3   The Evolution of Concepts about Agents: Or, What Do Animals Recognize When They Recognize an Individual?

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3.1   Introduction

We now know that the mind of a human infant is neither a blank slate nor, in William James's words, "one great blooming, buzzing confusion" (1890, 462). Instead, infants are born with what Carey (2010, 2011) has called a set of "innate, representational primitives" (2011, 113) that guide infants' learning and their expectations of how objects are likely to behave. Three *core systems* of knowledge have been suggested, each specialized for representing and reasoning about entities of different kinds (Carey and Spelke 1996). One core system deals with the causal and spatial relations among objects, another concerns number, and a third deals with agents. Here, we focus on core systems of knowledge about agents—their goals, attentional states, and the causal mechanisms that underlie their behavior.

The prevalence in human infants of a core system of knowledge about agents suggests that at some point in our evolutionary history, a predisposition to recognize certain entities in the world as capable of self-generated motion, with goals and the motivation to achieve them (Carey 2011; Frith and Frith 2012), gave some individuals a fitness advantage over others. In modern humans, the advantages to be gained from this style of thinking are obvious. How might it have benefited our nonhuman, prelinguistic ancestors?

Old World monkeys live in societies where survival and reproduction depend on social skills. To succeed, an individual must be able to predict the behavior of others, and to do this she must understand their social relationships. Here we propose that the demands of social life have favored individuals who can recognize other animals' social attributes and treat these properties as inextricable parts of an individual's identity. To illustrate our argument, we focus on female baboons and their recognition of other individuals' dominance rank and kinship.

Rank and kinship, we suggest, are examples of social concepts—baboons' representational primitives. Recognizing these attributes in others, however, poses a problem because there are no overt, physical markers of a female's social position. Instead,

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animals acquire this knowledge by observing other individuals' social interactions and learning the statistical regularities associated with them. Knowledge of other animals' rank and kinship, among their other attributes, permits baboons to predict how those animals are likely to behave when interacting with other group members. We can see in the social cognition of baboons the evolutionary origins of our theory of mind, our concepts about agents, and our inclination to classify other individuals in part according to both their social relationships and the intentions we attribute to them.

3.2   Individual Recognition

Individual recognition is widespread in animals (Tibbetts and Dale 2007). Many species have specialized brain cells that respond particularly strongly to faces (Tsao et al. 2006; Leopold and Rhodes 2010), voices (Petkov et al. 2008), and familiar speakers (Belin and Zattore 2003). Although such recognition has most often been documented in the auditory mode through playback experiments (e.g., Cheney and Seyfarth 1980; Rendall, Rodman, and Emond 1996), subjects in these experiments often seem to be engaged in more complex cross-modal or even multimodal processing. A baboon who looks toward the source of the sound when she hears her offspring's call (Cheney and Seyfarth 2007) acts as if the sound has created an expectation of what she will see if she looks in that direction.

The first evidence that animals might integrate multiple cues to form a representation of an individual came from work by Johnston and Bullock (2001) on hamsters. Golden hamsters have at least five different odors that are individually distinctive. In a typical experiment, a male familiar with females A and B was exposed (and became habituated to) the vaginal secretions of female A. He was then tested with either A's or B's flank secretions. Males tested with A's flank secretions showed little response (across-odor habituation); however, males tested with B's flank secretions responded strongly. The authors concluded that "when a male was habituated to one odor he was also becoming habituated to the integrated representation of that individual" (Johnston and Peng 2008, 122) and was therefore not surprised to encounter a different odor from the same animal. Hamsters, they suggested, have an integrated, multiodor memory of other individuals. Recent experiments indicate that direct physical contact with an individual—not just exposure to its odors—is necessary for such memories to develop (Johnston and Peng 2008).

