III Evolutionary Roots of Empathy

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6 Empathy in Primates and Other Mammals

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Definitions of empathy commonly emphasize two aspects, which are the sharing of emotions and the adoption of another's viewpoint. Empathy allows the organism to quickly relate to the states of others, which is essential for the regulation of social interactions, coordinated activity, and cooperation toward shared goals. Even though the cognitive capacity of perspective-taking assists in this, it is secondary. This is even true for our own species, as Hoffman (1981, 79) noted: "Humans must be equipped biologically to function effectively in many social situations without undue reliance on cognitive processes."

In the scientific literature, however, a mentalistic definition, closer to theory-of-mind, has become popular. Accordingly, empathy is a way of gaining access to another's mind by pretending to imagine yourself in their situation. For example Goldman (2006) sees empathy as a combination of simulation and projection: inside its own head, the subject simulates how it would feel being in the other's situation and proceeds to assign mental states of its own to the other. Similarly, Baron-Cohen (2005, 170) describes empathy as involving "a leap of imagination into someone else's headspace." Most of these definitions sound so cognitively demanding that it is hardly surprising that until recently animal empathy was rarely considered.

But what if the beginnings of empathy are simpler? What if it does not require the subject to sort through information gained from the other as well as digging inside itself to arrive at an evaluation of what might be going on with the other? What if subjects share in the other's state of mind via bodily communication? The immediacy of the empathic response hints at this possibility. If we see a child fall and scrape its knee, we flinch, and exclaim "ouch!" as if what happened to the child happened at the same instant to ourselves. This was already known to Theodor Lipps (1903), who developed the concept of empathy and aptly called it *Einfühlung* (German for "feeling into"). We are in suspense watching a high-wire artist, Lipps wrote, because we vicariously enter his body and thus share his experience. It is as if we are on the rope with him. We obviously cannot feel anything that happens outside of ourselves,

but by unconsciously merging self and other, the other's experiences echo within us as if they are our own. Such identification, argued Lipps, cannot be reduced to other capacities, such as learning, association, or reasoning. Empathy offers access to "the foreign self."

Empathy as feeling one with another's state, rather than some sort of cognitive deduction, was already a major point of discussion in early twentieth-century philosophy, from Wittgenstein to Max Scheler (Zahavi 2008). This bottom-up view has the advantage of explaining the unconscious reactions demonstrated by Dimberg et al. (2000) that are unexplained by the more cognitive view. With small electrodes registering facial muscle movements, investigators presented human subjects with pictures of angry and happy faces on a computer screen. Even if the pictures flashed too briefly for conscious perception, subjects still mimicked the faces and experienced corresponding emotions. Subjects exposed to happy faces reported feeling better than those exposed to angry ones, even though neither group was aware of what its members had seen. Clearly, empathy with the perceived emotions was brought about unconsciously without cognitive simulations or projections. Interpersonal emotional connections seem to run as much via bodies as minds (Niedenthal 2007).

If this is true for humans, it is probably even more true for other animals. We should not forget that mirror neurons, which some believe to facilitate these reactions (Gallese 2005), were first discovered not in humans but in monkeys (di Pellegrino et al. 1992), in which we must assume they serve a similar function. Bodily synchronization is as adaptive for prey as it is for cooperative predators. Social animals need to coordinate movements, collectively respond to danger, communicate about food and water, and assist others in need. Responsiveness to the behavioral states of conspecifics ranges from a flock of birds taking off all at once because one among them is startled by a predator to a mother ape returning to a whimpering youngster to help it from one tree to the next by draping her body as a bridge between the two. The first is a reflex-like transmission of fear that may not involve any understanding of what triggered the initial reaction, but one that is undoubtedly adaptive. The mother-ape example is more discriminating, involving anxiety at hearing one's offspring whimper, assessment of the reason for its distress, and an attempt to ameliorate the situation.

These synchronization responses are measurable in primates, for example, by demonstrating that they prefer experimenters who mimic their body movements over experimenters who do not (Paukner et al. 2009). It is also known that chimpanzees, like humans, yawn when they see another individual yawn (Anderson, Myowa-Yamakoshi, and Matsuzawa 2004), or even when they see an animated apelike drawing yawn (Campbell et al. 2009; figure 6.1). This kind of research is still in the beginning stages, but the reactions are strong and predictable and very much in line with what we know about the human tendency for mimicry.

