Putting the Altruism Back into Altruism: The Evolution of Empathy

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perception-action, perspective-taking, prosocial behavior, cooperation

Abstract

Evolutionary theory postulates that altruistic behavior evolved for the return-benefits it bears the performer. For return-benefits to play a motivational role, however, they need to be experienced by the organism. Motivational analyses should restrict themselves, therefore, to the altruistic impulse and its knowable consequences. Empathy is an ideal candidate mechanism to underlie so-called directed altruism, i.e., altruism in response to another's pain, need, or distress. Evidence is accumulating that this mechanism is phylogenetically ancient, probably as old as mammals and birds. Perception of the emotional state of another automatically activates shared representations causing a matching emotional state in the observer. With increasing cognition, state-matching evolved into more complex forms, including concern for the other and perspective-taking. Empathy-induced altruism derives its strength from the emotional stake it offers the self in the other's welfare. The dynamics of the empathy mechanism agree with predictions from kin selection and reciprocal altruism theory.

Contents

> Sympathy . . . cannot, in any sense, be regarded as a selfish principle.
> Smith (1759, p. 317)

> Empathy may be uniquely well suited for bridging the gap between egoism and altruism, since it has the property of transforming another person's misfortune into one's own feeling of distress.
> Hoffman (1981a, p. 133)

Altruism (biological definition): behavior that increases the recipient's fitness at a cost to the performers

Ultimate cause or goal: the benefits an organism or its close kin derive from a behavior, hence the probable reason why the behavior was favored by natural selection

Proximate cause: situation that triggers behavior and the mechanism (psychological, neural, physiological) that enables it

INTRODUCTION

Discussions of altruistic behavior tend to suffer from a lack of distinction between function and motivation. This is due to the contrasting emphasis of biologists and psychologists, with the former focusing on what a particular behavior is good for, and the latter on how it comes about.

Evolutionary explanations are built around the principle that all that natural selection can work with are the effects of behavior—not the motivation behind it. This means there is only one logical starting point for evolutionary accounts, as explained by Trivers (2002, p. 6): "You begin with the effect of behavior on actors and recipients; you deal with the problem of internal motivation, which is a secondary problem, afterward. . . . [I]f you start with motivation, you have given up the evolutionary analysis at the outset."

This is a perfectly legitimate strategy that has yielded profound insights into the evolution of altruism (e.g., Dugatkin 2006). Unfortunately, however, these insights have not come with a new terminology: Evolutionary biology persists in using motivational terms. Thus, an action is called "selfish" regardless of whether or not the actor deliberately seeks benefits for itself. Similarly, an action is called "altruistic" if it benefits a recipient at a cost to the actor regardless of whether or not the actor intended to benefit the other. The prototypical altruist is a honeybee that stings an intruder—sacrificing her life to protect the hive—even though her motivation is more likely aggressive than benign. This usage of the terms "selfish" and "altruistic" oftentimes conflicts with their vernacular meaning (Sober & Wilson 1998).

The hijacking of motivational terminology by evolutionary biologists has been unhelpful for communication about motivation per se. The way to clear up the confusion is to do what Trivers did when he decided that evolutionary analyses require that effects be considered separate from motivation. Conversely, motivational analyses require us to keep motivation separate from evolutionary considerations. It is not for nothing that biologists hammer on the distinction between ultimate and proximate (Mayr 1961, Tinbergen 1963). The ultimate cause refers to why a behavior evolved over thousands of generations, which depends on its fitness consequences. The proximate cause, on the other hand, refers to the immediate situation that triggers behavior, and the role of learning, physiology, and neural processes—typically the domain of psychologists.

Proximate and ultimate viewpoints do inform each other, yet are not to be conflated. For example, primate cooperation is

promoted by social tolerance. Through its effect on food-sharing, tolerance evens out payoff distributions (de Waal & Davis 2003, Melis et al. 2006). Tolerance likely is a proximate mechanism that evolved to serve the ultimate goal of cooperation, which is to yield benefits for all contributors.

