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# BABOON

METAPHYSICS

*The Evolution of a Social Mind*



SEVEN

## The Social Intelligence Hypothesis

If I be asked by what power the creator has added thought to so many animals of different types, I will confess my profound ignorance.

CHARLES DARWIN, 1838: NOTEBOOK C

Does the social intelligence of primates make them smarter than other animals? During the 18th and 19th centuries, both before and after the publication of *The Origin of Species*, scholars debated the merits of different animal minds. At issue was the general question of whether species should be ranked according to their utility to humankind or some other standard (Ritvo 1987). Mental ability seemed a compelling criterion for ranking animals, but even with their admittedly large brains the monkeys and apes did not always come out on top. Some scientists favored the orangutan, whereas others, like George Romanes (1881), argued for the “high intelligence” and “gregarious instincts” of the dog, which gave it a “more complex” psychology than monkeys. In 1883, Arabella Buckley, a friend of A.R. Wallace, published a children’s book entitled *The Winners in Life’s Race: or, The Great Backboned Family* in which she classified monkeys and apes with insectivores and rodents, rather than at the head of the animal kingdom. The “degenerate gorilla” was described as “equal neither in beauty, strength, discernment, nor any of the nobler qualities, to the faithful dog, the courageous lion, or the half-reasoning elephant” (Buckley 1883; Ritvo 1987).

## The social intelligence hypothesis

As we saw in Chapter 2, the notion that baboons' intelligence evolved to solve social problems first appeared in the idiosyncratic writings of Eugene Marais, who alone among his contemporaries observed baboons in their natural habitat. Years later, in 1953, the social intelligence hypothesis reappeared when the British psychologist Michael Chance suggested, on the basis of observations made at the London Zoo, that the near-continuous sexual receptivity of primate females created complex problems in behavioral control and social awareness for males. He postulated that "the enlargement of the neocortex is an anatomical adaptation to [these] circumstances" (Chance and Mead 1953:433). The idea lay dormant for thirteen years. In 1966, the hypothesis was reintroduced by Alison Jolly, one of the first scientists to study primates in their natural habitat. Jolly took a broader perspective than Chance, arguing that "the social use of intelligence" is crucially important to both male and female primates, and that "social integration and intelligence probably evolved together, reinforcing each other in an ever-increasing spiral" (Jolly 1966:504). But Jolly's hypothesis, like Chance's, was largely ignored by a psychological community that believed primate intelligence was best studied by presenting single animals in cages with problem sets comprised of blue squares and red triangles.

The modern renaissance of the social intelligence hypothesis began in 1976, when Nick Humphrey published a short paper entitled "The social function of intellect." Echoing Darwin, Humphrey argued that evolutionary biology and psychology could be combined to reveal the selective factors shaping the evolution of intelligence. He began by noting that natural selection is ruthlessly economical: traits, particularly energetically costly ones, do not evolve unless they serve some function. Years of laboratory testing had shown that monkeys and apes "possess impressive powers of creative reasoning." So what, precisely, were the demands of natural life that had made these animals so clever? Humphrey proposed that "the higher intellectual faculties of primates have evolved as an adaptation to social living" (1976:316) (Fig. 26).

The social intelligence hypothesis does not argue that baboons and other monkeys have little knowledge about their home range, the spatial and temporal distribution of trees, or the behavior of their predators. Indeed, a rigorous comparison of "social" and "nonsocial" skills would be difficult precisely because the two are inextricably entwined. A baboon's ability to acquire the most nutritious food depends, simultaneously, on



Figure 26. A young Sylvia sits next to her mother, Stroppey. Photograph by Joan Silk.

both her ecological knowledge of plants and her skill in competition with others. Her ability to detect and evade predators depends, simultaneously, on both her knowledge of predator behavior and her ability to live cooperatively in a large group, where she benefits from predator detection and defense. Instead, the hypothesis argues simply that all group-living animals confront a multitude of social problems, and that intelligence in primates—and perhaps many other species—must have evolved at least in part because natural selection has favored individuals who are skilled at solving these problems.

Below we review three kinds of evidence that support the social intelligence hypothesis. We then consider several kinds of evidence that might lead us to modify it and reconsider whether primates are unique among animals in their ability to monitor, or eavesdrop upon, other individuals' social relationships.

## Social complexity and brain size

Ethological studies have repeatedly shown that natural selection acts on both behavior and the neurological structures that support it. If a nutcracker can improve its survival by hiding pine seeds in the fall and recovering them during the winter, natural selection will simultaneously



favor behavior like hiding and searching and an enlarged hippocampus, the area of the brain devoted to spatial memory. Signs of the coevolution of behavior and brain morphology are clearly evident when we compare closely related species. Nutcrackers rely more on stored seeds than do their close relatives, scrub jays (*Aphelocoma californica*), and the nutcracker's hippocampus is correspondingly larger (Kamil et al. 1994).

The coevolution of behavior and brain morphology can also be seen when we compare males and females in certain species. In North American and European songbirds, where males do most of the singing, males also have much larger song control areas in their brains than do females (reviewed in Brenowitz and Kroodsma 1996). But in many tropical songbirds, where males and females sing equally, the sizes of male and female song control areas are more alike (Brenowitz and Arnold 1986). Song control areas in the brain have thus coevolved with behavior. Male baboons, who can increase their reproductive success by winning aggressive contests with rivals, have evolved large body size, large canines, and competitive vocal displays. Female baboons, whose reproductive success is much less influenced by fighting, have evolved neither the same morphology nor the same behavior.

Applying this logic to the social intelligence hypothesis, we might predict that species living in large, complex societies should exhibit both more sophisticated social knowledge and bigger brains than solitary species or species that live in small, monogamous groups. Alternatively, if large brains have evolved for some other reason, there should be no predictable relation between brain size, group size, and social intelligence. So why have large brains evolved? What are big brains for?

Across the animal kingdom, brain size increases with body size. Despite this common scaling principle, however, brain size-to-body weight ratios differ from one taxonomic group to another. Among mammals, primates have brains that are larger, on average, than the brains of similar-sized, nonprimate mammals.