But what about the representation of individuals across sensory modalities? Dogs (Adachi, Kuwahata, and Fujita 2007) and squirrel monkeys (Adachi and Fujita 2007) associate the faces and voices of their caretakers, rhesus macaques spontaneously match the faces and voices of familiar conspecifics and familiar humans (Adachi and Hampton 2011; Sliwa et al. 2011; Ghazanfar et al. 2005), and both horses and crows associate the vocalizations of a familiar group member with the sight of that individual

(Proops, McComb, and Reby 2009; Kondo, Izawa, and Watanabe 2012). Humans, of course, routinely integrate the perception of faces and voices to form the rich, multimodal concept of a person (Campanella and Belin 2007).

Supporting these behavioral observations, neurophysiological data reveal extensive connections between auditory and visual areas in mammalian brains (Cappe and Barone 2005), particularly between those areas involved in the recognition of voices and faces among rhesus macaques (Ghazanfar and Logothetis 2003; Ghazanfar et al. 2005; Sliwa et al. 2011) and humans (von Kriegstein et al. 2005; Blank, Anwander, and von Kreigstein 2011). These links between face- and voice-recognition areas provide further evidence, in both monkeys and humans, for a "cross-modal, cognitive representation" of individual identity (Sliwa et al. 2011, 1735).

3.3   Other Social Classifications

Many animals not only recognize individuals but also classify them into groups, organizing them according to their close social bonds, linear dominance ranks, and transient sexual relations. Baboons (*Papio hamadryas* spp.) provide some good examples.

Baboons live throughout Africa in groups of 50 to 150 individuals. Males and females have very different life histories. Males emigrate to other groups at around eight to ten years of age. Females, in contrast, remain in their natal group throughout their lives, maintaining close bonds with their matrilineal kin through frequent grooming, mutual support in coalitions, tolerance at feeding sites, and interactions with each other's infants (Cheney and Seyfarth 2007; Silk et al. 2010a). Adult females can also be ranked in a stable, linear dominance hierarchy that determines priority of access to resources. From birth, daughters acquire ranks similar to those of their mothers. As a result, the stable core of a baboon group consists of a hierarchy of matrilines, in which all members of, say, matriline B outrank or are outranked by all members of matrilines C and A, respectively. Rank relations are generally stable over time, with few reversals occurring either within or between families. When reversals do occur, however, their consequences differ significantly depending on who is involved. For example, if the third-ranking female in matriline B (B_3) rises in rank above her second-ranking sister (B_2), the reversal affects only these individuals; the B family's rank relative to other families remains unchanged. However, a rank reversal between females from different matrilines (for example, C_1 rising in rank above B_3) usually causes all members of matriline C to rise above all members of matriline B (Cheney and Seyfarth 1990, 2007). The ranked, matrilineal society of baboons is typical of many Old World monkeys.

Among baboon females, the ability to form stable, enduring social bonds can increase individuals' reproductive success. At two long-term study sites in Kenya and Botswana, females had highly differentiated relationships with other females in their group. Some pairs—usually but not always matrilineal kin—interacted often, maintaining close

bonds that lasted for many years, while others interacted infrequently. Those with the most stable, enduring relationships had higher offspring survival (Silk, Alberts, and Altmann 2003, Silk et al. 2009) and lived longer (Silk et al. 2010b) than females with weaker relationships. High dominance rank also had a significant effect on longevity but was a less powerful predictor than relationship quality.

Baboons, then, are born into a social world that is filled with statistical regularities: animals interact in highly predictable ways. Natural selection has favored individuals who can recognize these patterns, because knowing about other animals' relationships is both the best way to predict their behavior and essential to forming the kind of stable, enduring bonds that lead to high reproductive success. Field experiments have shown that, by the time she is an adult, a female baboon recognizes the close bonds among matrilineal kin (Cheney and Seyfarth 1999; see also below) and the linear rank relations both among females (Cheney, Seyfarth, and Silk 1995) and among males (Kitchen, Cheney, and Seyfarth 2005). When females hear the vocalizations of a juvenile involved in an aggressive interaction, they respond by looking at the juvenile's mother (Cheney and Seyfarth 1999; see also Cheney & Seyfarth 1980). Similarly, when baboons hear a sequence of aggressive and submissive calls that mimic a higher-ranking animal threatening a lower-ranking animal, they respond only briefly. If the calls of the participants are reversed, however, subjects respond significantly more strongly, as if the apparent rank reversal violates their expectations (Cheney, Seyfarth, and Silk 1995; a control sequence ruled out the possibility that the violating sequence evoked a stronger response simply because it was rare).