Cooperation and altruistic behavior are thought to have evolved to help family members and those inclined to return the favor (Hamilton 1964, Trivers 1971). Regardless of whether this is the whole explanation or not (see Sober & DS Wilson 1998, EO Wilson 2005), the point is that ultimate accounts stress return-benefits, i.e., positive consequences for the performer and/or its kin. Inasmuch as these benefits may be quite delayed, however, it is unclear what motivational role, if any, they play. This becomes clear if we consider more closely what drives directed altruism, i.e., altruistic behavior aimed at others in need, pain, or distress. There are three ways in which directed altruism may come about:

1. Altruistic impulse. Spontaneous, disinterested helping and caring in reaction to begging or distress signals or the sight of another in pain or need.
2. Learned altruism. Helping as a conditioned response reinforced by positive outcomes for the actor.
3. Intentional altruism. Help based on the prediction of behavioral effects. One prediction could be that the help will be reciprocated, hence that the act will produce a net benefit. Since the actor seeks to benefit itself, we may call this intentionally selfish altruism. The second possibility is help based on an appreciation of how one's own behavior will help the other. Since the actor seeks to benefit the other, we may call this intentionally altruistic altruism.

Some directed altruistic behavior is promoted by built-in rewards, such as the oxytocin release during suckling that may underpin maternal care (Panksepp 1998). Empathy-based altruism may have similar intrinsically rewarding qualities in that it offers the actor an emotional stake in the recipient's well-being, i.e., if helping the other ameliorates the helper's internal state (see Empathy as Evolved Proximate Mechanism, below). Extrinsic rewards, on the other hand, are less likely to play a role. By definition, altruism carries an initial cost, and positive consequences occur only after a significant time interval (e.g., the recipient reciprocates) or not at all (e.g., care for dependent kin), making for rather poor learning conditions.

Intentionally selfish altruism would require the actor to explicitly expect others to return the favor. Despite the lack of evidence for such expectations in animals, they are often assumed. The common claim that humans are the only truly altruistic species, since all that animals care about are return-benefits (e.g., Dawkins 1976, Fehr & Fischbacher 2003, Kagan 2000, Silk et al. 2005), misconstrues reciprocity as a motivation. It assumes that animals engage in reciprocal exchange with a full appreciation of how it will ultimately benefit them. Helpful acts for immediate self-gain are indeed common (Dugatkin 1997), but the return-benefits of altruistic behavior typically remain beyond the animal's cognitive horizon, i.e., occur so distantly in time that the organism is unlikely to connect them with the original act. This applies to most reciprocal altruism in the animal kingdom.

Once evolved, behavior often assumes motivational autonomy, i.e., its motivation becomes disconnected from its ultimate goals. A good example is sexual behavior, which arose to serve reproduction. Since animals are, as 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.

The altruistic impulse is to be taken very seriously, therefore, because even if altruistic behavior were partially learned based on

Directed altruism: helping or comforting behavior directed at an individual in need, pain, or distress

Intentional altruism: the altruist deliberately seeks to benefit either the other (intentionally altruistic altruism) or itself (intentionally selfish altruism)

Empathy-based altruism: help and care born from empathy with another

Empathy: the capacity to (*a*) be affected by and share the emotional state of another, (*b*) assess the reasons for the other's state, and (*c*) identify with the other, adopting his or her perspective. This definition extends beyond what exists in many animals, but the term "empathy" in the present review applies even if only criterion (*a*) is met

Motivational autonomy: independence of motivation from ultimate goals

Perception-action mechanism (PAM): automatically and unconsciously activated neural representations of states in the subject similar to those perceived in the object

Emotional contagion: emotional state-matching of a subject with an object

short-term intrinsic rewards or long-term extrinsic rewards, this by no means rules out the altruistic impulse. In fact, it presupposes this impulse given that a behavior's consequences cannot be learned without spontaneously engaging in it in the first place.

This review seeks to restore the altruism within altruism by exploring the role of empathy in the directed altruism of humans and other animals. Some definitions of empathy stress the sharing of emotions, whereas other definitions stress the capacity to put oneself into the other's "shoes." The latter definitions are so top-down, however, that they disconnect empathy from its possible antecedents. We follow a bottom-up approach instead, adopting the broadest possible definition, including mere emotional sensitivity to others. We first consider the various levels of empathy in animals and the underlying perception-action mechanism (PAM) proposed by Preston & de Waal (2002a). After this, we explore the relation between empathy and altruism.