Within the primate order, the picture is more complex. Martin (1990) uses the index of cranial capacity (ICC) as a means of comparison. The ICC is the ratio of a species' actual brain volume to that which would be expected for an animal of the same size if it were a basal insectivore—the basal insectivores being taken as a standard point of comparison. The ICC thus measures the extent to which a species diverges from the "typical" pattern for this group (see also Fuster 1997; Rilling and Insel 1999). Baboon brains average 177 cc in volume, giving them an ICC of 7.3, whereas chimpanzee brains average 393 cc, with an ICC of 8.2. Although this might suggest that all ape brains are relatively larger

than all monkey brains, there is considerable variation. The capuchin monkey (*Cebus* sp.), a New World primate, has an ICC of 11.7, whereas the gorilla, a great ape, has an ICC of 5.5. Overall, great apes closely fit the same scaling relationship as monkeys for brain:body size relations: their brain sizes are approximately what would be expected for a monkey scaled up to the appropriate body size (Martin 1990; Rilling 2006).

The brains of great apes may, however, differ from those of other primates on some qualitative, structural dimensions. Ape brains appear to exhibit a comparatively greater elaboration of the cerebellum and frontal lobes (Rilling 2006). In chimpanzees, a larger proportion of the brain is devoted to neocortex than in monkeys, which in turn have proportionately more neocortex than prosimians (Passingham 1982; Rilling and Insel 1999). Within the neocortex, ape (and especially human) brains have a particularly enlarged prefrontal cortex, an area known to be involved in many forms of abstract thought, decision making, rule learning, and reasoning about others' mental states (Deacon 1997; Fuster 1997; Rilling 2006).

Increases in the size of primate brains have come despite the fact that brain tissue is metabolically very costly. As we mentioned in Chapter 1, by one estimate the human brain uses energy at the same rate as the leg muscles of a runner during a marathon. Furthermore, large brains take a long time to develop. Monkeys experience a longer period of juvenile dependence and live longer than most other mammals of similar body size. Apes, in turn, experience a longer period of juvenile dependence and live longer than monkeys. Both of these life history traits are correlated with large brain size (van Schaik 2004). However, a prolonged period of prereproductive life is risky—you could easily die before you are able to reproduce. Large brains must therefore provide individuals with benefits that more than compensate for these costs. What are these benefits? When the question is applied to human evolution, answers typically focus on the adaptive advantages of technology (initially, stone tools) and language. But most monkeys rarely, if ever, use tools and lack language entirely, yet their brains are significantly larger than those of similar-sized mammals. At least in the case of monkeys, some other selective pressure must be at work.

Early studies found that brain weight:body weight ratios were higher in primate species with larger home ranges and larger in species that were fruit-eating or omnivorous than in leaf-eating species (Clutton-Brock and Harvey 1980; Milton 1988). These relationships suggested that fruit-eating primates face special problems in learning and memory because they depend on widely dispersed food that is ephemeral in both

space and time. Other data, however, argue against this explanation. In an analysis that involved many primate species, Barton and Dunbar (1997) showed that group size, not home range size, best predicted the size of a species' neocortex. They argued that group size is a good proxy for social complexity and concluded that primate brains have evolved in response to the demands of social life. Group size is important in part because, as we discussed in the previous chapter, the calculation of other individuals' social relationships becomes increasingly daunting as group size increases. Social competition might therefore offer one explanation for primates' unusually large brains. The hypothesis seems particularly compelling in the case of monkeys (if not apes), because monkeys rarely use tools but often live in relatively large groups.

So why do monkeys live in large groups? Some hypotheses stress the benefits of group life for predator detection and defense (e.g., van Schaik 1983), whereas others stress the need to defend food resources (e.g., Wrangham 1980). Still others suggest that both factors are important (e.g., Sterck et al. 1997). Whatever the reasons, these socioecological hypotheses propose that selection favoring large groups has resulted in societies that contain many different families, with social relationships simultaneously competitive and cooperative. This, in turn, places strong selective pressure on individuals' skills in managing social relationships.

Other hypotheses place less emphasis on group size and more emphasis on the details of primate feeding ecology. Kaplan and colleagues (2000) suggest that the need to forage in a complex three-dimensional environment for ephemeral fruit may have favored the evolution of cognitive abilities that served as preadaptations for the evolution of complex social relationships. Fruit-eating primates have relatively enlarged areas of the brain devoted to visual acuity, binocular vision, and color vision (Barton 1998). Thus, the cognitive demands of a frugivorous diet might have favored the evolution of large brains that could, in turn, support complex societies. On the other hand, it could also be argued that the need to process rapidly changing social interactions, such as those that occur during alliances, demands rapid visual processing and integration of information about individuals' behavior and gaze direction. Thus, social interactions might place just as strong, if not stronger, demands on vision and cognition.

It may never prove possible to determine whether social pressures, ecological pressures, or both drove the evolution of large brains in primates. Indeed, other selective pressures, such as social learning and technological innovations, may have exerted far greater influences, par-

ticularly in the ape and hominid lines (Reader and Laland 2002). Brain size is correlated with group size, but the causal origins of this correlation remain elusive. It even remains unclear whether primates differ from other animals in their "social intelligence."

### Brain specializations for social stimuli

Preliminary evidence in support of the social intelligence hypothesis as it applies to primates comes from the existence of brain areas specialized to deal with social stimuli. Monkeys, for example, have "face cells" in the temporal cortex that respond at least twice as vigorously to faces or components of faces (like eyes or mouths) than to other complex visual stimuli (Tsao et al. 2003, 2006). Face cells are surprisingly specialized. Those in the inferior temporal cortex (IT) seem most important for processing facial identity, whereas those in the superior temporal sulcus (STS) seem most important for processing facial expressions. IT and STS are extensively interconnected and probably share face-specific information (Weiss et al. 2002; Ghazanfar and Santos 2004). Face cells in STS respond not only to facial expressions but also to the direction of an individual's head orientation and gaze. Their response is greatest when head orientation and gaze direction are congruent, less strong when they are incongruent (Emery and Perrett 2000; Jellema et al. 2000; Perrett et al. 1992; Eifuku et al. 2004). The STS of rhesus macaques also includes neurons that fire when the monkey observes an individual walking, turning his head, bending, or extending his arm (Perrett et al. 1990). Particularly intriguing are "mirror neurons" in the inferior parietal lobule that show elevated activity both when the subject monkey executes a specific grasping action and when the monkey observes a human or other monkey execute a more or less similar grasp (Rizzolatti and Craighero 2004).