To test whether subjects classify females simultaneously according to both matrilineal kinship and dominance rank, Bergman and colleagues (2003) played sequences of calls mimicking within- and between-matriline rank reversals to subjects in matched trials. In one trial, subjects heard an apparent rank reversal involving two members of the same matriline: for example, female B_3 giving threat-grunts and female B_2 screaming. In another trial, the same subject heard an apparent rank reversal involving the members of two different matrilines: for example, female C_1 giving threat-grunts and female B_3 screaming. As a control, subjects heard a fight sequence that was consistent with the female dominance hierarchy. To control for the rank distance separating the subject and the individual whose calls were being played, each subject heard a rank reversal (either within or between family) that involved the matriline one step above her own (cf. Penn, Holyoak, and Povinelli 2008). Within this constraint, the rank distance separating apparent opponents within and between families was systematically varied.

Listeners responded with apparent surprise to sequences of calls that appeared to violate the existing dominance hierarchy. Moreover, between-family rank reversals elicited a consistently stronger response than did within-family rank reversals (Bergman

et al. 2003). Subjects acted as if they classified individuals simultaneously according to both kinship and rank. The classification of individuals simultaneously according to these two criteria has also been documented in Japanese macaques (Schino, Tiddi, and Polizzi di Sorrentino 2006).

These results are difficult to explain without assuming that, when one baboon hears another vocalize, the listener encodes information not just about the caller's identity but also about her dominance rank and family membership, among many other attributes. This encoding is immediate and occurs automatically: just as we cannot hear a word without thinking about its meaning, a baboon cannot hear a vocalization without thinking about the animal who is calling, what she looks like, and her rank and family membership. These features are an inextricable part of the caller's identity, bound together in much the same way that auditory and visual cues are bound together in a cross-modal cognitive percept. Individual recognition thus constitutes a form of *object perception* (e.g., Bregman 1990; Miller and Cohen 2010), in which a variety of disparate stimuli are linked together to form a coherent object. As a result, perception of one of the object's attributes (for example, her voice) creates a rich variety of expectations in the perceiver's mind of—for instance—what she will see when she looks toward the sound, whom the caller is likely to dominate, and who is likely to support her in an aggressive interaction. Individual recognition, then, is more than just the recognition of an individual. It includes the recognition of that individual's place in society.

3.4 Social Concepts

What mechanisms underlie animals' knowledge of the relations that exist among others? One hypothesis argues that memory and classical conditioning are entirely sufficient to explain primates' social knowledge. As they mature, baboons observe behaviors that link individuals in predictable ways. These associations, stored in memory, allow an observer to predict how others are likely to interact. According to this view, the baboons' knowledge should not be described as conceptual because, in contrast to the case among humans, we have no independent evidence for the existence of such concepts. Baboons' social knowledge is therefore best explained by relatively simple hypotheses based on learned associations and prodigious memory (e.g., Schusterman and Kastak 1998).

Explanations based on memory and associative learning are powerful and appealing under simplified laboratory conditions, but they strain credulity when applied to behavior in nature, where animals confront more complex sets of stimuli. A young baboon, for example, must learn thousands of dyadic (and tens of thousands of triadic) relations in order to predict other animals' behavior. The magnitude of the

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problem makes one wonder whether simple associations, even coupled with pro-
digious memory, are equal to the task (Seyfarth and Cheney 2001). Faced with the
problem of memorizing a huge, ever-changing dataset, humans (Mandler 1967) and
rats (Macuda and Roberts 1995) are predisposed to search for a higher-order rule that
makes the task easier. Why should other animals be any different?