A major question is whether evolution is likely to have selected empathy as proximate mechanism to generate directed altruism. Does empathy channel altruism in the direction that evolutionary theory would predict? So, even though motivation will be kept temporarily separate from evolutionary considerations, in the end the two will meet. Empathy may be motivationally autonomous, but it still needs to produce—on average and in the long run—evolutionarily advantageous outcomes. The central thesis to be argued here, then, is that empathy evolved in animals as the main proximate mechanism for directed altruism, and that it causes altruism to be dispensed in accordance with predictions from kin selection and reciprocal altruism theory.

ORIGIN OF EMPATHY

Empathy allows one to quickly and automatically relate to the emotional states of others, which is essential for the regulation of social interactions, coordinated activity, and cooperation toward shared goals. Even though cognition is often critical, it is a secondary development. As noted by Hoffman (1981b, p. 79), "[H]umans must be equipped biologically to function effectively in many social situations without undue reliance on cognitive processes."

The selection pressure to evolve rapid emotional connectedness likely started in the context of parental care long before our species evolved (Eibl-Eibesfeldt 1974 [1971], MacLean 1985). Signaling their state through smiling and crying, human infants urge their caregiver to come into action (Acebo & Thoman 1995, Bowlby 1958). Equivalent mechanisms operate in all animals in which reproduction relies on feeding, cleaning, and warming of the young. Avian or mammalian parents alert to and affected by their offspring's needs likely out-reproduced those who remained indifferent.

Once the empathic capacity existed, it could be applied outside the rearing context and play a role in the wider network of social relationships. The fact that mammals retain distress vocalizations into adulthood hints at the continued survival value of empathy-inducing signals. For example, primates often lick and clean the wounds of conspecifics (Boesch 1992), which is so critical for healing that adult male macaques injured during attempts to enter a new group often temporarily return to their native group, where they are more likely to receive this service (Dittus & Ratnayeke 1989).

LEVELS OF EMPATHY

Emotional Contagion

The lowest common denominator of all empathic processes is that one party is affected by another's emotional or arousal state. This broad perspective on empathy, which goes back as far as Lipps (1903), leads one to recognize continuity between humans and other animals as well as between human adults and young children. Emotional connectedness in humans is so common, starts so early in life (e.g., Hoffman 1975, Zahn-Waxler &

Radke-Yarrow 1990), and shows neural and physiological correlates (e.g., Adolphs et al. 1994, Decety & Chaminade 2003a, Rimm-Kaufman & Kagan 1996) as well as a genetic substrate (Plomin et al. 1993), that it would be strange indeed if no continuity with other species existed. Evolutionary continuity between humans and apes is reflected in the similarity of emotional communication (Parr & Waller 2007) as well as similar changes in brain and peripheral skin temperature in response to emotionally charged images (Parr 2001, Parr & Hopkins 2001).

A flock of birds taking off all at once because one among them is startled shows a reflex-like, highly adaptive spreading of fear that may not involve any understanding of what triggered the initial reaction. Similarly, when a room full of human newborns bursts out crying because one among them started to cry, there is an automatic spreading of distress (Hoffman 1975). At the core of these processes is adoption—in whole or in part—of another's emotional state, i.e., emotional contagion (Hatfield et al. 1993). Emotional contagion is not always a passive process, though: The object often aims to emotionally affect the subject, such as the extremely noisy temper tantrums of young apes when they are being rejected during weaning. Like human children (Potegal 2000), they exploit emotional contagion to induce maternal distress, which in turn may lead the mother to change her behavior to their advantage.

Emotional responses to displays of emotion in others are so commonplace in animals (de Waal 2003, Plutchik 1987, Preston & de Waal 2002b) that Darwin (1982 [1871, p. 77]) already noted that "many animals certainly sympathize with each other's distress or danger." For example, rats and pigeons display distress in response to perceived distress in a conspecific, and temporarily inhibit conditioned behavior if it causes pain responses in others (Church 1959, Watanabe & Ono 1986). A recent experiment demonstrated that mice perceiving other mice in pain intensify their own response to pain (Langford et al. 2006).