Finally, monkeys—like humans—process their own species' vocalizations in ways that are measurably different from the way they process other auditory stimuli. As is well known, most humans exhibit lateralization in their perception of speech. Because language is typically processed in the left hemisphere of the brain and the left hemisphere has its primary connections to the right side of the body, most humans are better at making rapid assessments of words and sentences when they hear them through their right ear. Their right-ear advantage disappears, however, when they are asked to identify other auditory stimuli (see Rogers and Andrews 2002 for review). Like humans, monkeys dis-

play a left-brain, right-ear advantage when processing their own species' vocalizations, but not when processing other sounds (Petersen et al. 1978; Hefner and Hefner 1984; Weiss et al. 2002; Poremba et al. 2004).

Specialized cells and unique brain mechanisms for dealing with social stimuli do not, by themselves, confirm the social intelligence hypothesis. Regardless of their degree of social complexity, all animals' brains respond selectively to stimuli produced by members of their own species. Solitary frogs respond selectively to their own species' calls, and monogamous birds respond selectively to their own species' song. But the special responsiveness of the monkey's brain to monkey voices, faces, gaze direction, and actions are just what we would expect if natural selection had acted with particular force to favor individuals skilled in solving social problems. Particularly intriguing is evidence that the STS and mirror neurons are also highly sensitive to intentional, goal-directed behavior, indicating that they may help monkeys assess other individuals' intentions. We discuss this issue further in Chapter 8.

### Social versus ecological "intelligence"

For 11 years during the 1970s and 1980s, we studied the social behavior of vervet monkeys in Kenya's Amboseli National Park (Fig. 27). Vervets

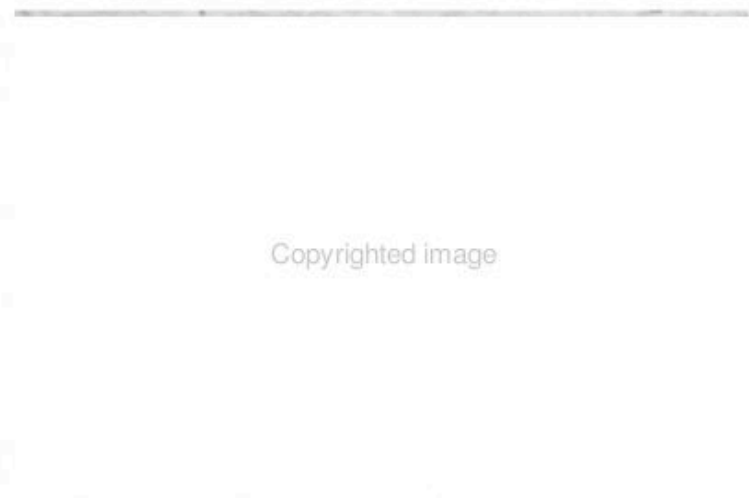


Figure 27. A matriline of vervet monkeys. Photograph by Dorothy Cheney.

live in smaller groups than baboons (10–25 on average), but their social organization is similar. Like baboons, they also display impressive knowledge of other individuals' dominance ranks and kinship relationships. They practice strategic alliances formation, curry favor with the members of high-ranking families, and keep track of who has been nice to them in the recent past (Cheney and Seyfarth 1990).

But we were equally struck by what the vervets seemed *not* to know. Take animal tracks, for example. Vervets in Amboseli regularly fall prey to pythons (*Python sebae*), large constrictors that hunt by concealing themselves in long grass or thick bush. Occasionally, though, the python's track gives away its location. When crossing open ground, pythons lay distinct, wide, straight tracks that cannot be mistaken for those of any other snake. Local humans recognize them easily, and it is relatively easy to find a concealed python by following its track.

Yet vervets seem unable to recognize that a fresh python track signals danger. On more than one occasion we watched as a vervet calmly followed a fresh track into a bush, only to leap out in surprise and alarm when it encountered the actual snake. The vervets' ignorance of python behavior was striking, because their daily life had certainly provided them with ample opportunity to watch pythons move across open areas laying down a track, and to associate this distinctive track with the animal itself. The association between a fresh track and a python was as statistically reliable as the association between two vervets in the same family who groom each other at high rates, but evidently more difficult for the vervets to learn.

Other gaps in the vervets' performance revealed that their knowledge outside the social domain was not what one would expect. Vervets are frequently attacked by leopards, which are abundant in Amboseli. Unlike other African cats, leopards carry their prey into trees, where it cannot be stolen by lions and hyenas. We had often seen vervets giving alarm calls as they watched a leopard haul the carcass of a gazelle into a tree. They clearly had the opportunity to learn that a carcass in a tree signaled the likely proximity of a leopard. But when we placed a stuffed carcass of a Thompson's gazelle (*Gazella thomsonii*) in a tree near the vervets' sleeping site before dawn, the monkeys showed no response. We might just as well have put a suitcase in the tree. It was not that the carcass was unrealistic; it did fool a tour bus operator. What was striking was that the monkeys failed even to show any curiosity about it (Cheney and Seyfarth 1985a). (We should note here that the local baboons also ignored the carcass. In fact, baboons are



not even especially alarmed when they see the carcass of a *baboon* cached in a tree by a leopard. Although they look at it with curiosity, they seem not to recognize that the carcass is associated with a leopard.)

This is not to say that vervet monkeys are oblivious to the signals provided by other species. They respond strongly to the alarm calls given by ungulates and birds, and even differentiate among the alarm calls given by birds to avian and terrestrial predators (Cheney and Seyfarth 1990). Similarly, they differentiate between the lowing of wildebeest (*Connochaetes taurinus*), which pose no threat, and the lowing of cows, which signal the approach of Maasai herders. Vervets are, therefore, not completely ignorant about their physical world. With training, they could also certainly learn to recognize the association between a python and its track, or a leopard and a carcass in a tree. But in the absence of such training they seem predisposed to attend to events in the social world in a way that they do not attend to events in the physical world. Vervets have a kind of laser-beam acuity; they make good psychologists but poor naturalists.