Figure 6.1
Because yawning is an involuntary reflex, yawn contagion is close to empathy. Chimpanzees are so sensitive to the yawns of others that even a three-dimensional animation of a yawning head, of which this drawing shows eight stages, induces yawns in chimpanzees watching it on a computer screen. (Animations by Devyn Carter, from Campbell et al. 2009)

Rodent Empathy

Emotional connectedness in humans is so common, starts so early in life (e.g., Hoffman 1975; Zahn-Waxler and Radke-Yarrow 1990), shows neural and physiological correlates (e.g., Adolphs et al. 1994; Decety and Chaminade 2003) as well as a genetic substrate (Plomin et al. 1993), that it would be strange indeed if no continuity with other species existed. Emotional responses to displays of emotion in others are in fact so commonplace in animals (Plutchik 1987; de Waal 1996) that Darwin (1982 [1871], 77) already noted that "many animals certainly sympathize with each other's distress or danger."

The selection pressure to evolve rapid emotional connectedness likely started in the context of parental care. Signaling their state through smiling and crying, human infants urge their caregiver to come into action, and equivalent mechanisms operate in other animals in which reproduction relies on feeding, cleaning, and warming of the young. Offspring signals are not just responded to but induce an agitated state, suggestive of parental distress at the perception of offspring distress (MacLean 1985). Avian and mammalian parents alert to and affected by their offspring's emotions must have outreproduced those who remained indifferent.

Once empathic capacities existed they could be applied outside the rearing context and play a role in the wider fabric of social relationships. The fact that mammals retain distress vocalizations into adulthood hints at the continued survival value of care-inducing signals. For example primates often lick and clean the wounds of conspecifics, which is so critical for healing that injured migrating adult male macaques have been observed to temporarily return to their native group, where they are more likely to receive this service (Dittus and Ratnayeke 1989).

One of the first experimental studies on animal empathy was Church's (1959) entitled "Emotional Reactions of Rats to the Pain of Others." Having trained rats to obtain food by pressing a lever, Church found that if a rat pressing the lever perceived another rat in a neighboring cage receive a shock from an electrified cage floor, the first rat would interrupt its activity. Why should this rat not continue to acquire food? The larger issue is whether rats that stopped pressing the lever were concerned about their companions or just fearful that something aversive might also happen to themselves.

Church's work inspired a brief flurry of research during the 1960s that investigated concepts such as "empathy," "sympathy," and "altruism" in animals. This included studies on monkeys, which showed a much more dramatic empathy response than rats. Monkeys will for many days refuse to pull a chain that delivers food to themselves if doing so delivers an electric shock to a companion (Masserman, Wechkin, and Terris 1964). In order to avoid accusations of anthropomorphism, however, authors often placed the topic of their research in quotation marks, and their studies went largely ignored in ensuing years.

Half a century after Church's study, however, there is a revival of interest in animal empathy, and a basic mechanism common to humans and other animals has been proposed. Accordingly, seeing another in a given situation or displaying certain emotions reactivates neural representations of when the subject was itself in similar situations or had experienced similar emotions, which in turn generates a bodily state resembling that of the object of attention. Thus, seeing another individual's pain may lead the observer to share the bodily and neural experience. The perception-action mechanism (PAM) seems to operate in both humans and other mammals (Preston and de Waal 2002).

Langford et al. (2006) put pairs of mice through a "writhing test." In each trial two mice were placed in two transparent Plexiglas tubes such that they could see one another. Either one or both mice were injected with diluted acetic acid, known to cause a mild stomach-ache. Mice respond to this treatment with characteristic writhing movements. The researchers found that an injected mouse would show more writhing if its partner was writhing, too, than it would if its partner had not been injected. Significantly, this applied only to mouse pairs who were cage mates.

Male (but not female) mice showed an interesting additional phenomenon while witnessing another male in pain: its own pain sensitivity actually dropped. This counter-empathic reaction occurred only in male pairs that did not know each other, which are probably also the pairs with the greatest degree of rivalry. Was that rivalry suppressing their reaction, or did they actually feel less empathy for a strange rival?

