (the "old action test" in which the ball still jumps when the barrier is removed rather than taking the shortest path; Gergely, Nádasdy, Csibra, & Bíró, 1995). Recognition of animacy and goal directedness may be a foundation for more complex forms of social cognition (Gigerenzer, 1997; Spelke & Kinzler, 2007).

Second, animals have eyes, and where they are looking is a good cue to what they will do next or where important things are in the
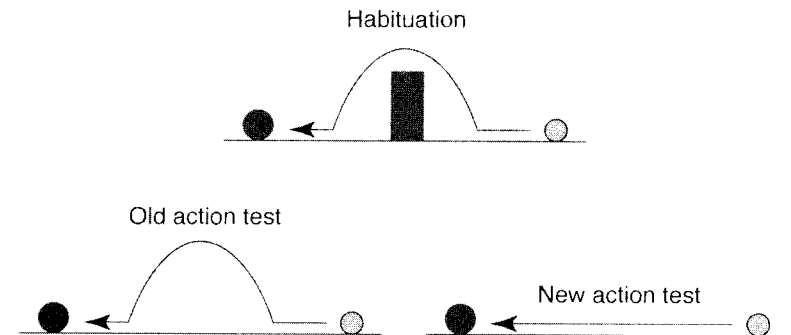

FIGURE **4.1.** Test for perception of intentionality. In each display, a single ball moves from the gray to the black position along the arrow. After habituation to the ball jumping over the barrier, the subject sees one of the lower displays. After Gergely et al. (1995) with permission.

environment. Accordingly, many mammals and birds are sensitive to the direction of other individuals' gaze. Apes, monkeys, goats, ibises, ravens, and others turn to look toward a distant location being gazed at by a human experimenter or conspecific (Byrne & Bates, 2010; Emery, 2000). But responding to gaze could be reflexive, in ethological terms a response to a sign stimulus. That is to say, importantly, *looking* or gazing is distinct from the mentalistic *seeing*: tracking gaze does not imply understanding others' experience of seeing. But what if an individual gazes toward a location you cannot see, for example at his side of a barrier placed between you? In such situations, apes, some monkeys (Amici, Aureli, Visalberghi, & Call, 2009), and ravens but not ibises (Loretto, Schloegl, & Bugnyar, 2010) move to look behind the barrier, as if aware their companion must be seeing something interesting. Even more strongly suggestive of this interpretation, if there is nothing behind the barrier apes (but not monkeys; Amici et al., 2009) "check back," looking again at a human experimenter (Rosati & Hare, 2009). It could be argued that this behavior reveals an expectation of seeing something that is conditioned to the basic gaze-following response, but the species differences here seem more compatible with apes having an understanding of gaze that other species lack. However, if gaze following is an adaptation for social life, it is not clear why gaze-following skills of apes should be different from those of other highly social primates (Rosati & Hare, 2009).

Theory of Mind

Sensitivity to the gaze of others is but one component of *theory of mind*, the understanding that others have knowledge, beliefs, desires, and the like (intentional states; Dennett, 1983). This central concept in social cognition was introduced by Premack and Woodruff (1978) in an article titled "Does the chimpanzee have a theory of mind?" but it has been studied most in young children. A key test here is the *false belief task*: a child sees a toy hidden by the experimenter, say in a basket, while a stooge, say a clown, looks on. The clown leaves the scene and the experimenter moves the toy to a second hiding place, say a box. The clown returns and the child is asked, "Where will he look for the toy?" Up to the age of about 4 years (see Apperly & Butterfill, 2009) children say the ignorant stooge will look in the box, as if unable to distinguish another's beliefs from their own knowledge about the true state of the world. Older children, like adults, predict the stooge will search the original hiding place. Notice, however, that a correct prediction need not imply theory of mind but could be based on behavioral cues. That is, a child could explain her prediction by saying, "Because he was looking there when you hid it" rather than "Because that's where he thinks it is." The distinction between use of behavioral cues alone and inference about others' mental states based on such cues—or behavior reading versus mind reading—is the root of the many controversies and challenges surrounding attempts to answer Premack and Woodruff's question.

To date, no nonhuman animal has unambiguously passed any form of false belief test (Byrne & Bates, 2010; Call & Tomasello, 2008). More often used has been the simpler *object choice test*. Here subjects choose between two containers that might hide food. In the original version for chimpanzees (Fig. 4.2; Povinelli & Eddy, 1996), a knowledgeable companion, usually a person, points toward or looks at the baited container. In versions with competition, the companion can see or has seen the food in one location, whereas the subject knows food is in both. When both animals are allowed to get the food, the subject should avoid competition by choosing the location the competitor does not know about.

Chimpanzees initially choose randomly in object choice tests like that depicted in Figure 4.2, although they eventually learn to use relevant cues such as whether the person is facing them (Povinelli & Eddy, 1996). However, pet dogs and some other domesticated animals immediately choose a container gestured toward or gazed at by a human. On one interpretation, domestication led to dogs evolving an innate or very early developing theory of the human mind. More consistent with the fact that selection works through modifying developmental programs is the view
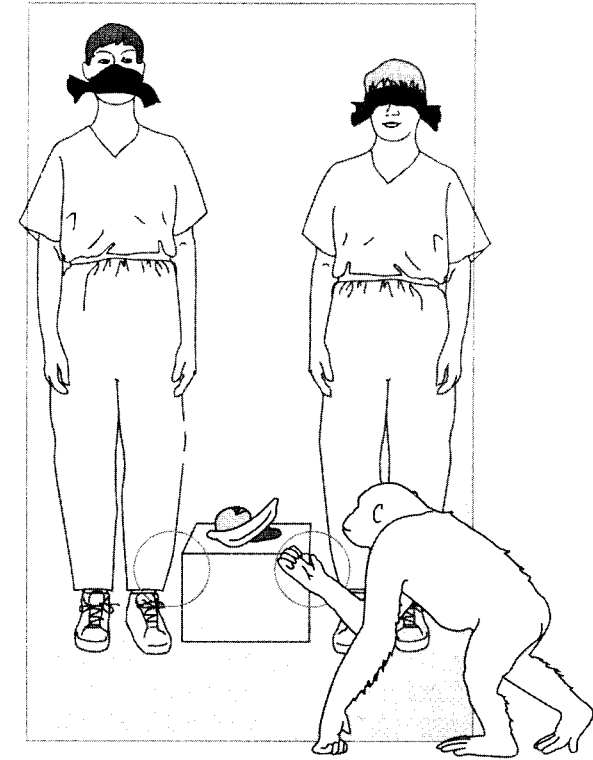
FIGURE **4.2.** Object choice test for chimpanzees. The animal will receive food for gesturing in front of the experimenter who can see him. After photographs in Povinelli and Preuss (1995) with permission.

that as a result of being selected not to fear humans and to attend closely to human behavior, pet dogs learn very early about the significance of human gestures (Reid, 2009; Udell, Dorey, & Wynne, 2010).