Such “attentive biases” are common among animals. Chickadees, for example, store seeds in the fall and, like nutcrackers, have excellent spatial memories. In one experiment, captive chickadees were trained to find food in a particular box located in an array of boxes positioned on a wall. The food might be located in a yellow box that was positioned third in line after a red box and a blue box, but before a green box. Once they had learned to choose the yellow box, the array was shifted along the wall and the boxes were scrambled. Now, say, the yellow box was first in line. When released into the aviary, most chickadees ignored both the color of the box and its relative position in the array. Instead, they flew to the box that was located at the same place on the wall where the yellow box had originally been (Brodbeck 1994). When learning which box contained food, the chickadees had apparently paid most attention to the box’s location on the wall, ignoring both its color and its relative position in the array. In contrast, juncos (*Junco hyemalis*), close relatives of chickadees that do not store food, chose the box according to its color. Chickadees are not completely oblivious to cues like color. When trained, they can learn to choose boxes according to their color. Instead, they seem biased to pay attention first and foremost to spatial cues. Other food-storing birds like nutcrackers display a similar bias (Olson et al. 1995). In a comparable way, vervets seem biased to be particularly attentive to social events.

## Critique of the argument thus far

To this point, the argument in favor of the social intelligence hypothesis, at least as it applies to primates, can be summarized as follows. Compared with other mammals, primates have larger brains relative to their body weight. Within the primate order, brain size is strongly correlated with group size. Since the complexity of an individual’s social relationships increases exponentially with increasing group size, large brains seem to have evolved in response to the demands of social life. Consistent with this hypothesis, we find that the primate brain contains many areas specialized for dealing with social stimuli, like the faces, movement, and voices of members of their own species; that baboons and other monkeys recognize each other’s dominance rank and social relationships; that female baboons’ social relationships are correlated with reduced stress and increased reproductive success; and that vervet monkeys’ knowledge of their social companions is impressive, whereas their knowledge of some ecological relations is underwhelming.

The argument can be challenged on at least four grounds. First, we have been discussing “intelligence” in primates and other animals without any attention to the behaviorists’ critiques mentioned in the last chapter. Knowledge of other individuals’ relationships might be acquired through relatively simple associative processes—processes that could easily be duplicated by even small-brained species.

Second, because primates have relatively larger brains than other species and large brains are presumed to have evolved to deal with social complexity, it follows that primate societies must in some fundamental way be more complex than those of other species. But we have thus far presented no evidence to support this view. Dolphins (*Tursiops truncatus*), elephants (*Loxodonta africana*), spotted hyenas (*Crocuta crocuta*), and pinyon jays (*Gymnorhinus cyanocephalus*)—to name just a few species—also live in complex societies comprised of multiple families and stable dominance hierarchies. Do they too recognize and monitor other individuals’ social relationships?

Third, the argument assumes that skills in recognizing social relationships have evolved in response to the challenges of living in large groups. Yet, as we will describe, recent studies have revealed similar skills in social intelligence in solitary animals and animals living in small family groups, such as monogamous birds. How do we reconcile these data with the social intelligence hypothesis?

Finally, within the primate order, social learning, innovation, and tool use are strongly correlated with brain size but not with group size.

In particular, chimpanzees and orangutans have larger brains than monkeys and use and manufacture tools more routinely than monkeys, but live in relatively small groups. Indeed, orangutans are frequently solitary. These relationships suggest that many of the selective pressures favoring enlarged brains in apes and humans may have been technological rather than social. We reevaluate the “social intelligence” hypothesis in light of this evidence at the end of the chapter.

### Are primates different?

Primates have, on average, larger brains for their body size than other vertebrates. Dunbar (2000, 2003) argues that this came about because primate social groups are not only larger but also more complex than those in other taxa. Primate groups are typically composed of many reproductively active males and females, and individuals interact with both kin and non-kin in both competitive and cooperative contexts. Such social complexity may place strong selective pressure on the ability to recognize other individuals’ ranks and social relationships.

Some comparative tests of captive apes, monkeys, pigeons, and other animals suggest that primates are more adept than nonprimates at classifying items according to their relative relations. In oddity tests, for example, a subject is presented with three objects, two of which are the same and one of which is different, and asked to choose the object that is different. Monkeys and apes achieve high levels of accuracy, even when tested with novel stimuli (reviewed by Tomasello and Call 1997; Shettleworth 1998). In all cases, subjects’ performance suggests the use of an abstract hypothesis, because concepts like *odd* specify a relation between objects independent of their physical features. In a similar manner, the concept *closely bonded* can be applied to any two individuals and need not be restricted to individuals that look alike. Although many animals, including honeybees (*Apis mellifera*; Giurfa et al. 2001), can learn to solve “delayed match-to-sample” (pick the stimulus that is the same as the previous one) and “delayed non-match-to-sample” (pick the stimulus that is different from the previous one) tasks, primates typically learn faster and generalize more accurately to novel stimuli (e.g., Harlow 1949; Strong and Hedges 1966; Wright et al. 1984). Furthermore, primates can be taught rules about how to respond: for instance, “If the tray is green, pick the odd item; if it’s red, pick the same one.”

Baboons and chimpanzees can also learn to make abstract judgments that involve comparing one relation with another (Premack 1983; Oden

et al. 1988; Fagot et al. 2001). In one study, the language-trained chimpanzee Sarah was tested on her ability to reason analogically. When Sarah was shown a lock and a key and asked to pick the appropriate object to accompany a can and complete the same relation, she correctly chose a can opener. She therefore completed the analogy “key is to lock as can-opener is to can.” (This test will doubtless bring back dark memories to all American readers who remember the analogical reasoning portion of the SAT featuring questions like “flounder is to telephone booth as yak is to (a) democracy, (b) the Vietnamese pot-bellied pig, (c) summer, (d) Kant’s *Critique of Pure Reason*, (e) none of the above, (f) all of the above.”)

The ability to make judgments based on relations among items has been demonstrated more often in primates than in other animals, and primates seem to recognize abstract relations more readily than at least some other animals. Although it is possible to train pigeons (*Columba livia*) to recognize relations such as *same*, the procedural details of the test appear more critical for pigeons than they are for monkeys. Rather than attending to the relations among stimuli, pigeons seem predisposed to focus on the physical features of the stimuli and to form item-specific associations (reviewed by Shettleworth 1998). Similarly, in tests of transitive inference, monkeys and apes appear to acquire a representation of serial order that allows them to rank items even when some items in the list are missing (D’Amato and Colombo 1989; Treichler and van Tilburg 1996). So, for example, having learned the series  $A > B > C > D$ , monkeys have little difficulty recognizing that  $B > D$ . In contrast, many—but not all—birds seem to attend primarily to the association between adjacent pairs, which limits their ability to add or delete items from a list (von Fersen et al. 1991; Zentall et al. 1996).