Finally, Langford et al. (2006) exposed pairs of mice to different sources of pain—the acetic acid as before and a radiant heat source. Mice observing a cage mate writhing due to the acid injection withdrew more quickly from the heat source. In other words

their reactions could not be attributed to mere motor imitation but involved emotional contagion because seeing a companion react to pain caused sensitization to pain in general.

Preconcern

Once an organism is sensitive to another's pain or distress, the next step is to approach and provide comfort. This goes beyond "personal distress" (i.e., self-focused distress in response to another's distress) in that it is other-oriented, even though the motivation behind it may still be to comfort oneself. Seeing someone else cry, we get upset, so that by contacting the other we also reassure ourselves. I am quite familiar with such behavior in young rhesus monkeys. Once, when an infant had been bitten because it had accidentally landed on a dominant female, it screamed so incessantly that it was soon surrounded by other infants. I counted eight of them climbing on top of the poor victim, pushing, pulling, and shoving each other as well as the first infant. That obviously did little to alleviate its fright. The infant monkeys' response seemed automatic, as if they were as distraught as the victim and sought to comfort themselves as much as the other (de Waal 1989).

This cannot be the whole story, though. If these monkeys were just trying to calm themselves, why did they approach the victim? Why did they not run to their mothers? Why seek out the actual source of distress and not a guaranteed source of comfort? Surely, this is more than emotional contagion. The latter can explain a need for comfort—but not the magnetic pull toward a crying peer.

In fact both animals and young children often seek out distressed parties without any indication that they know what is going on. They seem blindly attracted, like a moth to a flame. We like to read concern about the other into their behavior, but the required understanding may not be there. I will call this blind attraction *preconcern*. It is as if nature has endowed the organism with a simple behavioral rule: "If you feel another's pain, get over there and make contact."

One might counter that such a rule would prompt individuals to waste energy on all sorts of distraught parties, many of which they would far better stay away from. Approaching others in a predicament may not be the smartest thing to do. But I do not think we need to worry about this given the evidence that emotions are picked up more readily between parties with close ties than between strangers. This was the case in the above-mentioned mouse study (Langford et al. 2006) and is well known of many species, including humans (reviewed in Preston and de Waal 2002). A simple approach rule would automatically propel individuals toward those distressed parties that matter most to them, such as offspring and familiar companions.

If true, the sort of behavior that we associate with sympathy arose in fact before sympathy itself. If this seems like putting the cart before the horse, it is really not as

strange as it sounds. There are other examples of behavior preceding understanding. Language development, for example, does not start with children naming things or expressing thoughts. It starts with *babbling:* babies crawl around uttering nonsensical strings of "ba-ba-ba-ba-ba," advancing to "do-ko-yay-day-bu." When our species claims to be the only talking primate, babbling is obviously not what we have in mind, but this is no reason to belittle it. The fact that everyone's linguistic career starts with this baby *lingua franca* illustrates how deeply ingrained language is. It develops out of a primitive urge without any of the refinements of the final product, exactly what I am proposing for the impulse to attend to someone else's distress.

Preconcern goes beyond personal distress, but not by far, since it does not require imagining yourself in the other's situation, and indeed the capacity to do so may be wholly absent, such as when a one-year-old child is already drawn toward upset family members (Zahn-Waxler and Radke-Yarrow 1990). Children of this age are not yet capable of grasping someone else's situation. Preconcern may also explain why certain animals, such as household pets, contact others in pain (Zahn-Waxler, Hollenbeck, and Radke-Yarrow 1984), or why infant monkeys pile on top of a hapless vocalizing peer.

Perspective-Taking

With preconcern in place learning and intelligence can begin to add layers of complexity, making the response ever more discerning until full-blown sympathy emerges. Since this is the level of sympathy that we, human adults, are familiar with, we think of it as a single process, as something you either have or lack, but in fact it consists of many layers added by evolution over millions of years. Most mammals show some of these—only a handful show all of them.

Some large-brained animals may share the human capacity to put themselves into someone else's shoes. Whether they do or do not has been debated ever since an American primatologist, Emil Menzel (1974), conducted his pioneering studies. Do chimps have any inkling of what others feel, want, need, or know? Menzel's work is rarely mentioned anymore, but he was the very first to see the importance of this issue.