The studies with dogs underline the fact that theory of mind tasks like that in Figure 4.2 test responses to cues from helpful humans. A more natural task for chimpanzees is responding to cues from another chimpanzee who is competing for food. Indeed, in such tasks chimpanzees do keep track of what a competitor sees or saw, and hence knows about, by preferentially approaching alternative sources of food (Hare, Call, Agnetta, & Tomasello, 2000). An analogous situation confronts a food-storing bird when a competitor watches it caching, and accordingly ravens and scrub jays discriminate

between caches observed by another bird and those not so observed (Emery & Clayton, 2009a). For instance, when recovering caches in private, a scrub jay is more likely to recache items another bird witnessed it caching, a behavior that should help to defeat pilfering. Moreover, when recovering in the presence of another bird, they behave differently toward caches that individual watched them make, apparently encoding "who" along with what, when, and where in their episodic-like memory (Chapter 2; Dally, Emery, & Clayton, 2006). Similarly, when a competitor that witnessed hiding of a given cache is nearby, a raven will move more quickly to retrieve it than if an ignorant competitor is present (Bugnyar & Heinrich, 2005).

The studies just summarized and many others (cf. Byrne & Bates, 2010; Emery & Clayton, 2009a) reveal sophisticated responses to present and/or remembered cues to what other individuals know, intend, or want, but none of them compels us to conclude that the subjects understand knowing, intending, wanting, or the like as mental states. This viewpoint (Penn & Povinelli, 2007; Povinelli & Vonk, 2004) suggests that sophisticated social behavior is supported by *behavioral abstractions*, concept-like representations (Chapter 2) that integrate information about a possible competitor's identity, past and present gaze direction, and the like to control behavior in a flexible and appropriate way.

If behavioral abstractions do the same job as theory of mind without attributing to animals the ability to reason about the unseen mental causes of behavior, is there any way to isolate behavior based specifically on theory of mind? One suggestion (Penn & Povinelli, 2007) involves a complex object choice task with multiple locations designed to distinguish reasoning about theory of mind from both control by observable cues alone and random choice. Another is based on the controversial notion that theory of mind requires generalizing from one's own experiences to those of others. For instance, because I experience seeing when I gaze at something, I infer that others do. This view inspired Heyes (1998) to suggest a paradigm in which animals are first taught that one kind of visor allows them to see things whereas another kind is opaque. If subjects infer others' experiences from their own, then in an object choice task they will treat another individual wearing the see-through visor as knowledgeable and one wearing the opaque visor as ignorant. Reportedly, this test has been tried unsuccessfully with chimpanzees, but young children pass it (see Penn & Povinelli, 2007). Yet another approach is to suggest that full-blown theory of mind has multiple components, with understanding of goals and intentions distinct from understanding of knowledge and beliefs, and that chimpanzees have the former but not the latter (Call & Tomasello, 2008). Chimpanzees and some other primates are indeed sensitive to cues to a person's intention, for instance, responding differently to apparently accidental as opposed to intended acts, but these findings seem explicable in terms of sensitivity to behavioral cues.

This last approach is consistent with a growing appreciation that "Do animals have theory of mind?" is one of those all-or-nothing questions like "Do animals count" that is better answered by asking instead, "What are the components of this ability, which are shared across which species, and why?" Current comparative research seems to be moving in this direction (Emery & Clayton, 2009a). In that, it is converging with new research and theorizing about human theory of mind, which suggests that in adults it has two components: a fast, efficient, early-developing, behavior-reading process and a slower, gradually developing, mind-reading process (Apperly & Butterfill, 2009). The former is used in ongoing social interactions, when we respond rapidly to social signals, whereas the latter comes into play for reasoning about and explaining other people's behavior. The former, but not the latter, is present in very young infants and nonhuman animals. Both are present in adults, as shown by the effects of making them conflict. For example, adult subjects report the number of objects in a display more slowly if the scene includes an avatar whose gaze takes in a different number of objects from the subject's, as if another's viewpoint is processed automatically and unconsciously. Such findings (see Apperly & Butterfill, 2009) indicate that just as nonverbal numerosity discrimination is not replaced by verbal counting during human development (Chapter 3), fast automatic behavior reading is not replaced by mind reading but exists in parallel with it.

Cooperation and Prosocial Behavior

Helping others potentially increases their fitness at a cost to one's own. Because evolutionary theory emphasizes that natural selection occurs primarily at the level of genes promoting the fitness of individuals, altruism is therefore a puzzle. Nevertheless, three kinds of helpful behavior could still evolve by individual selection alone (Trivers, 1971). The study of animal cooperation has generally focused on documenting examples of them rather than analyzing their underlying psychology. However, each kind of altruistic behavior implies particular cognitive and/or emotional mechanisms, most of which are among the basic cognitive tools discussed in Chapter 2.

The least problematic in evolutionary terms is helping relatives. Even if the helper incurs a substantial cost, it may be able to enhance its own fitness by increasing the chances that those who share its genes will

reproduce. Thus, altruism could evolve by *kin selection*. A helper does not understand kinship as such but is simply more likely to perform potentially helpful behavior in the presence of individuals possessing some feature shared by its relations. For example, Belding's ground squirrels are more likely to alarm call—thus attracting a predator's attention to themselves—when in the presence of conspecifics raised in the same nest with them, a feature correlated with kinship in natural conditions (Holmes & Mateo, 2007).

A second cognitively undemanding form of cooperation is *mutualism*, an interaction from which both individuals gain an immediate benefit as in "you scratch my back while I scratch yours." Some chimpanzees hunt cooperatively (Boesch & Boesch-Acherman, 2000), and in the lab pairs of apes or monkeys can learn to work together to obtain food from an apparatus that neither could operate by itself (Noë, 2006). Such interactions imply the ability to recognize other individuals and their behaviors and to learn through reinforcement. Mutualistic exchanges need not be with conspecifics. The best-studied example is that of some cleaner fish and their "clients" (Bshary & d'Souza, 2005) on tropical reefs. By eating parasites from larger fish, cleaners get a meal; by making their clients more comfortable, they reinforce clients for visiting. Clients learn to visit particular cleaners at their stations on the reef, using both individual experience and information gained from observing cleaners' behavior toward others. This is a remarkably fine-tuned and complex system, but one based only partly on specifically social cognition.

Reciprocal altruism is arguably a different story. Consistent with evolution by individual selection, reciprocal altruists both benefit from cooperating, but some of the benefits are delayed, as in "You scratch my back now and I'll give you food later." Reciprocity seems to pose cognitive challenges (Cheney, 2011; Stevens & Hauser, 2004): participants must be sensitive to delayed rewards, which are generally not very effective (Chapter 3), and in a social group of any size, they seem to need sophisticated mental balance sheets. Perhaps because of this, there are few if any clear cases of reciprocal altruism between nonrelatives (Clutton-Brock, 2009). Moreover, individuals may interact frequently because they stay close together for some extraneous reason so analysis of relevant field data needs to control for the possible confound of proximity. Models based solely on proximity (Hemelrijk, 2011) serve as a null hypothesis against which to evaluate claims that reciprocation reflects memory for past exchanges. Nevertheless, some recent analyses of data from primates

in the field convincingly show animals consistently choosing specific partners to exchange support in aggressive interactions, grooming, and food (Cheney, 2011; Schino & Aureli, 2009). The mechanism that sustains it could be a partner-specific emotional memory, similar to associative strength in summarizing past costly and beneficial interactions in a single value. Episodic memory for the details of past exchanges is not required.