Recent experiments by Earl Miller and colleagues have begun to elucidate the neural basis of abstract judgments in rhesus macaques. In a typical test, subjects first saw a picture and received a cue: as they viewed the picture they either received a drop of juice or heard a tone. Then they were shown a second picture. If they had been given juice, they were to respond only if the second picture was the same as the first. If they had heard a tone, they were to respond only if the second picture was different from the first. Thus the monkeys had to learn the abstract rule “juice drop means *same* and tone means *different*” and apply this rule regardless of what the pictures actually showed. The monkeys readily learned to do this. Underlying their behavior was neural activity in the prefrontal cortex (PFC), where individual nerve cells appeared to exhibit rule specificity. Some cells sharply increased their firing when

the *same* rule was in force, whereas others increased their firing when the *different* rule was in force. The cells' selective firing could not be explained by the physical features of the pictures because these were different in different trials. Nor could selective firing be linked to the monkeys' anticipation of their response, because at the time they received the cue and learned which rule was in force the monkeys did not yet know how they would respond. Instead, the selective neurons seemed to function in the encoding of an abstract rule (Freedman et al. 2001; Wallis et al. 2001; Miller et al. 2002). Complementing these data, recall that the relatively greater size of primate brains is particularly pronounced in the prefrontal cortex.

Taken together, these data argue that the primate brain—particularly the prefrontal cortex—and primates' cognitive skills—particularly the ability to make abstract judgments—have evolved together, presumably in response to the demands of a socially complex society. As a result, modern nonhuman primates have both larger brains and greater cognitive abilities than other animals. We might be tempted to conclude that cognitive skills in primates are qualitatively and hence fundamentally different from those in all other animals.

### Social cognition in gregarious mammals and birds

This conclusion, however, may be premature. If the ability to recognize and monitor other individuals' social relationships confers a selective advantage, we should expect to find evidence of social intelligence and increased brain size not just in primates but also in any animal species that lives in large social groups, particularly those that contain individuals of different dominance ranks and varying degrees of genetic relatedness. Conversely, selection should have acted less strongly on social intelligence and brain size in solitary species and species living in small, family groups. If true, the ability to recognize the close associates of others should be evident in nonprimate species like hyenas and dolphins and lacking or less highly developed in the less social apes, including gorillas and orangutans. Studies to test this hypothesis are only beginning to be conducted. Indeed, one of the great lacunae in cognitive studies of apes (including chimpanzees) is the absence of any research on apes' ability to monitor other individuals' social relationships.

There is, in fact, good evidence that social complexity and large brains have coevolved in nonprimate species as well as in monkeys and apes. As we mentioned earlier, primate species that live in large

groups have a relatively larger neocortex than those that are solitary or live in small groups. A similar relation is found in carnivores (Barton and Dunbar 1997), toothed whales (Connor et al. 1998; Marino 1998), and ungulates (Perez-Barberia and Gordon 2005), supporting the hypothesis that sociality has driven the evolution of large brains in many taxonomic groups. Differences in social complexity may exert their effect even in species that lack a cortex entirely. In paper wasps (*Polistes dominulus*), for example, there is a significant increase in the size of the antennal lobes and collar (a substructure of the calyx of the mushroom body in the insect brain) in females that nest colonially, with other queens, as opposed to solitary breeders (Ehmer et al. 2001). This increase in neural volume may have been favored because sociality places increased demand on the need to discriminate between familiar and unfamiliar individuals and to monitor other females' dominance and breeding status. Changes in brain size occur even within individuals, according to the size of their behavioral repertoires. The brains of queen ants are significantly smaller than those of virgin females during their nuptial flight. Queen ants are also much less socially active and much less reliant on vision (Julian and Gronenberg 2002). Clearly, therefore, neural correlates of sociality are not restricted to higher mammals.

Given their relatively large brains, it is not surprising that highly social nonprimate mammals also display sophisticated knowledge of other individuals' social relationships. When competing over access to females, male dolphins form dyadic and triadic alliances with specific other males, and allies with the greatest degree of partner fidelity are most successful in acquiring access to females (Connor et al. 1992, 1999, 2001). The greater success of high-fidelity alliances raises the possibility that males in newly formed alliances, or in alliances that have been less stable in the past, recognize the strong bonds that exist among others and are more likely to retreat when they encounter rivals with a long history of cooperative interaction.

Similarly, spotted hyenas live in baboon-like social groups made up of matrilineal units in which daughters inherit their mothers' dominance ranks (Smale et al. 1993; Engh et al. 2000). Holekamp and colleagues (1999) played recordings of cubs' *whoop* calls to mothers and other clan members. Like vervets and baboons, hyena females responded more strongly to the calls of their offspring and close relatives than to the calls of unrelated cubs. In contrast to vervets and baboons, however, unrelated animals did not look at the cubs' mothers.

One explanation for these negative results is that hyenas are unable to recognize other individuals' kin relations, despite living in social



groups that are superficially similar to those of many primates. It is also possible that hyenas are simply uninterested in the calls of unrelated cubs. In fact, hyenas' patterns of redirected aggression suggest that they do recognize other individuals' kin (or close associates). Like monkeys, hyenas sometimes "redirect" aggression toward other, previously uninvolved animals after they have been in a fight. When redirected aggression occurs, hyenas are most likely to attack a relative of their former opponent (Engh et al. 2005).

Hyenas also seem to make transitive inferences about other individuals' dominance ranks. When competing over meat, hyenas often solicit support from other individuals, and they typically solicit aid from allies that are dominant to their opponent (Fig. 28). Similarly, when choosing to join an ongoing skirmish, a hyena that is dominant to both of the contestants almost always supports the higher-ranking of the two (Engh et al. 2005). If the hyena is intermediate in rank between the two opponents, it inevitably supports the dominant. These data provide the first evidence that individuals in a nonprimate species base their decision to join an alliance on both their own and the other individuals' rank relations. Like monkeys, hyenas appear to monitor other individuals' interactions and learn about other animals' ranks from their observations.