In fact, several results suggest that, even if it begins with relatively simple Pavlov-
ian associations, primates' social knowledge is rapidly organized into units of thought
that resemble our concepts (Dasser 1988). Consider, for example, the speed of animals'
reactions to events. When a baboon hears a sequence of vocalizations that violates the
dominance hierarchy, she responds within seconds (Cheney and Seyfarth 2007). When
a macaque or capuchin monkey involved in a fight tries to recruit an ally, she seems to
know almost immediately which individuals would be the most effective partners (Silk
1999; Perry, Barrett, and Manson 2004; Schino, Tiddi, and Polizzi di Sorrentino 2006).
The speed of these reactions suggests that animals are not searching through a mas-
sive, unstructured database of simple, dyadic associations but have instead organized
their knowledge about individuals into categories, including what we call dominance
hierarchies and matrilineal (family) groups.

These categories share many features with human concepts. For example, they
cannot be reduced to any one, or even a few, perceptual attributes. High-ranking females
are not older or larger than low-ranking females, nor do they live in larger kin groups.
Males change dominance ranks often. Family members do not always look alike, sound
alike, or share any other physical features that make them easy to tell apart. None of
this variation, however, affects other animals' classifications: a three-legged member of
family B is still a member of family B.

Nor is the classification of individuals into family groups based on different types
or rates of interaction. The members of high-ranking families are not necessarily more
aggressive than others, nor do they feed in different areas, forage together, or groom
or play more often. In fact, grooming within families can be highly variable (Silk et al.
2010a), yet this has no effect on other animals' perception of who belongs in which
family.

Social categories, moreover, persist despite changes in their composition. Among
baboons, for instance, the recognition of a linear, transitive hierarchy persists despite
demographic changes in the individuals who occupy each rank. Linear, transitive rank
orders and matrilineal kin groups thus qualify as concepts because, in the mind of a
baboon, their existence is independent of the individuals that compose them.

Finally, the classification of individuals is a cognitive operation that affects behavior.
When a listener hears vocalizations from two individuals interacting elsewhere, her
response depends not just on the animals' identities but also on their ranks and family
membership (Bergman et al. 2003). Such data support the view that social concepts are
units of thought with causal power: they determine how individuals behave.

3.5   Concepts, Expectations, and the Attribution of Motives to Others

If the formation of social concepts is adaptive, however, individuals confront a problem because, as already noted, the entities that make up these concepts are heterogeneous. We propose that, faced with this dilemma, natural selection has favored those individuals who analyze social interactions according to causal relations between behaviors, and who categorize others at least in part according to their perceived intentions. Here are some experiments that lead us to these conclusions.

3.5.1   Rank Reversal and the Violation of Expectation

The rank reversal experiments described above (Cheney, Seyfarth, and Silk 1995; Bergman et al. 2003; Kitchen, Cheney, and Seyfarth 2005) all relied on the violation-of-expectation method: the listener responded more strongly to "D_2 threatens and B_1 screams" than to "B_1 threatens and D_2 screams" because the former sequence violated the listener's expectations about how these individuals ought to behave toward each other. But this logic holds only if the listener assumes both that B_1's scream *was caused by* D_2's threat-grunt, and that D_2's threat-grunt indicates an aggressive intent toward B_1. Without this assumption of causality, there would be no violation of expectation.

Rank reversal experiments also suggest that listeners attribute intentions and motives toward others: D_2 has aggressive intentions toward B_1, and this attribution of intent, combined with knowledge of D_2's and B_1's relative ranks, causes the strong response. By contrast, an alternative, simpler explanation makes no reference to a theory of mind: D_2's threat-grunts simply indicate impending or probable aggressive behavior toward B_1. In sections 3.5.2–3.5.4, we describe experiments designed to test between these two hypotheses. In section 3.5.5, we review some of the relevant neurophysiological data.