Although the primary force in evolution is individual selection, natural selection can also operate at the level of the group (Wilson & Wilson, 2008). Under conditions arguably resembling those early in hominid evolution, groups of cooperating individuals have an advantage, and this may account for the presence in humans of what is known as *strong reciprocity* or a sense of fairness. In simple economic games, people worldwide exhibit a sense of fairness, tending to divide resources evenly rather than taking all for themselves even when there is no penalty for doing so and wanting to punish others who do not do the same. Such prosocial (or other-regarding) behavior implies a basic ability to perceive what others are getting and compare it to one's own payoffs. Evidence for it in nonhuman primates is mixed (Silk & House, 2012). In one candidate demonstration (Brosnan & de Waal, 2003) capuchin monkeys seeing a neighbor rewarded with a preferred grape when they received only cucumber rejected the cucumber more often than when both got the same reward for their efforts. But several factors other than aversion to social inequity may play a role in tests like this one (Brosnan, Talbot, Ahlgren, Lambeth, & Schapiro, 2010). For example, in itself seeing grapes or memory of past grape rewards may increase rejection of cucumber (Wynne, 2004).

A test free of this confound allows the animal to choose between delivering reward to itself and for the same effort delivering that reward to itself and one to another nearby individual. Because chimpanzees are phylogenetically closer to humans than are other nonhuman primates except for the rarer bonobos (see Fig. 1.2 in Chapter 1), they have been tested the most for this kind of prosocial behavior. However, despite evidence that human children prefer fairness by the age of 3 or 4 years, chimpanzees seem to care only what they themselves are getting (Silk & House, 2012; Warneken & Tomasello, 2009). For example, in the experiment depicted in Figure 4.3, a version of the so-called ultimatum game for testing humans, chimpanzees making the first choice chose the allotment giving them more raisins, and recipients accepted any allotment with at least one raisin for themselves (Jensen, Call, & Tomasello, 2007). However, some monkeys choose to benefit others in tests of prosociality.
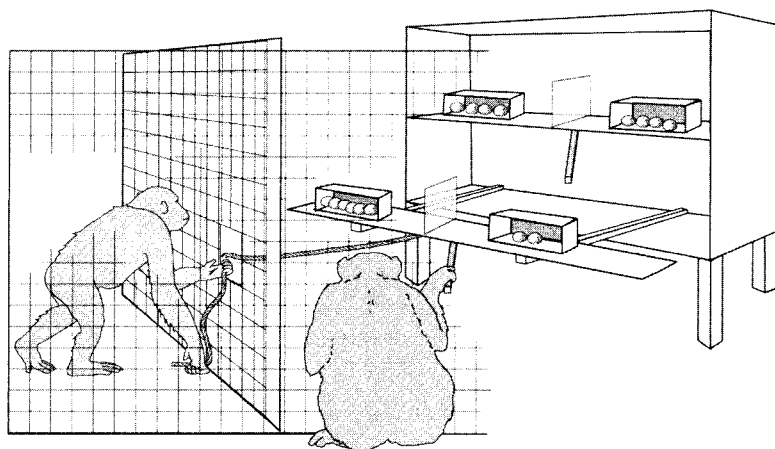
Figure 4.3. Ultimatum game for chimpanzees. The animal on the left (the proposer) has chosen the lower tray, giving him the larger proportion of the eight raisins. The animal on the right (the responder) can complete delivery of this unfair allotment, six raisins to the proposer and two to himself, by pulling the vertical rod, or he can refuse to pull. After Jensen et al. (2007) with permission.

Understanding the species differences in this relatively new area of research is a challenge for the future (Silk & House, 2012). Testing methods may also be crucial. Chimpanzees given a less elaborate test than the one depicted in Figure 4.3 did choose to benefit a partner at somewhat above chance levels (Horner, Carter, Suchak, & de Waal, 2011).

Suggestions that chimpanzees are indifferent to others' welfare have been controversial because they seem inconsistent with observations of spontaneous species-typical helpful behaviors in naturalistic situations, such as a chimpanzee placing an arm over the shoulder of the loser in a fight. These have sometimes been taken as evidence for empathy (de Waal, 2008), that is, an emotional reaction to others' distress that motivates helping. Many animals, including mice and fish, respond physiologically and/ or behaviorally to witnessing conspecifics in pain or acting fearfully or aggressively. As we see in the next section, such empathic responses may support Pavlovian conditioning, but even if they occur in the situations used to test prosociality there may be limits to the arbitrary instrumental responses they can support (de Waal, 2008; Silk & House, 2012).

Social Learning

The Basics

Social learning is any learning from other individuals. It is thus a generic term covering a variety of learning mechanisms, some also used in non-social situations. Similarly, *copying* refers to doing what others are doing, regardless of mechanism. *Imitation*, performing an act because of seeing it done, is perhaps the most cognitively complex form of copying. Learning by imitating was traditionally the holy grail of social learning studies, while other kinds of social learning were dismissed as uninteresting alternatives to be ruled out in attempts to demonstrate imitation. Perhaps as a result, authors do not always agree on terms and definitions for these other processes (Hoppitt & Laland, 2008).

Notwithstanding its importance in human development, imitation is rare in other species, but other kinds of social learning often contribute to mate choice, foraging, enemy recognition, and other behaviors (Kendal, Galef, & van Schaik, 2010; Laland, Atton, & Webster, 2011; Whiten, Hinde, Stringer, & Laland, 2011). Appreciation of this fact together with interest in whether any other species have an analog to human culture has inspired mathematical models dealing with such issues as when and what to learn from others (see Rendell et al., 2011). But although a benefit of sociality is the opportunity to learn from others, behavior would not track environmental change very well if everyone learned socially and no one from individual experience. This insight has stimulated functional models and experimental studies of tradeoffs between socially and individually acquired information. For example, what does an animal do when it learned for itself that A is a more profitable foraging option but others are choosing B (Galef, 2009a; Laland et al., 2011; Rieucau & Giraldeau, 2011)? Findings in this area are generally interpreted functionally, in terms of "social learning strategies," but they raise interesting mechanistic questions. For instance, do they reflect basic mechanisms of attention or memory or rather species-specific predispositions for weighting social versus other cues?

Any test of social learning requires one or more *demonstrators*, animals that perform the behavior of interest, and one or more groups of naive *observers* exposed to the to-be-learned behavior or—as in the example shortly to be discussed—some product of it. Observers are then tested for performance of the target behavior in the absence of demonstrators. Perhaps the most thoroughly analyzed example of

mammalian social learning in the laboratory, social transmission of food preferences in rats (Galef, 2007), provides an illustration. Demonstrator rats eat one of two flavored foods, say cinnamon or chocolate, and then interact with observer rats in the absence of food. Observers later given both cinnamon- and chocolate-flavored foods eat a larger proportion of the food eaten by their demonstrator than do observers whose demonstrators ate the alternative. The key to this phenomenon is that when rats meet they engage in face-to-face contact, allowing one to experience the odor of whatever the other has been eating simultaneously with the odor of carbon disulphide, a component of rat breath. The resulting social learning is robust enough that preference can be transmitted across several successive groups or "generations" of observers in the laboratory.