Copyrighted image

Figure 28. Two hyenas form a coalition against a third. Photograph by Kay Holekamp.

Ultimately, the best way to test whether sociality has favored specialized cognitive skills is to conduct comparative tests on closely related social and nonsocial species, similar to the ones that have been conducted on bird species that do and do not store food. For example, Clark's nutcrackers have prodigious spatial memory for storing and recovering food and a bias to attend to spatial, rather than nonspatial, cues. But although they outperform closely related jay species in radial maze and cache retrieval tasks, they are less accurate than other jays when the tests require memory of color (Olson et al. 1995). They are also relatively inattentive to social cues.

Clark's nutcrackers are relatively asocial. Although they form monogamous groups during the breeding season, during the fall and winter they search for and store seeds alone. By contrast, their close relatives, Mexican jays (*Aphelocoma ultramarina*), live in highly structured flocks numbering several dozens of birds. In addition to storing their own seeds, Mexican jays also pilfer from the caches of others. In experiments where birds could recover seeds from sites that either they themselves had created or they had observed another bird create, nutcrackers were more accurate at recovering their own caches than at recovering other birds' caches. Mexican jays, on the other hand, were as accurate at recovering seeds from caches they had observed another bird create as ones that they had created themselves (Bednekoff and Balda 1996). Perhaps because they almost always store seeds alone, nutcrackers are not very attentive observers, and they more accurately remember what they do than what others do. For the more social Mexican jays, however, it pays to spy on your neighbor. As a result, Mexican jays attend to and remember not just what they do but also what others do (see also Lefebvre et al. 1996 for similar data on gregarious pigeons and territorial doves). We return to this interesting question in Chapters 8 and 9.

The social intelligence hypothesis predicts that species living in large social groups should be able to track other individuals' relationships and ranks more accurately than closely related species living in small family groups. Alan Bond, Al Kamil, and their colleagues tested this hypothesis on two species of jay with markedly different social organizations.

Pinyon jays are highly gregarious—they are sometimes referred to as "avian baboons." They live in stable flocks of 50 to 500 birds, each containing individuals that are linked by kinship and arranged in a linear dominance hierarchy. By contrast, western scrub jays (like nutcrackers) live either alone or in small monogamous family groups. The two species are closely related and sympatric throughout much of Colorado

and Arizona. The birds were tested on their ability to make transitive inferences—that is, to recognize that if A is dominant to B and B is dominant to C, then A must be dominant to C. Transitive inference is crucial to the recognition of relative rank in a dominance hierarchy.

In the first experiment, each bird was presented with two stimuli, A and B (denoted by different colored circles), and rewarded for selecting A. Once the bird had reached a certain level of performance, it was presented with a novel pairing, B and C, and rewarded for selecting B (note that B is the incorrect answer when paired with A, but the correct answer when paired with C). After reaching criterion on the B/C pairing, they were tested with C/D (C was rewarded), D/E (D rewarded), and E/F (E rewarded). Pinyon jays performed significantly better than scrub jays, especially as more items were added to the list.

In the next experiment, the birds were tested with nonadjacent stimuli like B and D. Both species performed well, especially on nonadjacent pairs like B/D that were drawn from the top part of the hierarchy. But when the birds were tested with nonadjacent stimuli, like D/F, toward the bottom of the hierarchy, a striking difference emerged: scrub jays responded quickly but were often wrong, whereas pinyon jays took much longer to respond but were usually correct. Apparently, during training the scrub jays had memorized each combination of pairs, whereas the avian baboons, the pinyon jays, had memorized the ranked list. As a result, although the pinyon jays seemed to have to “recite” the entire list in their heads before making a choice, they were more accurate than scrub jays at recognizing the relative relation between nonadjacent pairs (Bond et al. 2003).

A subsequent experiment has shown that pinyon jays use transitive inference to calculate their own dominance status relative to that of a stranger they have observed interacting with their group-mates. In this study, four jays were placed in each of two cages and allowed to form their own dominance hierarchies. We will call the dominance hierarchy in the first group  $A > B > C > D$  and the one in the second  $1 > 2 > 3 > 4$ . The cages were kept in separate rooms, so the jays were unfamiliar with the members of the other group. A bird (say, bird 3) was then temporarily removed from its group and allowed to witness two paired encounters (Fig. 29). In the first A dominated B; in the second B dominated 2 (note that only bird 2 was familiar to bird 3). Next, bird 3 was placed in the same cage as bird B. In all cases, bird 3 deferred to B. The bird acted as if he had made the transitive calculation “B may be subordinate to A, but he’s clearly dominant to 2. Given that 2 is dominant to me, I’d better be submissive to B.” The bird could only have made this

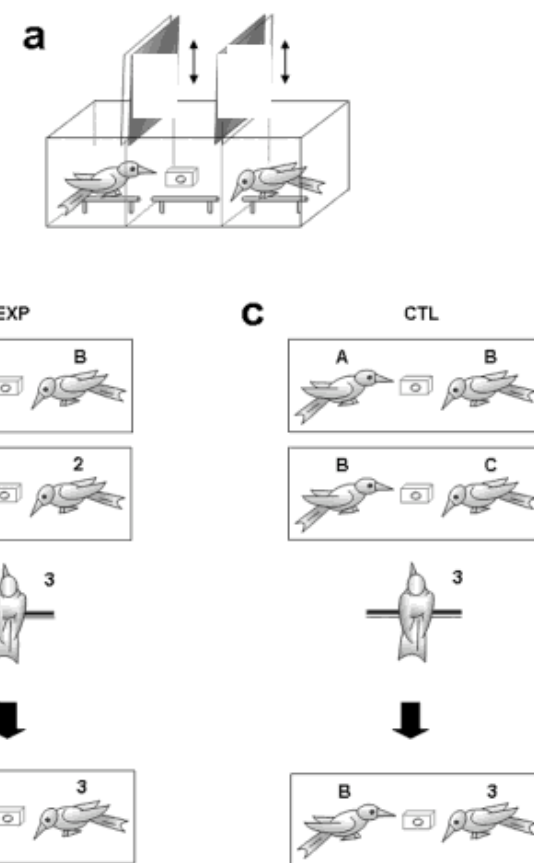


Figure 29. The protocol for tests of transitive inference in pinyon jays. (a) All dyads in two social groups were first tested in competitive interactions to establish their relative dominance ranks. In one group,  $A > B > C$ , etc. In the other group,  $1 > 2 > 3$ , etc. Next, a bird (e.g., bird 3) from one group observed a staged competitive encounter between two other contestants. If bird 3 was in the test condition (b), he observed  $A > B$  and  $B > 2$ , where only 2 was familiar to 3. If bird 3 was in the control condition (c), he observed  $A > B$  and  $B > C$ , where all three birds were unfamiliar to 3. In either case, bird 3 was then tested with bird B. Bird 3 was significantly more likely to behave subordinally to B in the test condition. Figure provided by G. Paz-y-Miño.

calculation by taking a non-egocentric perspective and recognizing the relative ranks that exist among others (Paz-y-Miño et al. 2004).