3.5.2   Judging the "Directedness" of a Vocalization

Primates are constantly required to make judgments about other animals' intentions. This demand is particularly striking in the context of vocal communication, when listeners must make inferences about the intended recipient of another animal's calls. Primate groups are noisy, tumultuous societies, and an individual could not manage her social interactions if she assumed that every vocalization she heard was directed at her. Of course, listeners can often draw inferences about the intended target of a vocalization from the direction of the caller's gaze; however, such cues are not always available. Even in the absence of visual signals, monkeys are able to make such inferences based on their knowledge of a signaler's identity and the nature of recent interactions.

In one study, for example, subjects heard an aggressive threat-grunt from an individual shortly after they had either exchanged aggression or groomed with that individual. Subjects who heard a female's threat-grunt shortly after grooming with her ignored the call: that is, they acted as if they assumed that the female was threatening

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another individual. But subjects who heard the same call after receiving aggression responded strongly: they acted as if they assumed that the call was directed at them and signaled further aggression (Engh et al. 2006). This result could not be explained by a simple contingency judgment, since the prior event—the vocalization—was the same in each case. Nor could results be explained by assuming that any prior interaction with individual X "primed" subjects to expect further interaction with X, because prior aggression and prior grooming affected the subjects' responses to the vocalization in different ways. Finally, the effects of prior behavior were specific to the subject's former partner: hearing the partner's threat-grunt did not affect the subject's behavior toward other, previously uninvolved individuals. The simplest explanation would seem to be that female baboons make inferences about the target of a vocalization even in the absence of visual cues, and that the nature of prior interactions creates an expectation on the part of the subject—an expectation that is based on the attribution of intentions to another. After a fight, the subject assumes that her rival has aggressive intentions toward her; after grooming, she draws the opposite conclusion (Cheney and Seyfarth 2007).

3.5.3   Judging the Intent to Reconcile

Tests of *reconciliatory* grunting in baboons provide further suggestion that listeners' responses to vocalizations depend not only on the identity of the caller but also on their assessment of the caller's motives and the intended target of the call. In many species of primates, aggressors will occasionally "reconcile" with their victims by extending a friendly gesture toward them shortly after the fight. Among baboons, reconciliation most commonly occurs in the form of a grunt. Grunts are signals of benign intent; they lower the probability of subsequent aggression and facilitate friendly interactions (Cheney, Seyfarth, and Silk 1995; Silk, Cheney, and Seyfarth 1996). In one playback experiment, a female baboon that had recently been threatened heard within minutes either the grunt of her aggressor or the grunt of another dominant female unrelated to her aggressor. After hearing her former aggressor's grunt, the female was more likely to approach her aggressor and to tolerate her aggressor's approach than after hearing the grunt of the other, uninvolved dominant female. She acted as if she attributed friendly motives to the aggressor, and therefore treated the call as a reconciliatory signal that renewed aggression was unlikely (Cheney and Seyfarth 1997).

In a subsequent experiment, victims were played the grunt of a close relative of their aggressor. In this case, too, they treated the grunt as a signal of reconciliation, responding as they would have if the aggressor herself had grunted: they were more likely to approach the aggressor or the reconciling relative and more likely to tolerate either individual's approach. By contrast, females who heard the grunt of a dominant female unrelated to the original aggressor showed no such response. Here again, subjects acted as if they assumed that the grunt by the aggressor's relative was directed at them as a

signal of benign intent, and they accepted this grunt as a proxy of reconciliation with their opponent. In other words, they acted as if they attributed some kind of shared intention to the aggressor and her relative—one that they did not attribute to the unrelated female who vocalized in the control condition (Wittig, Crockford, Wikberg, et al. 2007). The alternative, behaviorist explanation based solely on learned contingencies seems increasingly unlikely. If, after receiving aggression from B_1, subjects respond as if they expect further aggression from B_1 (Engh et al. 2006), but after receiving aggression from B_1 and hearing a grunt from B_2, subjects respond as if they expect no further aggression from B_1 (Wittig, Crockford, Wikberg, et al. 2007), the difference cannot be based on B_1's prior reconciliatory behavior because B_1 has not reconciled. The difference can only be explained if we assume that subjects have different expectations—or ascribe different motives—to B_1.