Working outdoors with nine juvenile chimpanzees, Menzel would take one of them out into a large, grassy enclosure to reveal hidden food or a scary object, such as a (toy) snake. After this he would bring this individual back to the waiting group and release all the chimps together. Would the others appreciate that one among them knew something of importance, and if so, how would they react? Could they tell the difference between the other having seen food or a snake?

They most certainly could. They eagerly followed a chimpanzee who knew a food location, but they were hesitant to stay close to one who had seen a hidden snake

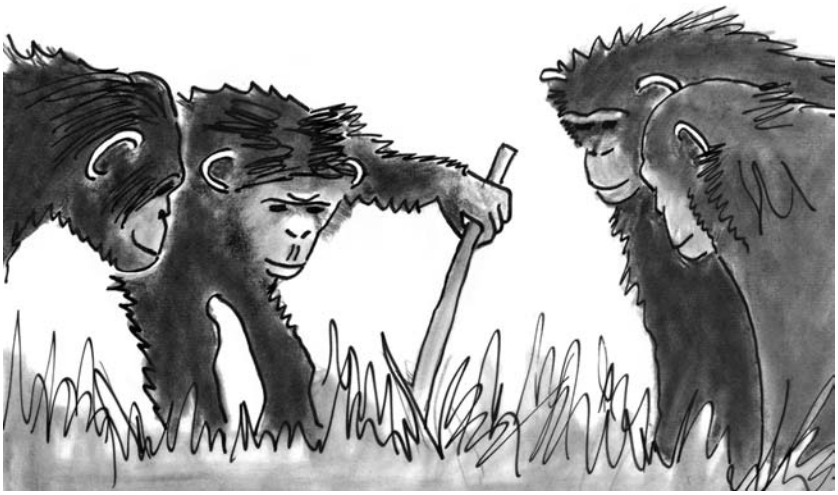

Figure 6.2
The very first theory-of-mind research was conducted by Emil Menzel (1974) with a focus on emotional body language to see what apes know about what others know. One juvenile chimpanzee, poking with a stick at a snake in the grass, is the only one who knows what is there. Before having seen the danger themselves, the onlooking apes know to be cautious from this individual's body language. (Drawing by Frans de Waal)

(figure 6.2). This was emotional contagion in action: they copied the other's enthusiasm or alarm. Menzel's guesser versus knower test has inspired a huge following as reflected in numerous studies on children, apes, birds, dogs, and so on. Unfortunately, the topic was soon redefined with a more abstract focus, such as knowing what others know (Premack and Woodruff 1978). The precise mechanism of such "theory of mind" (ToM) remained unaddressed, however, and to this date it is questionable if the process is as bodiless and theoretical as implied by the chosen terminology (de Gelder 1987; Hobson 1991).

The acquisition of ToM probably starts with emotional connections. Children pass traditional ToM tasks around the age of four, but they appreciate the feelings, needs, and desires of others already at the age of two or three (Wellman, Phillips, and Rodriguez 2000). They often rely on emotional communication to deduce what kind of situation the other faces, showing reactions similar to Menzel's (1974) apes, who recognized if one among them had spotted hidden food or danger. It should not surprise, therefore, that after many studies in which apes were challenged to guess what human experimenters knew or did not know, the greatest research progress arrived when scientists adopted a more emotionally relevant approach by testing how one ape perceives the knowledge of another in a dominance-subordination context (Hare, Call,

and Tomasello 2001). For further experimental evidence for ape ToM see Shillito et al. (2005) and Hirata (2006).

An important spontaneous manifestation of empathic perspective-taking is "targeted helping," which is help fine-tuned to another's specific situation (de Waal 1996). For an individual to move beyond being sensitive to others toward an explicit other-orientation requires a shift in perspective. The emotional state induced in oneself by the other now needs to be attributed to the other instead of the self. A heightened self-identity allows a subject to relate to the object's emotional state without losing sight of the actual source of this state (Hoffman 1982; Lewis 2002). The required self-representation is hard to establish independently, but one common avenue is to gauge reactions to a mirror. The *co-emergence hypothesis* (de Waal 2008) predicts that mirror self-recognition (MSR) and advanced expressions of empathy appear together in both ontogeny and phylogeny.