In the wild several additional mechanisms help to insure that naive rats eat foods being safely eaten by others in their colony. For instance, rats approach other rats that are feeding, or even fresh rat droppings. They are thereby exposed to the flavors of safe foods, reducing their neophobia toward them. In social learning terms, the effect of cues from other feeding rats is an example of *local* or *stimulus enhancement*. That is, the activities of other animals increase the attractiveness of a location or stimulus, respectively, which the observer may then learn about on its own. The learning instigated by local or stimulus enhancement often depends on species-specific preferences. Chickens approach other chickens pecking and peck the same colored grain they are pecking at, but they are probably not interested in rat excrement or rat breath.

Cues with species-specific motivational or reinforcing properties also contribute to *observational conditioning*, but here initially neutral cues are associated with a demonstrator's behavior or the motivational state it arouses in observers. One well-studied example involves the mobbing behavior that small birds show toward predators. In mobbing, birds approach a predator in a group, often with special calls and postures. Mobbing alerts others to the presence of the predator and may drive it away. Young blackbirds learn what to mob by seeing what others are mobbing. In a laboratory setup, mobbing by a demonstrator toward a stuffed owl elicits mobbing by an observer who sees only a harmless object such as a milk bottle. The observer starts mobbing the milk bottle, and when later tested alone, it still does so (Curio, 1988). Monkeys acquire fear to objects they see other monkeys reacting fearfully toward (Mineka & Cook, 1988), and they do so more quickly if

the object is a snake than a flower, an example of belongingness in associative learning (Chapter 2). There is some evidence that people have a similar adaptive predisposition for fear learning (Öhman & Mineka, 2001).

Imitation

Unlike mobbing or fearful responses to a predator, imitative behaviors are often novel or unusual behaviors for a species, though they need not be. Many candidate examples are behaviors judged difficult to learn by trial and error, as in tool using. One of the original tests of animal imitation learning, Thorndike's study of chicks described in Chapter 1, introduced a design that is key in more recent experimental work: two responses are available (turning left or right in a maze in Thorndike's study); some observers see one demonstrated, some see the other. All are then compared in the absence of demonstrators to see whether observation influences their responses. In one contemporary example of what is now known as *the two-action test*, quail or pigeons that have watched conspecifics operate a treadle for food by either pecking or stepping on it are subsequently more likely to perform the action they saw than are those who saw the alternative. Here both actions are directed toward the same part of the same object, so this two-action test controls for local or stimulus enhancement (see Hoppitt & Laland, 2008).

Because imitation seems so important in human development and because, as will be discussed shortly, chimpanzees exhibit many complex skills in the wild, chimpanzees have been common subjects in studies of imitation learning. Figure 4.4 comes from a direct comparison of children and chimpanzees in a two-action test with an "artificial fruit," a box that could be opened by twisting or poking two bolts. The results are typical in that chimpanzees imitated to some extent but young children were more likely to do so (Whiten, Custance, Gomez, Teixidor, & Bard, 1996). Indeed, children are more likely to engage in blind (or over-) imitation, copying extraneous nonfunctional aspects of a demonstration (see Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009).

Rather than imitating in box-opening or tool-using tasks, chimpanzees sometimes show *emulation* or *affordance learning*. In emulation, the animal appears to learn that there is a goal to be obtained (goal emulation) or that an object has to be used to obtain it. The resulting behavior is not an exact copy of the demonstrator's action but a crude approximation,
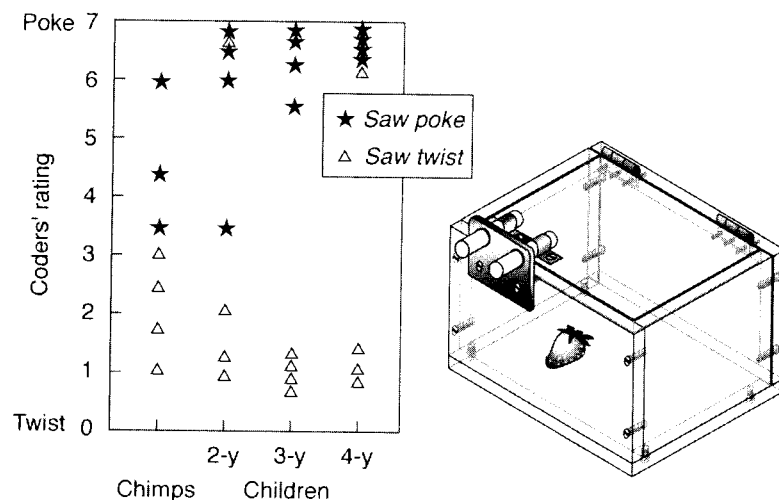
FIGURE **4.4.** Data from chimpanzees and 2-, 3-, and 4-year-old children presented with the "artificial fruit" at right as a function of whether the subjects had seen a human adult demonstrator poke or twist the cylindrical bolts on its upper left corner. Each data point represents one subject, rated as to whether actions on the bolts more resembled poking or twisting. Redrawn from Whiten et al. (1996) with permission.

such as picking up a rake tool upside down (Tomasello, Davis-Dasilva, Camak, & Bard, 1987). Affordance learning implies learning how something works (what actions it affords), information that may generate the same action as a demonstrator's but not because of seeing the demonstrator. The nonsocial character of affordance learning is revealed by "ghost controls" (Hopper, 2010), in which an apparatus is operated remotely as if by a ghost. For example, pigeons, chimpanzees, and children that watch a door slide to the left or to the right to reveal a reward tend to push it in the direction they saw. Affordance learning may have contributed when New Caledonian crows that had made an apparatus deliver food by poking their beak or a stick into a tube spontaneously dropped stones down the tube (Chapter 3). It deserves deeper analysis in nonverbal creatures: how does seeing something happen translate into making it happen oneself?

The mechanism of true imitation has been more deeply analyzed. The basic issue is *the correspondence problem*, that is, what cognitive mechanism allows me to perform the same action I see you perform?

The correspondence problem is most acute with perceptually opaque actions like facial or whole-body movements, because the observer cannot see how well its own actions match those of the demonstrator. By the same token, probably the most widespread form of imitative learning in nature, song learning by birds (Bolhuis, Okanoya, & Scharff, 2010), is not considered cognitively challenging because young birds can (and do) learn by matching the sounds they hear themselves make to the sounds of adults. Discovery of *mirror neurons* in the monkey premotor cortex at first appeared to solve the correspondence problem (see Iacoboni, 2009; Rizzolatti & Fogassi, 2007). Mirror neurons fire both when the monkey performs a particular action and when it sees another individual perform the same action or hears distinctive sounds such as lip smacking associated with the action. Less direct evidence indicates that humans also have mirror neurons. By representing "my actions" and "others' actions" in a unitary way, mirror neurons provide a mechanism for translating between self and other, but they are not a complete neural mechanism for imitation.