3.5.4   Judging the Intention of Alliance Partners

Finally, in a test of *vocal alliances* among baboons, a subject who had recently been threatened by a more dominant female heard either the aggressive threat-grunt of a close relative of her opponent or the threat-grunt of a female belonging to a different matriline. Subjects responded more strongly in the first condition, avoiding both the signaler, the original antagonist, and other members of her family for a significantly longer time than in the control condition (Wittig, Crockford, Seyfarth, et al. 2007). Once again, subjects changed their behavior toward another individual based on an interaction not with the individual herself but with one of the individual's close kin. Subjects acted as if they attributed some kind of shared intention to closely related individuals—a motivation that they did not attribute to others who belonged to different matrilines.

3.5.5   The Attribution of Motives

When deciding "Who, me?" upon hearing a vocalization, baboons must take into account the identity of the signaler (who is it?), the type of call given (friendly or aggressive?), the nature of their prior interactions with the signaler (were they aggressive, friendly, or neutral?), and the correlation between past interactions and future ones (does a recent grooming interaction lower or increase the likelihood of aggression?). Learned contingencies doubtless play a role in these assessments. But because listeners' responses depend on simultaneous consideration of all these factors, it seems likely that these assessments are also based at least in part on inferences about other individuals' motives and intentions.

Neurobiological research supports this hypothesis. In both monkeys and humans, the perception of gaze direction and goal-directed behavior appear to activate the same areas of the brain, including the superior temporal sulcus (STS) and the amygdala. The STS is particularly sensitive to the orientation of another individual's eyes (Jellema

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et al. 2000; Emery and Perrett 2000). Mutual gaze evokes greater activity in the STS than does averted gaze, suggesting that the STS facilitates the processing of social information (Pelphrey, Viola, and McCarthy 2004). In both monkeys and humans, STS also responds to goal-directed actions and perceptions. Cells in monkeys' STS show particularly increased activity to goal-directed hand movement when the actor they are observing is gazing at his or her hand (Jellema et al. 2000; Lorincz et al. 2005). It therefore seems possible that STS may be involved in representing what others see and what their actions and intentions are (Gallagher and Frith 2003). Similarly, in both monkeys and humans. the amygdala responds strongly to social stimuli, particularly aversive ones. It also seems to be important for processing information about gaze direction (Adolphs, Russell, and Tranel 1999; Kawashima et al. 1999; Fine, Lumsden, and Blair 2001; Santos, Flombaum, and Phillips 2006).

Other areas of monkeys' brains seem to be sensitive to the intentions that underlie behavior. As in humans, *mirror* neurons in the inferior parietal lobule (IPL) of monkeys' brains are activated both when a monkey performs a specific action and when it observes someone else performing that action. Furthermore, neurons that code for specific acts, such as grasping, seem to be context dependent. Some mirror neurons in monkeys respond more when they grasp a piece of food to eat it than when they grasp the same food to place it into a container. This same context dependence is preserved when monkeys observe *another* individual performing these actions. Significantly, many neurons begin to fire *before* the other individual actually performs a specific action—that is, before grasping to eat as opposed to grasping to place. Thus, it seems possible that these neurons encode not only the specific motor act but also the actor's intentions (Fogassi et al. 2005; see also Nakahara and Miyashita 2005; Rizzolatti and Craighero 2004; Rizzolatti and Buccino 2005). These results are perhaps not surprising, given the benefits of being able to predict what others are going to do.