Ontogenetically, there is compelling support for the co-emergence hypothesis in human children (Bischof-Köhler 1988, 1991; Zahn-Waxler et al. 1992; Johnson 1992). Gallup (1983) was the first to propose phylogenetic co-emergence, a prediction empirically supported by the contrast between monkeys and apes, with compelling evidence for both MSR, consolation, and targeted helping only in the apes (see below). Apart from the great apes, the animals for which we have the most striking accounts of consolation and targeted helping are dolphins and elephants (reviewed in de Waal 2009), which are also the only mammals other than the apes to pass the mark test in which an individual needs to locate a mark on itself that it cannot see without a mirror (Reiss and Marino 2001; Plotnik, de Waal, and Reiss 2006; figure 6.3).

Sympathetic Concern

Yerkes (1925) reported how a young bonobo showed intense concern for his sickly chimpanzee companion, and Ladygina-Kohts (2001 [1935], 121) noticed similar tendencies in her home-reared chimpanzee toward herself:

> If I pretend to be crying, close my eyes and weep, Yoni immediately stops his play or any other activities, quickly runs over to me, all excited and shagged, from the most remote places in the house, such as the roof or the ceiling of his cage, from where I could not drive him down despite my persistent calls and entreaties. He hastily runs around me, as if looking for the offender; looking at my face, he tenderly takes my chin in his palm, lightly touches my face with his finger, as though trying to understand what is happening, and turns around, clenching his toes into firm fists.

What better evidence for the power of simian sympathy than the fact that an ape who would refuse to descend from the roof of the house for food that is waved at him would do so instantly on seeing his mistress in distress? Ladygina-Kohts also described

Figure 6.3
An Asian elephant with a visible X-shaped mark on the right side of her head and an invisible sham mark on the left side, touches the visible mark with the tip of her trunk thus indicating self-recognition, which is thought to correlate with perspective-taking. This still image was collected by a lipstick video camera embedded in the mirror. (Video still from Plotnik et al. 2006)

how Yoni would look into her eyes when she pretended to cry: "the more sorrowful and disconsolate my crying, the warmer his sympathy" (2001 [1935]). If she would slap her hands over her eyes, he tried to pull them away, extending his lips toward her face, looking attentively, slightly groaning and whimpering. She described similar reactions for her son, Roody, adding that he went further than the ape in that he would actually cry along with her. Roody cried even when he would notice a bandage over the eye of his favorite uncle or when he would see the maid grimace while swallowing bitter medicine.

A monkey or rat reacting to another's pain by stopping the behavior that caused it may simply be "turning off" unpleasant signals. But such self-protective altruism cannot explain Yoni's reaction to his surrogate mother. First, because he had not caused her distress himself and second, because he could easily have moved away when he saw her crying from the roof of the house. If self-protection were his goal, he also should have left her hands where they were when she cried behind them. Clearly, Yoni was not just focusing on his own situation: he felt an urge to understand what was the matter with Kohts.

Yoni's reaction is typical of apes. The *consolation* he showed is the best documented nonhuman-primate example of what in humans is known as *sympathetic concern*.

Figure 6.4
Consolation is common in humans and apes but largely absent in monkeys. A juvenile chimpanzee puts an arm around a screaming adult male, who has been defeated in a fight. The latest analyses suggest that this behavior expresses sympathetic concern. (Photograph by Frans de Waal)

Consolation is usually defined as reassurance provided by an uninvolved bystander to one of the combatants in a previous aggressive incident. For example, a third-party goes over to the loser of a fight and gently puts an arm around his or her shoulders (see figure 6.4). After the first few studies of chimpanzee consolation (de Waal and van Roosmalen 1979; de Waal and Aureli 1996), other studies have confirmed this behavior in different ape species (Palagi, Paoli, and Borgognini 2004; Cordoni, Palagi, and Borgognini 2004; Mallavarapu et al. 2006). But when de Waal and Aureli (1996) set out to apply the same observation protocol to detect consolation in monkeys, they failed to find any, as did others (Watts, Colmenares, and Arnold 2000). The consolation gap between monkeys and the hominids (i.e., humans and apes) extends even to the one situation where one would most expect consolation to occur: macaque mothers fail to comfort their own offspring after a fight (Schino et al. 2004).