One reason is that monkeys are not very good imitators, although—like people—they do respond positively toward others who imitate them (Paukner, Suomi, Visalberghi, & Ferrari, 2009). Moreover, although normal humans do not overtly imitate everything they see, they have a strong unconscious tendency to imitate, as revealed when automatic imitation conflicts with a required action (Heyes, 2009). For instance, a picture of an open hand beside the instruction to "make a fist" slows closing the hand, whereas a picture of a fist accelerates it. Dogs and budgerigars also show evidence of automatic imitation (Range, Huber, & Heyes, 2011). So why is overt imitation normally inhibited, and if it is, what are mirror neurons and automatic imitation for anyway? A provisional answer (see Iacoboni, 2009; Rizzolatti & Fogassi, 2007) is that mirror neurons play a more general role in social cognition in representing the actions of others and perhaps promoting cooperation with those who mirror one's own actions (Paukner et al., 2009).

Evidence that human newborns copy mouth movements suggests that mirror neurons are innate connections between sensory and motor representations of actions. However, the skilled and generalized imitation characteristic of human adults develops gradually and depends on imitative experience, and in other species the actions copied are generally just a few species-typical behaviors (Catmur, Walsh, & Heyes, 2009). These observations are consistent with the proposal (Heyes, 2010) that mirror neurons develop in social species through learning in which sensory input from

performing and/or seeing others perform a given action becomes associated with the motor commands for that action, in a process of *associative sequence learning.* For instance, birds copy pecking actions because having often pecked in the company of pecking conspecifics, as when a flock fed together, they have acquired an association between the sight of pecking and the motor commands for it. Support for this proposal comes from demonstrations that in dogs (Range et al., 2011) and people (see Catmur et al., 2009) training to counterimitate (e.g., to spread the fingers when told to "make a fist" and the reverse) reduces or even reverses automatic imitation of the actions involved. Of course, showing a capacity can be modified in adulthood does not rule out that it developed very early in life, before relevant experience, and indeed there could well be a predisposition to acquire the associations embodied in primate mirror neurons. Nevertheless, associative sequence learning theory has the attraction of showing how an apparently special "higher" cognitive process could be constructed from the bottom up, from basic species-general mechanisms.

Do Nonhuman Animals Teach?

This question shifts the focus from learning by observers to cognition and behavior of demonstrators. Teaching in humans implies theory of mind—the teacher understands what the pupil knows and behaves accordingly. Studies of teaching in other species are guided by a functional definition based strictly on behavior (Caro & Hauser, 1992): for teaching to have occurred, experienced animals must incur a cost, and no immediate gain, by engaging in behavior that allows naive individuals to learn something more quickly or that they would not learn otherwise. "Cost" here is used in the behavioral ecological sense of resources contributing to fitness, such as energy used or time spent foraging. Thus, the rat that has just eaten cinnamon-flavored food is not teaching other rats to eat it because rats normally sniff each other's faces when they meet. Most examples of social transmission in wild animals similarly do not imply any special teaching-like behaviors but rather mechanisms in observers that promote learning from the normal activities of experienced conspecifics (Thornton & Raihani, 2010). The primary exceptions involve carnivorous birds and mammals bringing half-dead prey which their young appear to practice killing (see Caro & Hauser, 1992). Such behavior that increases the cost of foraging in the short run could evolve by conferring long-term benefits via offspring that become independent sooner or are more successful predators.

So far the best-documented example of teaching occurs in wild meerkats (*Suricata suricatta*), small social mammals that live in the Southern African semidesert digging in the sand for scorpions and other invertebrate prey (Hoppitt et al., 2008; Thornton & McAuliffe, 2006). Groups cooperate to feed their young, who follow foraging adults around emitting begging calls. Initially adults offer pups mostly dead or disabled prey. Over a couple of months they offer more intact prey, but scorpions that can sting are less likely than other prey to be offered intact. Because giving live prey to the young has a cost in time spent monitoring the pups' feeding and recapturing escapees, meerkats fulfill two of the criteria for teaching. *(1)* They engage in special behavior toward naive animals that *(2)* has an immediate net cost. Experiments provide evidence for the third criterion for teaching: facilitating learning by the young. For 3 days researchers gave pups in groups matched for age and litter either four extra live scorpions, four dead ones, or an equivalent amount of hard-boiled egg. In a test at the end, those in the first group were most successful in subduing live scorpions. Adult meerkats are not, however, responding to the pup's skill but rather to their begging signals, which change with pup age. Adults with young pups bring more intact prey after hearing recorded calls of older pups, whereas the calls of younger pups stimulate adults to bring more dead prey.

Contemporary research on animal social learning and—as discussed in the next section—the possibility of animal cultures, has uncovered two other candidates for teaching, each in a different animal group. In birds, pied babblers behave so as to allow their nestlings to associate a special costly "purr" call with feeding, a call that summons the young to food once they leave the nest (Raihani & Ridley, 2008). And in ants (*Temnithorax albipennis*), naive foragers follow experienced "teachers" to food (Franks & Richardson, 2006). Leaders incur a cost, in that they slow down when being followed, but what the "pupils" learn has not been well documented. Nevertheless, these findings with species not closely related to humans together with the fact that teaching is rare or nonexistent in chimpanzees and other wild primates (Thornton & Raihani, 2010) compel the conclusion that teaching in other species is not an evolutionary precursor (i.e., homologous) to human teaching. Animals with certain kinds of life histories may teach one thing, whereas in humans theory of mind and other cognitive or motivational capacities make teaching a domain-general skill (Premack, 2007).

Animal Cultures?

Applied to humans, *culture* refers to group-wide, population-specific customs and beliefs transmitted from one generation to another through teaching, language, and in more subtle ways. Culture is thus a product

of social cognitive processes. Nonhuman species also have a variety of socially transmitted behaviors (Kendal et al., 2010; Whiten et al., 2011), but these tend to stay the same from one generation to the next. Human culture stands apart from such traditional behaviors in ratcheting up, with one generation improving on (or at least modifying) what it learned from the one before, resulting in products that become ever more complex (Richerson & Boyd, 2005). This suggests it is underpinned by some cognitive and/or motivational mechanism(s) unique to humans (Tomasello, Carpenter, Call, Behne, & Moll, 2005). The quest to characterize them and understand their evolution—and debates about whether there are such mechanisms—has focused most sharply on population-specific behaviors of chimpanzees in the field and comparisons between chimpanzees and human children in the laboratory, but it is increasingly enriched by studies of traditional behaviors by other primates, cetaceans, birds, and even fish (see Laland & Galef, 2009; Whiten et al., 2011).

Key data here are differences in tool use and other behaviors among seven geographically separated groups of wild chimpanzees (Whiten et al., 1999). Over 30 cases were judged unlikely to reflect ecological differences between sites in prey availability and the like but rather to be "cultural," that is, originated by one or a few individuals and transmitted by social learning. This claim is controversial, in part because on some conceptions even multiple behavioral traditions do not add up to culture (Laland & Galef, 2009). Moreover, ecological causes for population differences may not be obvious. For instance, one candidate cultural behavior is "ant dipping," in which the chimpanzee stimulates ants to crawl up a twig or grass stalk and removes them with the hand or mouth. It turns out, however, that more aggressive species of ants are more safely captured with longer tools and use of the hand (Humle & Matsuzawa, 2002). Thus, population differences in techniques may be at least partly explained by how the local ant species shape individual learning (see Mobius, Boesch, Koops, Matsuzawa, & Humle, 2008).