Miller et al. (1959) published the first of a series of pioneering studies on the transmission of affect in rhesus macaques. These monkeys tend to terminate projected pictures of conspecifics in a fearful pose even more rapidly than negatively conditioned stimuli. Perhaps the most compelling evidence for emotional contagion came from Wechkin et al. (1964) and Masserman et al. (1964), who found that monkeys refuse to pull a chain that delivers food to them if doing so delivers an electric shock to and triggers pain reactions in a companion. Whether their sacrifice reflects concern for the other (see below) remains unclear, however, as it might also be explained as avoidance of aversive vicarious arousal.

Sympathetic concern: concern about another's state and attempts to ameliorate this state (e.g., consolation)

Cognitive empathy: empathy combined with contextual appraisal and an understanding of what caused the object's emotional state

Personal distress: self-centered distress born from empathy with another's distress

Sympathetic Concern

The next evolutionary step occurs when emotional contagion is combined with appraisal of the other's situation and attempts to understand the cause of the other's emotions. De Waal (1996) speaks of "cognitive empathy" when the empathic reaction includes such contextual appraisal.

The psychological literature distinguishes sympathy from personal distress, which in their social consequences are each other's opposites. Sympathy is defined as "an affective response that consists of feelings of sorrow or concern for a distressed or needy other (rather than sharing the emotion of the other). Sympathy is believed to involve an other-oriented, altruistic motivation" (Eisenberg 2000, p. 677). Personal distress, on the other hand, makes the affected party selfishly seek to alleviate its own distress, which mimics that of the object. Personal distress is not concerned, therefore, with the other (Batson 1991). A striking nonhuman primate example is how the continued screams of a punished infant rhesus monkey will cause other infants to embrace, mount, or even pile on top of the victim. Thus, one infant's distress spreads quickly to its peers, which then seek to reduce

Consolation: comforting behavior directed at a distressed party, such as a recent victim of aggression

their own negative arousal (de Waal 1996, p. 46).

Concern for others is different in that it relies on a separation between internally and externally generated emotions. This separation is observable in many mammals. In a study that sought to document children's responses to family members instructed to feign sadness (sobbing), pain (crying), or distress (choking), striking similarities emerged between the reactions of one-year-old children and pets, such as dogs and cats. The latter, too, showed comforting attempts, such as putting their head in the lap of the "distressed" person (Zahn-Waxler et al. 1984).

Yerkes (1925, p. 246) reported how his bonobo, Prince Chim, showed such concern for his sickly chimpanzee companion, Panzee, that the scientific establishment might reject his claims: "If I were to tell of his altruistic and obviously sympathetic behavior towards Panzee I should be suspected of idealizing an ape." Ladygina-Kohts (2001 [1935]) noticed similar tendencies in her young home-reared chimpanzee. She discovered that the only way to get him off the roof of her house (better than reward or threat of punishment) was by acting distressed, hence by inducing concern for herself in him.

Perhaps the best-documented example of sympathetic concern is consolation, defined as reassurance provided by an uninvolved bystander to one of the combatants in a previous aggressive incident (de Waal & van Roosmalen 1979). For example, a third party goes over to the loser of a fight and gently puts an arm around his or her shoulders (**Figure 1**). De Waal & van Roosmalen (1979) analyzed

Figure 1

Consolation is common in humans and apes, but virtually absent in monkeys. Here a juvenile chimpanzee puts an arm around a screaming adult male, who has just been defeated in a fight. Photograph by the author.

hundreds of consolations in chimpanzees, and de Waal & Aureli (1996) included an even larger sample. These studies show that bystanders contact victims of aggression more often than they contact aggressors, and bystanders contact victims of serious aggression more often than they contact those who had received mild aggression.