Spontaneous consolation is so common in apes that scientists have collected data on literally thousand of cases. Studies confirm that this behavior reduces the

recipient's arousal, is biased toward socially close individuals, and shows a sex difference, with females showing more of it than males (Fraser, Stahl, and Aureli 2008; Romero, Castellanos, and de Waal 2010) consistent with sex differences in human empathy (Zahn-Waxler et al. 1992; Han, Fan, and Mao 2008). Given the morphological similarity between ape consolation behavior and expressions of sympathetic concern in young children, which also touch and embrace distressed individuals, we follow the Darwinian principle of parsimony that if two related species show similar behavior under similar circumstances the psychology behind their behavior is likely similar, too (de Waal 1999).

Altruistic Behavior

An old female named Peony spends her days with other chimpanzees in a large outdoor enclosure near Atlanta, Georgia. On bad days when her arthritis is acting up she has great trouble walking and climbing. But other females help her out. For example, Peony is huffing and puffing to get up into the climbing frame in which several chimpanzees have gathered for a grooming session. An unrelated younger female moves behind her, places both hands on her ample behind and pushes her up with quite a bit of effort until Peony joins the rest.

Even though there are abundant examples of spontaneous helping among primates, the modern literature still depicts humans as the only truly altruistic species, since all that animals care about are return benefits (e.g., Dawkins 1976; Kagan 2000; Fehr and Fischbacher 2003). The problem with this view is that the evolutionary reasons for altruistic behavior are not necessarily the animals' reasons. Do animals really help each other in the knowledge that this will ultimately benefit themselves? To assume so is cognitively demanding in the extreme, requiring animals to anticipate the future behavior of others and to keep track of what they did for others versus what others did for them. Thus far there is little or no evidence for such expectations. Helpful acts for immediate self-gain are indeed common, but it seems safe to assume that future return benefits remain largely beyond the animal's cognitive horizon.

Once evolved, behavior often operates with *motivational autonomy*, that is, its motivation is relatively independent of evolutionary goals (de Waal 2008). A good example is sexual behavior, which arose to serve reproduction. Since animals are, so far as we know, unaware of the link between sex and reproduction, they must be engaging in sex (as do humans much of the time) without progeny in mind. Just as sex cannot be motivated by unforeseen consequences, altruistic behavior cannot be motivated by unforeseen payoffs such as inclusive fitness or return benefits in the distant future.

The helping impulse must therefore stem from immediate factors, such as sensitivity to the emotions and/or needs of others. Such sensitivity would by no means contradict self-serving reasons for the evolution of behavior so long as it steers altruistic

behavior into the direction predicted by theories of kin selection and reciprocal altruism. Apart from assisting an aging female in her climbing efforts, chimpanzees occasionally perform extremely costly helping actions. For example, when a female reacts to the screams of her closest associate by defending her against a dominant male, she takes enormous risks on behalf of the other. Note the following description of two long-time chimpanzee friends in a zoo colony: "Not only do they often act together against attackers, they also seek comfort and reassurance from each other. When one of them has been involved in a painful conflict, she goes to the other to be embraced. They then literally scream in each other's arms" (de Waal 1982, 67). Or take high-risk helping such as when Washoe, the world's first language-trained chimp, heard another female scream and hit the water. Fouts and Mills (1997, 180) describe how Washoe raced across two electric wires, which normally contained the apes, to reach the victim and waded into the slippery mud to reach the wildly trashing female and grab one of her flailing arms to pull her to safety. This was a courageous act given that chimpanzees do not swim and are extremely hydrophobic. Washoe barely knew this female, having met her only a few hours before.