A further objection to equating population-specific behaviors with culture is that *traditional* implies social transmission, and the required information about development of complex behaviors in natural populations is rarely available (Galef, 2009b). Moreover, on some conceptions culture involves teaching and imitation. As we have seen, there is little evidence for teaching in any nonhuman species, and although field observations such as those of young animals watching intently as adults use tools (observations which are not unique to chimpanzees; Ottoni & de Resende, 2005) support the involvement of some form of social

learning, that need not be imitation. Indeed, even when young animals observe tool-using adults, they take time to develop skilled use of tools for extracting prey from shells or crevices, evidently through trial-and-error learning (for an example see Bluff et al., 2010).

The obstacles to studying social transmission in wild primates are circumvented in experiments on social transmission in captive groups (Whiten et al., 2009). The basic type of study employs two groups of animals and an apparatus like that illustrated in Figure 4.4 that affords two actions for extracting a reward. An individual from one group is taught one action, and an individual from the other, the other. Then these demonstrators rejoin their respective groups to test whether others adopt the action of the demonstrator. Ideally a third group is also introduced to the apparatus with no trained demonstrator to see whether they learn to open it spontaneously and if so with which technique. Several different tasks have been transmitted among chimpanzees in this way. Similar results come from studies of transmission chains in which one observer learns from a trained demonstrator and then becomes the demonstrator for the next individual and so on (Whiten et al., 2009). Thus, group differences of the sort documented in the field can be supported by the social learning mechanisms available to chimpanzees, but these need not include imitation. Studies like that illustrated in Figure 4.4 suggest that chimpanzees use imitation, emulation, and/or other processes, depending on the task. In comparisons to young children, their imitative responses may not be particularly rigid or long-lasting, and they are less likely than young children to rigidly copy functionally irrelevant features of a task, such as poking a stick into an empty hole before using it to open a door with food behind it. In contrast, once a copied method has become habitual, chimpanzees are less likely than children to copy a different but more rewarding method (Whiten et al., 2009). Such findings suggest that a variety of species differences contribute to the uniqueness of human culture.

Communication

Research on animal communication ranges from analyzing natural communication systems like the honeybee "dance language" to training captive parrots and chimpanzees to use human words. In the context of this book the most important questions are the following: What cognitive processes are involved in animal communication? Which are shared with human language, and what can the answer to this question reveal about how human language evolved?

In the last part of the twentieth century, much effort was expended attempting to teach forms of human language to apes. The animals' accomplishments were greeted as evidence they could use sign language or systems of tokens comparably to very young children, but in fact they largely learned to use them instrumentally, to get things they wanted. They did not communicate to acquire or share information, nor did they develop grammar in any meaningful sense. Most researchers have now concluded that these studies are most instructive for what the animals did *not* do (for reviews see Fitch, 2010; Shettleworth, 2010a). Just as young song sparrows exposed to swamp sparrow song do not learn to sing it (Marler & Peters, 1989), so apes exposed to the species-typical experiences of human children do not acquire human language. Contemporary research has moved on to examine the degree to which specific components of language are shared with other primate and nonprimate species. Such research receives most attention here. First, however, we review the basics of animal communication.

Animal Communication: Concepts and Controversies

Any instance of communication involves a *signaler* and a *receiver*. A *signal* in this context is "any act or structure that alters the behaviour of other organisms, which evolved because of that effect, and which is effective because the receiver's response has also evolved" (Maynard Smith & Harper, 2003, p. 3). Examples of communicative structures are the warning colors of Monarch butterflies and poison-arrow frogs, i.e. conspicuous colors and patterns signaling distastefulness to predators, evolved because predators readily learn to avoid them (Ruxton, Sherratt, & Speed, 2004). *Cues*, in contrast, are correlated with some feature of an animal but have not evolved specifically because of it. For example, visible symptoms of sickness like a slow gait would not be regarded as signals even though predators may learn to use them to target weak individuals.

Two contrasting views of animal communication are exemplified by the approach of classical ethology on the one hand and the philosophical analysis of human language on the other. As documented by Tinbergen, Lorenz, and other ethologists, social interactions of courting or fighting birds, fish, and other animals are intricate chains of stimulus and response. The stimuli are provided by *displays*, distinctive postures and/or calls by one member of a pair that elicit specific responses by the other. These in turn might elicit further responses by the first signaler, and so on until mating occurs or a fight is resolved. Everyday examples are the bowing and cooing of a courting male pigeon or the growling and teeth-

baring of a hostile dog, an example compared by Darwin (1879/2004) to human emotional expression.

The ethological approach to communication is behavioristic: what is the signal, under what circumstances is it given, and what is the response? Behavioral ecology continues this tradition but focuses on evolution and function. For example, what are the fitness benefits of conspicuous, energy-demanding displays and structures like the tails of peacocks and how can these outweigh their obvious costs? But communication via human language involves intentionality and representations in the minds of signaler and receiver: I have something in mind and I want you to know it (see Dennett, 1983). Communicating thus implies theory of mind: a speaker adjusts his communication to what he believes the audience already knows. This framework has influenced much recent research on animal communication, in some views too much so (Rendall, Owren, & Ryan, 2009; but see Seyfarth et al., 2010). It has, however, led to discoveries that arguably would not have been made otherwise, some involving important differences between animal signaling systems and human language. Current research points toward a synthesis of ethological and cognitivist or informational views, as can be seen in examples from some well-studied animal communication systems.

Honeybee "Dance Language"

When a honeybee returns to the hive from a successful foraging trip, she performs a *waggle dance* on the vertical surface of a honeycomb, while other bees crowd around her (Fig. 4.5). The dance consists of a straight run during which the bee buzzes and waggles her abdomen from side to side, followed by circling back to the start, first to one side then to the other, in a figure 8. The angle of the straight run to vertical matches the angle between the sun's azimuth and the straight-line path to food (see Fig. 4.5), and its duration corresponds to the distance to food. The dance thus carries information about where the forager has just found nectar or another resource, and several kinds of experiments show that bees can use it (Dyer, 2002). In pioneering studies of the dance, Karl von Frisch (1953) found the largest numbers of new recruits at the distance or direction signaled by the dancer. In later experiments the location signaled was not a location recently visited by bees, eliminating the possibility recruits use some environmental cue such as odors of recent visitors. For example, recruits follow the dance of a robot bee or of a live bee induced to "lie" (see Dyer, 2002). Recruited bees caught as they leave the hive and released a few hundred meters away fly the distance and direction
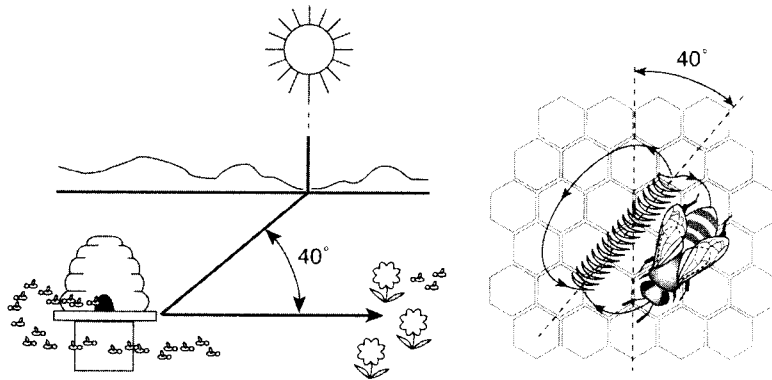
FIGURE 4.5. The waggle dance of the honeybee showing how its angle to the vertical is related to the angle between the path to the food and the sun's azimuth (the point on the horizon directly below the sun). Redrawn from Seeley (1985) with permission.

indicated by the dance and then start circling around as if searching for the expected nectar source, suggesting they treat the dance as a set of flying instructions rather than information about a location on a cognitive map (Riley, Greggers, Smith, Reynolds, & Menzel, 2005).