In less social settings, many gregarious species of birds and mammals can make similar relational distinctions. For example, the African



gray parrot (*Psittacus erithacus*), Alex, is reported to make explicit same/different judgments about sets of objects (Pepperberg 1992). Sea lions and dolphins have been taught to respond to terms such as *left*, *right*, *dark*, and *bright* that require them to assess relations among a variety of different objects (Schusterman and Krieger 1986; Schusterman et al. 1993; Herman et al. 1993a; Mercado et al. 2000). And a number of species, including parrots and rats, are able to assess quantities, suggesting that relatively abstract concepts of number and transitivity may be pervasive among animals (Pepperberg 1994; Church and Meck 1984; Capaldi 1993; Suzuki and Kobayashi 2000; reviewed by Shettleworth 1998).

Finally, birds and nonprimate mammals like dogs seem to be at least as adept as monkeys and apes at gleaning information from other individuals' direction of gaze, at recognizing other individuals' perspectives and motives, and at concealing their behavior from others. The ability to read other individuals' minds—if only at a very rudimentary level—constitutes a crucial component of social intelligence. We discuss this question at length in Chapters 8 and 9.

Taken together, the data from studies of dolphins, hyenas, and several species of birds raise the possibility that monkeys appear to have a greater capacity to recognize other individuals' relationships only because they have received more attention than nonprimate species living in similarly large groups. Once this imbalance in research has been redressed, the difference between primates and other animals will disappear, to be replaced by a difference that depends primarily on group size and composition.

### Social cognition in more solitary species

It is also possible that neither phylogeny nor group size has determined an individual's ability to gain information about others. There may, in effect, be no substantive differences across species in "social" intelligence. After all, much information about other individuals' social relationships can be acquired through relatively simple processes of association and transitivity. If animal A outranks B, and B outranks C, it is not too difficult to conclude that A will outrank C. Highly social species like baboons, hyenas, and pinyon jays might appear to excel in their ability to recognize other individuals' relative ranks only because their large social groups allow them to display this knowledge. Solitary animals, or animals that live in small family groups, might be just as

skilled but fail to display their knowledge because the opportunity to monitor interactions among many other individuals rarely arises.

Recent research on "eavesdropping" by birds and fish has shown that animals living in small social groups are indeed capable of acquiring detailed information about other individuals' relative dominance or attractiveness as a mate. Like their North American relatives the chickadees, great tits (*Parus major*) in Denmark form monogamous pairs in which the male defends his territory against other males by singing. When an intruder encroaches onto a male's territory, the resident typically engages in a singing contest with his rival. In great tits, dominance takes the form of interruption. If a male—either the territory holder or his challenger—feels that he can dominate his rival, he will challenge him by singing over his song. Subordinate males, in contrast, will politely remain silent when their rival is singing.

To test whether male tits acquire information about potential opponents by eavesdropping on other males' interactions, Peake and colleagues (2002) used playback experiments to simulate an encounter between a male subject and an intruder (A). A loudspeaker was placed onto the subject's territory and A's song was played. (Note that A is not a real bird, only a vocal representation of one.) When the subject answered with his own song, a computer manipulated the timing of A's response in such a way that in some contests A won the singing match, while in others the subject did. Fifteen minutes after this playback, the experimenters simulated a singing contest between A and another strange bird, B, outside the subject's territory by broadcasting A's and B's songs from two loudspeakers. In some of these simulated contests, A won the contest; in others B won. The loudspeaker was then moved back onto the subject's territory and B's song was broadcast to the subject.

If the subject had previously dominated A, and A had dominated B, the subject responded only weakly to B's intrusion. He appeared to regard B as someone who posed little threat. But if A had dominated the subject and B had dominated A, the subject responded to B's intrusion by singing at a high rate, as if he recognized that B represented a significant challenge to his territory. Subjects behaved as if they had acquired information about B's dominance relative to their own by noting B's relationship with A and integrating this information with their own experience with A (Peake et al. 2002). They behaved, in other words, as if they were guided by the transitive rule "if I can dominate A, and A can dominate B, then B is no threat to me."

Eavesdropping on the singing contests of other males allows males to assess a rival's status without engaging in a potentially costly conflict.

It also allows females to assess their mate's relative dominance. In an experiment conducted on Canadian chickadees that parallels the study on great tits, females were given the opportunity to eavesdrop on simulated singing contests between their mate and a neighboring male. In some playbacks, the mate appeared to win the contest; in others, he appeared to lose. Subsequent paternity tests on the pairs' offspring showed clearly that females were paying attention. The males who had won the simulated encounters fathered all the chicks in their nest. In contrast, the nests of males who had lost their encounters contained many chicks that had been fathered by the neighboring male (Mennill et al. 2002).

Fish, too, eavesdrop on other individuals' competitive displays when assessing their chances of beating an opponent. In one experiment, male Siamese fighting fish (*Betta splendens*) observed an aggressive interaction between two unfamiliar males from behind a transparent partition. Observers subsequently avoided the winner of the contest at a significantly higher rate than the loser, suggesting that they had gained information about the two fishes' fighting ability through their observations (Oliveira et al. 1998).