Subsequent studies have confirmed consolation in captive apes (Cordoni et al. 2004; Fuentes et al. 2002; Koski & Sterck 2006; Mallavarapu et al. 2006; Palagi et al. 2004, 2006), wild chimpanzees (Kutsukake & Castles 2004, Wittig & Boesch 2003), large-brained birds (Seed et al. 2007), and human children (Fujisawa et al. 2006). However, when de Waal & Aureli (1996) set out to apply the same observation protocol to detect consolation in monkeys, they failed to find any, as did others (Watts et al. 2000). The consolation gap between monkeys and the Hominoidea (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). O'Connell's (1995) content analysis of hundreds of reports confirms that reassurance of distressed others is typical of apes yet rare in monkeys. It still needs to be established, however, that this behavior actually does reduce the distressed party's arousal.

Empathic Perspective-Taking

Psychologists usually speak of empathy only when it involves perspective-taking. They emphasize understanding of the other, and adoption of the other's point of view. In this view, then, empathy is a cognitive affair dependent on imagination and mental state attribution, which may explain the skepticism about nonhuman empathy (Hauser 2000, Povinelli 1998). Perspective-taking by itself is, of course, hardly empathy: It is so only in combination with emotional engagement. The latter here is called "empathic perspective-taking," such as in one of the oldest and best-known definitions by Smith (1759, p. 10) "changing places in fancy with the sufferer."

Menzel (1974) was the first to investigate whether chimpanzees understand what others know, setting the stage for studies of nonhuman theory-of-mind and perspective-taking. After several ups and downs in the evidence, current consensus seems to be that apes, but probably not monkeys, show some level of perspective-taking both in their spontaneous social behavior (de Waal 1996, 1998 [1982]) and under experimental conditions (Bräuer et al. 2005; Hare et al. 2001, 2006; Hirata 2006; Shillito et al. 2005).

A major manifestation of empathic perspective-taking is so-called targeted helping, which is help fine-tuned to another's specific situation and goals (de Waal 1996). The literature on primate behavior leaves little doubt about the existence of targeted helping, particularly in apes (see From Empathy to Altruism, below). A mother ape who returns to a whimpering youngster to help it from one tree to the next—by swaying her own tree toward the one the youngster is trapped in and then drape her body between both trees—goes beyond mere concern for the other. Her response likely involves emotional contagion (i.e., mother apes often briefly whimper themselves when they hear their offspring do so), but adds assessment of the specific reason for the other's distress and the other's goals. Tree bridging is a daily occurrence in orangutans, with mothers regularly anticipating their offspring's needs (van Schaik 2004, p. 104).

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.

Empathic perspective-taking: the capacity to take another's perspective—e.g., understanding another's specific situation and needs separate from one's own—combined with vicarious emotional arousal

Targeted helping: help and care based on a cognitive appreciation of the other's specific need or situation

Mirror self-recognition (MSR): recognizing that one's own body is reflected in the mirror

The coemergence hypothesis predicts that mirror self-recognition (MSR) and advanced expressions of empathy appear together in both development and phylogeny.

Ontogenetically, the coemergence hypothesis is well-supported (Bischof-Köhler 1988, Johnson 1992, Zahn-Waxler et al. 1992). The relation between MSR and the development of empathic perspective-taking holds even after the data have been statistically controlled for age (Bischof-Köhler 1991). Gallup (1982) was the first to propose phylogenetic coemergence, a prediction empirically supported by the contrast between monkeys and apes, with compelling evidence for MSR, consolation, and targeted helping only in apes.

Apart from the great apes, the animals for which we have the most striking accounts of consolation and targeted helping are dolphins and elephants (see From Empathy to Altruism, below). Gallup (1983) had already predicted MSR in dolphins and elephants, and these predictions have now been confirmed by the mark test, in which an individual needs to locate a mark on itself that it cannot see without a mirror (Plotnik et al. 2006, Reiss & Marino 2001). MSR is believed to be absent in the rest of the animal kingdom (Anderson & Gallup 1999).

It should be added that self-representation is unlikely to have appeared de novo in a few large-brained animals. The framework of developmental psychologists, according to which self-representation emerges in small incremental steps (Lewis & Brooks-Gunn 1979, Rochat 2003), may apply also to phylogeny. Instead of adhering to an all-or-nothing division of self-representation, some animals may reach an intermediate stage similar to that of pre-MSR human infants (de Waal et al. 2005).