For both practical and ethical reasons, however, there is a scarcity of experiments on emotionally charged situations that could trigger costly altruism. This is not only true for animal altruism but equally so for human altruism. Instead, experiments usually concern low-cost altruism, sometimes called "other-regarding preferences." A typical paradigm is to offer one member of a pair the option to either secure food for itself by manipulating part A of an apparatus or to secure food for both itself and the other by manipulating part B of the same apparatus. In the first such experiment Colman, Liebold, and Boren (1969) found one of four tested macaques to be consistently other-regarding. When replications failed to find the same tendency in chimpanzees, however, this led to the suggestion that other-regarding preferences may be uniquely human (Silk et al. 2005). It is impossible to prove the null hypothesis, however, and recent studies with different methodologies have yielded results more in line with what we know about naturalistic primate behavior.

In one chimpanzee study investigators tried to rule out reciprocity by having the apes interact with humans they barely knew, and on whom they did not depend for food or other favors, and found significant expressions of altruism (Warneken et al. 2007). Spontaneous helping has also been experimentally demonstrated in both capuchin monkeys (de Waal, Leimgruber, and Greenberg 2008; Lakshminarayanan and Santos 2008) and marmosets (Burkart et al. 2007). In our study two capuchin monkeys were placed side by side separated by mesh. One of them needed to barter with us with small plastic tokens, which we would first give to a monkey, after which we would hold out an open hand to let them return the token for a tidbit (figure 6.5). The critical test came when we offered a choice between two differently colored tokens with different meaning: one token was "selfish," the other "prosocial." If the bartering

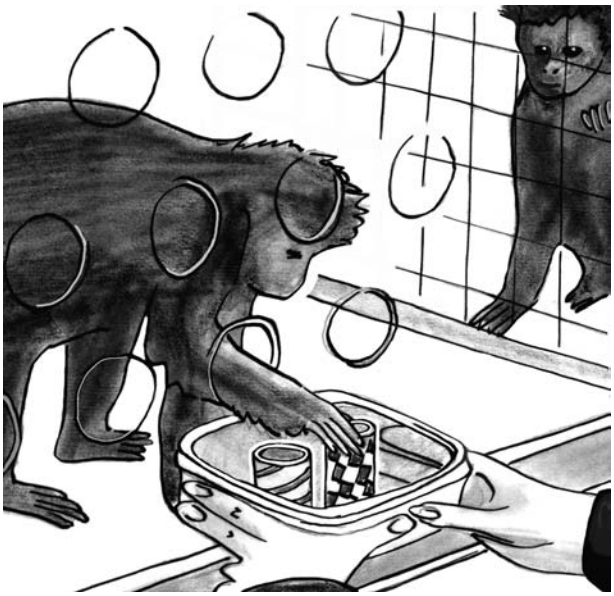

Figure 6.5
One capuchin monkey reaches through an armhole to choose between differently marked pieces of pipe while her partner looks on. The pipe pieces can be exchanged for food. One token feeds both monkeys; the other feeds only the chooser. Capuchins typically prefer the "prosocial" token (de Waal et al. 2008). (Drawing from video by Frans de Waal)

monkey picked the selfish token, it received a small piece of apple for returning it, but its partner remained unrewarded. The prosocial token, on the other hand, rewarded both monkeys with apple at the same time. Since the monkey who did the bartering was rewarded either way, the only difference was in what the partner received.

Monkeys preferentially bartered with the prosocial token. This preference could not be explained by fear of future punishment, because dominant partners (which have least to fear) proved to be more prosocial than subordinate ones. Familiarity biased the choices in the predicted direction: the stronger the social tie between two monkeys, as measured by how much time they associated in the group, the more they favored the prosocial token (de Waal et al. 2008).

In short there is mounting evidence from both naturalistic observations and experiments that primates care about each other's welfare, and they follow altruistic impulses that are probably based on empathy, which in both humans and other animals increases with familiarity. The empathy mechanism automatically produces a stake in the other's welfare, that is, the behavior comes with an intrinsic reward, known in the human literature as the *warm-glow* effect. Actions that improve another's condition

come with pleasant feelings (Andreoni 1989), so that humans report feeling good when they do good and show activation of reward-related brain areas (Harbaugh, Mayr, and Burghart 2007). It will be important to determine if the same self-reward system extends to other primates.