Even relatively unsocial species, then, have a sophisticated knowledge of other animals' relations. This behavior is clearly adaptive, because it allows listeners to assess a rival's skills at very little cost to themselves. As we mentioned earlier, however, it is difficult to ascertain whether the social intelligence of solitary or monogamous species is equivalent to that of more social species, because under natural conditions these less social species simply do not have the opportunity to monitor the ranks of more than two or three other individuals. Comparative tests conducted in the laboratory, like those of Bond et al. (2003) on pinyon and scrub jays, lend some support to the hypothesis that social complexity is correlated with superior performance in some cognitive tasks. But more data are needed from both natural and laboratory studies before we can make any definitive conclusions about cognitive differences between primates and other animals, or between species living in large as opposed to small groups.

### Reconciling "social" and "technological" intelligence

Finally, we must consider the possibility that large brains in apes and humans—if not in monkeys—evolved as a result of selective pressures favoring social learning and technological innovation rather than skill in social interactions. Recently, Reader and Laland (2002) accumulated

data on 116 primate species and looked for evidence of innovation (defined as apparently novel solutions to environmental or social problems), social learning (the acquisition of information from others), and tool use. They assumed that the frequency of such behaviors, corrected for the amount of time that had been devoted to studying each species, would provide a useful measure of a species' behavioral flexibility and that behavioral flexibility is a good measure of intelligence. They found significant positive correlations between brain size and all three behaviors. There was also a close relation between innovation and social learning. Group size, however, was not closely related to any of these behaviors. The lack of a strong correlation between group size and innovation was due primarily to three primates: New World capuchin monkeys, chimpanzees, and orangutans (Fig. 30). All three have large brains, use tools in a variety of contexts, but live in comparatively small groups—in the case of orangutans, sometimes no group at all. These correlations suggest that tool use and behavioral flexibility, not the complexity of social groups, have driven brain evolution in apes and humans (Reader 2003; for a similar argument, see Kaplan et al. 2000; van Schaik 2004).



Figure 30. As her infant looks on, a chimpanzee in the Tai Forest of the Ivory Coast uses a rock to crack open a palm nut. Photograph by Roman Wittig and Cathy Crockford.



Reader and Laland's results remind us that ecological and social skills are difficult to distinguish in present-day species and unlikely to have played entirely separate roles during evolution. Social learning, after all, can help individuals to acquire food, and tool use can have social as well as ecological benefits. Jane Goodall (1968), for example, describes a male chimpanzee who rose in rank after he learned to bang together garbage can lids in dominance displays. Because innovation and tool use are highly dependent on social learning, perhaps the most appropriate conclusion to make is that "social" and "technological" intelligence should not be contrasted as alternatives, but as selective forces that are inextricably linked. In any case, the absence of any data on apes' knowledge of other individuals' social relationships makes it impossible to contrast the two sorts of intelligences in apes.

Another hypothesis—first proposed by Alison Jolly (1966) and one to which we return to at the end of this book—argues that the technological and innovative skills that we see in rudimentary form among chimpanzees (and hyperbolically so in humans) have their roots in the selective forces that originally favored the evolution of social skills. Technological innovations require planning and the kind of "what-if" contemplations that can arise only through introspection. The propagation of innovative technology demands, in turn, the ability to recognize other individuals' goals and motives, to imitate, and in at least some cases also to teach. Chimpanzees routinely manufacture and use simple tools. They also show evidence of planning and imitation. Baboons and other monkeys rarely if ever manufacture tools, but they may have a limited capacity to access and monitor their own knowledge and to attribute mental states to others (Chapters 8 and 9). Indeed, inferences about other individuals' intentions—or at least their intention to behave in certain ways—guide almost every component of baboons' social behavior, including especially their vocal communication. In addition to placing computational demands on their participants, therefore, social groups may require individuals to make inferences about other group members' intentions and to plan alternative scenarios for future behavior. It seems highly plausible, as Reader and Laland suggest, that the "ability to learn from others, invent new behaviors, and use tools may have played pivotal roles in primate brain evolution" (2002:4436). It also seems likely, though, that these skills piggybacked and built upon mental computations that had their origins in social interactions.

## Are monkeys different from other animals?

What, then, are the differences between monkeys' social knowledge and that of other species? The short answer is that we just do not know. It is now clear that gregarious species like hyenas and pinyon jays recognize other individuals' relative ranks; hyenas may also recognize other individuals' kin. In their basic knowledge of others' ranks and kinship relations, therefore, there may not be many differences between monkeys and nonprimates. However, there are at least five other components of baboons' (and by extension, other monkeys') social knowledge that have not thus far been documented in birds or nonprimate mammals, and which might yet reveal qualitative differences.

First, baboons are able to track short-term changes in the status of transient relationships like sexual consortships (Chapter 6). Although it seems likely that other animals are also capable of monitoring transient social relationships, the necessary experiments have not yet been conducted.

Second, monkeys appear to classify other group members simultaneously according to both their individual attributes (like rank) and their membership in higher-order groups (like matrilineal families) (Chapter 6). The ability to classify others into hierarchical categories allows baboons to take into account other individuals' rank and kinship at the same time. Although animals such as hyenas, elephants, and dolphins may live in groups with similarly nested hierarchical structures, we do not yet know whether nonprimate animals make the same simultaneous assessments.

Third, although female baboons group other females into matrilineal, or "equivalence classes" (Schusterman and Kastak 1998), they nonetheless recognize the members of a matriline as distinct individuals who are not mutually substitutable. Recall, for example, that when female baboons hear the reconciliatory grunt of their opponent's kin, they change their disposition toward their opponent and that relative but not toward other members of the opponent's matriline (Chapter 6). Reconciliation is specific to the opponent and the relative whose grunt they hear. Future research may (or may not) show that other animals make the same subtle distinctions within members of the same equivalence class.

Fourth, in treating the grunts of their opponent's relative as a proxy for reconciliation with the opponent herself, baboons show that they assume that the grunt is directed *at them* and is causally related to the dispute. They make this causal inference even though they have not interacted with the signaler. Whether or not other animals are capable

of making similar indirect causal inferences when evaluating social signals remains to be determined.

Finally, baboons seem almost irresistibly compelled to recognize other individuals' social relationships, even when these social relationships involve the members of another species. Dogs herd sheep and goats, but it is not known whether even breeds like border collies, which have been specifically selected as herders, are as skilled as the baboon Ahla in recognizing the mother-offspring relationships among their charges (Chapter 2). Perhaps the best way to answer these questions will be to rear dogs, hyenas, dolphins, and pinyon jays with goats, and then sit back to see whether they can resist the temptation to reunite kids with their mothers.