Furthermore, like the behavioral evidence for cross-modal visual-auditory recognition, the behavioral evidence for the simultaneous recognition of identity and motives receives support from the neurophysiological literature. In humans, one region of the fusiform gyrus, the fusiform face area (FFA), is more engaged by human faces than by any other visual stimulus (Kanwisher, McDermott, and Chun 1997; Kanwisher 2000). While the FFA was originally thought to be activated only by faces, however, some recent studies have shown that this activation depends on other factors, including the attribution of motives to the stimuli involved. Healthy adults showed heightened FFA activation when they were asked to observe three geometric figures engaged in "movements intended to suggest a sense of personal agency" and "interactions that were meant to be easily interpreted as social" (Schultz et al. 2003, 417). Subjects were then asked to state when the "interaction" was friendly or not. Activation of the FFA was therefore not restricted to faces but limited instead to those stimuli that had an animate, social character. The authors conclude that the fusiform gyrus and FFA encode

information not only about facial identity but also about the "semantic attributes of people because of repeated perceptual experiences with faces that occur during social interactions" (Schultz et al. 2003, 423). Making much the same argument as we have here, the authors speculate that "the nature of the information stored in the FG might … [include] anything that would be helpful in defining faces. … There would be a measure of efficiency from this arrangement … that is, having representations and computations of more abstract attributes of people interdigitated with front-end perceptual processes about physical attributes" (Schultz et al. 2003, 423–424). Farah and Heberlein (2010) review evidence that the human brain contains a dedicated system for representing "the appearance, actions, and thoughts of people" that is innate, autonomous, and functions with a great deal of automaticity. This is just what we would expect to find if natural selection had acted strongly throughout primate evolution to favor a brain and perceptual system that innately, simultaneously, and automatically merged information about an individual's identity and motives.

In all the baboon experiments just mentioned, baboons that heard a vocalization rapidly assessed the type of vocalization and the identity of the caller, and integrated this information with their memory of recent events and their knowledge of the relationships among all the individuals involved. Based on these data, they appeared to attribute motives to the participants and to judge the motives of different individuals to be similar or different. When dealing with individuals perceived to share motives (typically matrilineal kin), they responded in particular ways; when dealing with individuals perceived not to share motives (usually unrelated animals), they reacted differently. If the call was aggressive and came from a relative of an individual with whom the listener had just fought, the call appeared to create in the listener's mind the expectation of an alliance directed against her, because the opponent and the caller, being members of the same kin group, were assumed to have similar motivations and were expected to act in concert. The listener therefore moved away. By contrast, if the call was aggressive and came from an individual who was unrelated to the previous opponent, it created no such expectation, because most alliances occur within families. Females therefore behaved as if they assumed that the call was directed at someone else.

3.6   Summary

For millions of years our ancestors lived in highly social groups where they saw, heard, and interacted with the same individuals over extended periods. Under these conditions, another animal's identity becomes inseparable from its social position and its intentions toward others. As a result, natural selection seems to have favored among baboons and other primates a perceptual system in which the recognition of an individual activates a rich cognitive network of information—about how the individual

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looks and sounds, its dominance rank, its family membership, and its motivation to behave toward specific others in particular ways. Individual recognition thus constitutes a form of object perception, in which many different stimuli are bound together to create a single coherent object—the individual—who behaves in predictable ways toward other objects or individuals. In baboons, the predictable ways are defined in part by the rules of close bonds among matrilineal kin and a linear dominance hierarchy. The object perception of others has been shaped by natural selection to be automatic, effortless, and accurate—if it were not, the individual could not succeed in its social environment.