Empathy as Umbrella Term

At the core of the empathic capacity lies a mechanism that provides the subject with access to the subjective state of another through the subject's own neural representations. When the subject attends to the other's state, the subject's neural representations of similar states are automatically activated. This lets the subject get "under the skin" of the other, bodily sharing its emotions and needs. This neural activation, which Preston and de Waal (2002) dubbed the perception-action mechanism of empathy, fits with Damasio's (1994) somatic marker hypothesis of emotions, Prinz's (1997) common coding theory of perception and action, as well as evidence for a link at the cellular level between seeing and doing, such as the mirror neurons first discovered in macaques.

This view of empathy is a layered one. Instead of driving wedges between, let us say, emotional contagion and empathy, compassion and sympathy, or automatic and deliberate empathy, all of these capacities are connected, I believe. None of them could probably exist without the others. For example, what would empathy be without emotional engagement? Psychopaths may be capable of perspective-taking that superficially looks like empathy, but given their lack of emotional investment they cannot truly be called empathetic (Mullins-Nelson, Salekin, and Leistico 2006). Instead of viewing emotional contagion, personal distress, and other emotional reactions as distinct from empathy, I see them as being at the heart of it.

In the Russian Doll model visualized in figure 6.6, empathy is the *umbrella term* that encompasses all levels. Adult humans show all of them, but many animals show only a few layers as do human infants. I see perspective-taking as another level of empathy, not as separate. In normal development (and also in evolution) perspective-taking is *added* to the emotional processes. The child begins to wonder what causes emotions in others, rather than just being affected by them, and so begins to focus on the situation of the other. The same applies to some large-brained animals. They add perspective-taking to the emotional process, without replacing it. Since it is integrated with the emotional core, I speak of empathetic perspective-taking.

This reflects a typically biological way of thinking, stressing the unity behind a phenomenon and the realization that evolution rarely throws out anything. It rarely replaces one trait with another. Traits are transformed, modified, co-opted for other functions, or "tweaked" in another direction in what Darwin called "descent with modification." Thus, the frontal fins of fish became the front limbs of land animals,

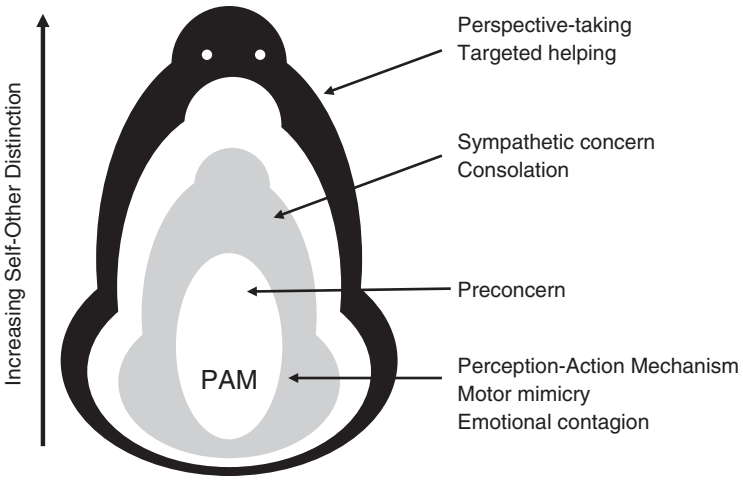

Figure 6.6
The Russian doll model of empathy and imitation. Empathy induces a similar emotional state in the subject as the object. At the core of emotional contagion is the perception-action mechanism (PAM). The doll's outer layers, starting with preconcern and followed by sympathetic concern and targeted helping, build on this hard-wired socio-affective basis. The complexity of empathy grows with increased self-other distinction and perspective-taking abilities. Even though the doll's outer layers depend on learning and prefrontal functioning, they remain fundamentally linked to its inner core.

which over time turned into hoofs, paws, wings, hands, and flippers. In the case of empathy this means that the simple forms remain present in the advanced ones.

Even the most advanced forms of human empathy, which do not require physical closeness and body language, are never fully independent from these simpler processes since we have learned over our lifetime to internalize what happens to others and how to react. Even if we just read about another's situation in a novel, our reaction still draws on well-established neural representations of similar situations that we have encountered, allowing us to have empathy for a fictional character based on our imagination. Human empathy is truly remarkable, but as argued here, it is hardly unprecedented in the animal kingdom.

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