The dance language has a history of controversy (Dyer, 2002). Most recently this has revolved around not whether bees *can* use the information in the dance but the extent to which they *do* use it (Grüter & Farina, 2009). Instead of visiting a novel location indicated by the dance, experienced foragers may be stimulated by floral odors on the dancer to visit a familiar site with the same odor, as if having had their memory of it reactivated. Still, as the foregoing summary indicates, the honeybee dance fits the classical ethological description of communication very well.

Audience Effects

Because animals should not evolve to expend energy and attract the attention of predators by signaling unless a receiver is within range, senders should be sensitive to the presence of conspecifics. But such sensitivity does not require theory of mind. Like associatively learned responses (Chapter 2), signaling may be conditional upon contextual cues. For instance, after finding nectar of a given concentration, a returning honeybee forager dances longer when resources are more needed in the hive, as indicated by how fast workers unload her (Seeley, 1995). What would

more conventionally be called audience effects are shown by alarm calling roosters (Zuberbühler, 2008). They give more "aerial alarm" calls to a video hawk overhead when a hen is visible than when alone or with a quail as audience, even when the hen "audience" is presented on video so the rooster cannot be influenced by her direct response to the predator (Karakashian, Gyger, & Marler, 1988). Food calling, part of roosters' courtship, also shows audience effects (Evans & Marler, 1994). But such effects do not mean the rooster or any other animal signals with intent to inform. Indeed, consistent with the lack of other evidence for animal theory of mind, there is little evidence from any nonhuman species for sensitivity to receivers' need to know. For example, animals may keep on alarm calling even when receivers have already spotted the predator themselves (Seyfarth & Cheney, 2003; Zuberbühler, 2009).

Functional Reference

The discovery that vervet monkeys have different alarm calls for snakes, eagles, and leopards (Seyfarth, Cheney, & Marler, 1980) suggested that animal vocalizations are like words in referring to things in the world (Radick, 2007). Many other species are now known to have predator-specific alarm calls (Zuberbühler, 2009), but it is hard to know what representation, if any, such calls evoke in receivers (Manser, 2009). Just as in the study of metamemory, planning, and elsewhere, the solution to this problem is to develop clear behavioral criteria, here for *functional reference*. A functionally referential vocalization is, first, given under a restricted set of conditions, that is, it is production specific. Production specificity is demonstrated when the sender is alone, uninfluenced by receivers' responses to whatever caused his signal. For instance, in the laboratory setup described earlier, roosters give different alarm calls to a raccoon at the side of the cage than to the aerial predator. On the receiver's side, functionally referential calls by themselves, in the absence of whatever elicits them, evoke distinctive behaviors. For instance, a caged hen hearing a recorded "aerial alarm" crouches down and looks up, whereas on hearing the "ground predator alarm" she stands tall and looks from side to side (C. S. Evans, Evans, & Marler, 1993).

Responses to a functionally referential alarm call are not necessarily mediated by a representation of the predator, nor need they be entirely learned. A "leopard alarm" might directly elicit running to the nearest tree (the appropriate defense) or it might evoke thoughts of a leopard in the receiver's mind and thereby cause running. Higher orders of representation are conceivable, if unlikely. For instance, the receiver infers

that the sender sees a leopard nearby and wants him to run to the trees (Dennett, 1983). The habituation/dishabituation method introduced in Chapter 2 provides a way to address this issue, using acoustically different vocalizations which signal the same event. An excellent example comes from Diana monkeys.

On sighting a leopard or eagle, a male Diana monkey gives a predator-specific call, and nearby females respond with a series of alarm calls of their own. If the male calls again a few minutes later, females show habituation, calling less than the first time, but their calling is renewed if they hear the male alarm associated with a different predator. This dishabituation is due to the change in predator signaled (the "meaning" of the call) rather than to a mere acoustic change, as shown by making use of the fact that females also alarm call in response to the predators' own vocalizations (Zuberbühler, Cheney, & Seyfarth, 1999). Females heard a recorded male eagle alarm, the shriek of an eagle, or male leopard alarms and 6 minutes later, the shriek of an eagle. The first two groups showed equally little alarm calling to this standard probe stimulus. Similarly, the growl of a leopard elicited little alarm calling if the females had recently heard a leopard growl or male leopard alarms. It is as if a common representation of information provided by the calls mediates responding to them, as in category learning or many-to-one matching to sample (Chapter 2).

The aptness of this comparison is confirmed by the observation that species living in close proximity, experiencing similar threats, learn to respond to each other's alarm calls. Some of this learning is quite subtle, as when Diana monkeys respond with silent escape to guinea fowl alarms after hearing people in the area but with leopard alarm calls when they have recently heard leopard growls, as if inferring whether a person or a leopard caused the birds to call (see Zuberbühler, 2009). Here, members of the heterospecific monkey "audience" are eavesdropping on the guinea fowl (Peake, 2005). More generally *eavesdropping* refers to any case in which a third party acquires information from a communicative interaction between other individuals. The information might also be about social relationships (Cheney & Seyfarth, 2005a; Seyfarth & Cheney, 2010), as when animals learn about others' dominance relationships by watching them interact (Chapter 3).

Urgency and Emotion
Predator-specific alarm calls should evolve when the environment affords different evasive responses for different predators, as in climbing higher

to avoid leopards versus descending from the tree canopy to avoid eagles (Donaldson, Lachmann, & Bergstrom, 2007). But when the habitat affords only one means of escape, the only important information about an approaching predator is how near and/or dangerous it is, and this can be communicated by a single type of alarm call varying in intensity (e.g., loudness or repetition rate). For instance, open grassland species such as Belding's ground squirrels have one alarm call whose intensity reflects the urgency of need to break off other activities and run to the burrow (see Furrer & Manser, 2009). Similarly, black-capped chickadees' alarm calls have more "dee" notes for more dangerous predators (Templeton, Greene, & Davis, 2005). Urgency-based alarm calling fits a traditional notion that signals are expressions of emotion (here, fear) that directly elicit receivers' responses (Rendall et al., 2009). But referential alarm calling can also reflect urgency. For instance, like vervet monkeys, meerkats have acoustically distinct alarm calls for snakes, other ground predators, and aerial predators, but each call type varies in intensity with the strength of threat posed by the given predator. Call intensity determines the completeness and duration of receivers' responses (see Furrer & Manser, 2009).