To achieve these goals, natural selection has favored in baboons a mind that organizes data on individuals according to concepts—in the baboons' case, concepts that we humans label with names like *matrilineal family* and *linear dominance rank order*. The baboons have no such names, but they do have the concepts. Not explicit concepts, of course—we have no evidence that baboons can attach labels to different social relations, or that they are consciously aware of kin categories or their own knowledge of them—but implicit knowledge about which animals go together, how they are likely to interact, and the extent to which their motives are shared. Young children exhibit implicit knowledge when they learn and remember facts but cannot explain how they came to know them. When three-year-old children, for example, were shown the contents of a drawer, they could easily recount the drawer's contents at a later date, but they could not explain how they acquired this knowledge—they explained that they "just knew," or that they had always known what was in the drawer (reviewed in Nelson 2005). Children's knowledge at this age, like that of the baboons', is implicit, not explicit, but no less effective for all that.

3.7   Implications

3.7.1   For Research on Theory of Mind

There is at present some controversy over the extent of a theory of mind in animals. Much of the debate focuses on whether apes can attribute knowledge or false beliefs to others (Call and Tomasello 2008). There are, however, many more rudimentary ways in which animals might attribute a mental state to another, and some of these attributions may be considerably more widespread in the animal kingdom.

Baboons and other monkeys do not seem able to attribute knowledge or beliefs to each other (Cheney and Seyfarth 2007). They do, however, seem to attribute motives and intentions, as illustrated by the many experiments reviewed here. Indeed, there is growing evidence that many animal species routinely attend to other individuals' visual attention and intentions (e.g., Flombaum and Santos 2005; Bugnyar and Heinrich 2005; Burkhart et al. 2012; MacLean and Hare 2012), and even distinguish deliberate acts from accidental ones (e.g., Buttleman et al. 2007). Like young children

(Repacholi and Gopnik 1997), monkeys appear to attribute likes, dislikes, and intentions to others despite their failure to appreciate more complex mental states.

3.7.2   For Research on the Perception of Group Membership

Among social psychologists. there is considerable interest in the ways in which humans classify others into groups, because such classifications may lead to stereotypes, prejudice, and conflict (e.g., Brewer 1999; Spelke and Kinzler 2007; Fiske 2010). What are the origins of this tendency? It has been known for years that birds (Brooks and Falls 1975), primates (Cheney and Seyfarth 1982; Cheney 1987), and many other species recognize individuals outside their own group and associate them with particular areas. Conflict between groups, sometimes lethal, is well documented among hyenas (Smith et al. 2010), lions (Mosser and Packer 2009), and chimpanzees (Mitani, Watts, and Amsler 2010). Mahajan and coauthors (2011) add to this literature by showing that semi-free-ranging rhesus monkeys associated a novel object with a specific social group and appeared to attach a positive valence to members of their own group but a negative valence to members of a neighboring group. These distinctions between the members of one's own versus the members of another group could, however, be based on familiarity versus unfamiliarity, rates of interaction, or association with a particular range or territory.

The experiments reviewed here indicate that classification of others into distinct social units is ubiquitous in the everyday life of baboons, and indeed is essential for the formation of social bonds, offspring survival, and longevity. This classification occurs among individuals who live in the same group, range over the same area, see each other every day, and interact with each other often. Perhaps most important for those interested in comparison with humans, a baboon's classification of others seems to be based at least in part on the intentions she attributes to them—specifically, how she expects them to behave toward her and toward each other.

3.7.3   For Neurophysiological Studies of Primate Cognition

We have argued that a variety of information is bound together in the perception of primate vocalizations: information about the caller's identity, appearance, social relationships, and behavioral intentions. This view is consistent with the hypothesis that object knowledge—in both monkeys and humans—"may be represented in multiple cortical areas that store information about different object attributes, such as form … and motion" (Chao and Martin 2000, 478; see also Mahon and Caramazza 2009; Coutanche and Thompson-Schill 2013). If this hypothesis proves correct, and if similar mechanisms underlie the recognition of objects and individuals, then it should be possible to identify areas in the brain that are specialized not only for the identification of familiar voices, faces, and their integration but also for the identification of appropriate social interactions or, conversely, the detection of interactions that violate the social

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order. The recent paper by Kumaran, Melo, and Emrah (2012) represents a first step in this direction.

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