Animal Communication and Human Language
Attempts to teach human language to apes (see Fitch, 2010; Shettleworth, 2010a) essentially asked, "Can another animal learn language?" In the early twenty-first century, this all-or-nothing question has been replaced by asking which components of language, or communicative ability, are shared with other species, to what degree, and why. For example, animal signals contain information, in that particular signals are correlated with particular states of the world (Seyfarth et al., 2010), and receivers use this information, but signalers do not seem to signal with the intent to inform. Another difference from human language is that although we can communicate an infinity of messages, even the graded signals of alarm-calling ground squirrels or dancing honeybees communicate about only a few things. Not only does any human language have many more words than any known nonhuman communication system has signals, words are combined according to implicit grammatical rules to make new messages, whereas in only a few known cases do nonhuman species combine discrete signals in predictable ways. Moreover, it still is unclear whether sequences of two different alarm calls or the like necessarily have "meaning" systematically related to their components (see Zuberbühler, 2009).

This sort of broad comparative approach to language was prominently articulated by Hauser, Chomsky, and Fitch (2002), who proposed that the human language "faculty" in the broad sense includes sensory-motor, conceptual-intentional, and computational components, many of which are shared with other species and not specific to language. The abstract computational capacity by means of which an infinity of meaningful sentences is generated from a finite set of words is referred to by Hauser, Chomsky, and Fitch (2002) as the faculty of language in the narrow sense. Crucially, it includes the ability to comprehend and generate recursive structures, an ability Hauser et al. suggest is unique to humans. Recursion refers to the embedding of a unit inside another unit of the same kind, as in "The rabbit the fox saw ran." Formally, interpreting any such sentence with an AABB structure (where any number of As are subjects and the same number of Bs are predicates) requires a *phrase structure grammar*, an implicit understanding that respective As are matched with respective Bs. Cognitively less demanding is stringing elements together, or *finite state grammar*, ABAB..., as in "The fox saw the rabbit that ran."

Although the proposal that recursion is the key unique feature of the human language faculty is controversial (Fitch, 2005; Pinker & Jackendoff, 2005), phrase structure grammar is generally agreed to be a key characteristic of human language. This view has inspired tests of whether animals can discriminate strings of sounds with a simple recursive structure such as AABB from equal-length strings of the same sounds obeying a finite state grammar (e.g., ABAB). In the most thorough study to date (van Heijningen, deVisser, Zuidema, & ten Cate, 2009) zebra finches learned to discriminate five strings of one type from five of the other, where the stimuli were "artificial songs" constructed of elements from natural zebra finch song. The birds transferred, with some decrement, to new exemplars constructed with the same song units. However, tests with sequences of two new song units (i.e., C and D) showed that they were not in fact responding to the overall structures but to local features such as whether the stimulus ended in two Bs.

As evidenced by the attention given this and similar studies (see, e.g., Corballis, 2007), shifting the focus from a global ability such as language (or numerical cognition, planning, etc.) to its components does not bring an end to all-or-nothing debates. Here, the question has shifted from "Do any animals have language?" to "Do any have recursion?" but researchers still confront the potentially endless task of finding a species that passes an unassailable test. In any case, not all agree

that recursion alone makes human language unique. Rather, language may be a unique combination of components, coevolved under special conditions in early hominid society (Pinker & Jackendoff, 2005). Just as assumed by the tests of recursion, some concepts expressed in or implicit in language may be present in other cognitive domains even if not expressed in communication. For instance, Cheney and Seyfarth (2005b) suggest that studies of baboon social cognition (e.g., Bergman et al., 2003) reveal implicit understanding of hierarchical classification. They also suggest that baboons' responses to sequences of vocalizations representing social interactions imply understanding of simple narrative structure like "A is approaching B and B is rebuffing her." Other candidates include aspects of spatial and numerical cognition and sensitivity to sequential organization (Hauser et al., 2002). The last of these has been shown very well by dolphins trained to respond to a complex system of commands. For example, in one of the few demonstrations of animal sensitivity to syntax, they discriminated between sequences such as "take the ball to the hoop" and "take the hoop to the ball" (Herman & Uyeyama, 1999; Kako, 1999).

The fact that apes extensively exposed to forms of human language learn to produce it in only a very limited way indicates that learning language requires some specialized process(es) unique to humans. Candidates include theory of mind together with a motivation to share information that communicating chimpanzees rarely if ever seem to display (Tomasello et al., 2005). As for possibly specialized learning processes per se, what allows young children to increase vocabulary at seemingly astronomical rates is *fast mapping*. Encountering a novel word together with a novel object or event, the child implicitly understands that the word refers to the object or event and thereby learns its meaning (see Pilley & Reid, 2010). Fast mapping goes beyond learning by exclusion, a capacity shared by sea lions among others (Kastak & Schusterman, 2002), to an understanding of reference, as demonstrated by immediate use of the word in multiple contexts. For instance, having learned "wug," when asked, "bring me the wug," the one new toy among three, a child could later "put the wug beside the teddy." It turns out that this ability is shared with at least one other mammal, a border collie named Chaser (Pilley & Reid, 2010), suggesting that it emerges in some way from extensive experience learning word-object associations. Over 3 years, Chaser learned the names of more than 1,000 objects as well as verbs for several actions he could perform. With the experimenter in a separate room to eliminate Clever Hans effects, he

could correctly choose any familiar object from a bigger collection. Like a previously studied border collie, Chaser showed evidence of fast mapping, though like children he did not retain the new associations well without practice. More important, he also correctly pawed, nosed, or took newly named objects the first time he was commanded to do so, thus exhibiting behavior consistent with understanding of reference.

We have so far dealt only with receptive aspects of language, but of course learning to produce language depends on vocal imitation, at least for hearing humans. Evidently crucial elements of the vocal mechanisms and cognitive capacity required for acquiring spoken language were absent in the last common ancestor of chimpanzees and humans and have evolved more recently (Fitch, 2005). Indeed, evidence that learning to produce words vocally, whether by imitation or otherwise, was beyond the abilities of chimpanzees inspired the studies in which apes were taught gestural and other nonvocal systems of communication. But some birds share our ability to acquire an extensive vocal repertoire by imitation, and it turns out that birdsong learning has many instructive similarities to human language learning (see Bolhuis et al., 2010). As already mentioned, both are compelling examples of interactions between experience and species-typical predispositions for learning. Like human babies, songbirds imitate species-typical vocalizations which they hear early in life, at first crudely in a period of subsong analogous to babbling. The brain circuits involved in song learning and production are well understood and have some instructive parallels to those involved in language. In evolutionary terms, the many similarities between birdsong and speech development are not homologies between birds and humans but analogies (i.e., not descended from a common ancestor but convergently evolved), likely reflecting basic constraints on the control and development of complex vocal signals.

The topic of communication thus brings us back to where we began in Chapter 1, with Darwin's claim that human "mental powers" differ in degree and not in kind from those of other animals. In this chapter we seem to have uncovered one "difference in kind," namely the presence in humans of the ability to acquire and use language, a "mental power" that Darwin also pondered (see Seyfarth & Cheney, 2010). Full-blown theory of mind seems to be another candidate, along with a motivation to cooperate in certain ways. Contemporary discussions of Darwin's claim are a major subject of Chapter 5.

Suggestions for Further Reading

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