Possibly, the link between MSR and perspective-taking is relatively loose. Perspective-taking has recently been reported for species that appear to lack MSR, both mammals (Kuroshima et al. 2003, Virányi et al. 2005) and birds (Bugnyar & Heinrich 2005, Emery & Clayton 2001). These reports concern the finding or hiding of food, however, hence not empathic perspective-taking. In the future, we may be able to address the self-other distinction more directly through neural investigation (Decety & Chaminade 2003b). In humans, the right inferior parietal cortex, at the temporo-parietal junction, underpins empathy by helping distinguish between self- and other-produced actions (Decety & Grèzes 2006).

UNDERLYING MECHANISMS

Perception Action Mechanism

Preston & de Waal (2002a) propose that at the core of the empathic capacity lies a mechanism that provides an observer (the subject) with access to the subjective state of another (the object) through the subject's own neural and bodily representations. When the subject attends to the object's state, the subject's neural representations of similar states are automatically and unconsciously activated. The more similar and socially close two individuals are, the easier the subject's identification with the object, which enhances the subject's matching motor and autonomic responses. This lets the subject get "under the skin" of the object, bodily sharing its emotions and needs, which in turn may foster sympathy and helping. Preston & de Waal's (2002a) PAM fits Damasio's (1994) somatic marker hypothesis of emotions as well as evidence for a link at the cellular level between perception and action, such as the mirror neurons discovered in macaques by di Pellegrino et al. (1992).

Human data suggest that a similar physiological substrate underlies both observing and experiencing an emotion (Adolphs et al. 1997, 2000), and that affect communication creates matching physiological states in subject and object (Dimberg 1982, 1990; Levenson & Reuf 1992). Recent investigations of the neural basis of human empathy confirm the PAM in that they report neural similarity between self-generated and vicarious emotions

(Carr et al. 2003, Decety & Chaminade 2003a, Decety & Jackson 2006, de Gelder et al. 2004, Singer et al. 2004), such as activation of the anterior ventral insula both when we are disgusted and when we see another person expressing disgust (Wicker et al. 2003).

The idea that perception and action share representations is anything but new. Accordingly, empathy is a rapid routine, as confirmed by electromyographic studies of muscle contractions in the human face in response to pictures of facial expressions, even if presented so briefly that they cannot be consciously perceived (Dimberg et al. 2000). Accounts of empathy as a cognitive process often neglect such automatic reactions, which are far too rapid to be under voluntary control.

Russian Doll Model

Empathy covers all the ways in which one individual's emotional state affects another's, with simple mechanisms at its core and more complex mechanisms and perspective-taking abilities as its outer layers. Because of this layered nature of the capacities involved, we speak of the Russian doll model, in which higher cognitive levels of empathy build upon a firm, hard-wired basis, such as the PAM (de Waal 2003). The claim is not that PAM by itself explains sympathetic concern or perspective-taking, but that it underpins these cognitively more advanced forms of empathy, and serves to motivate behavioral outcomes. Without emotional engagement induced by state-matching, perspective-taking would be a cold phenomenon that could just as easily lead to torture as to helping (Deacon 1997, de Waal 2005).

Perception-action mechanisms are well known for motor perception (Prinz & Hommel 2002, Wolpert et al. 2001), so that we may assume PAM to underlie not only emotional state matching but also motor mimicry. This means that the Russian Doll also relates to doing as others do, including bodily synchronization, coordination, imitation, and emulation (**Figure 2**). If PAM is involved in both imitation and empathy, one expects correlations between both capacities. Highly empathic persons are indeed more inclined to unconscious mimicry (Chartrand & Bargh 1999) and humans with autism spectrum disorder are not only deficient in empathy but also imitation (Charman 2002, Charman et al. 1997). Functional magnetic resonance imaging studies neurally connect motor mimicry, such as contagious yawning, with empathic modeling (Platek et al. 2005).

Other primates, too, yawn when they see conspecifics yawn (Anderson et al. 2004, Paukner & Anderson 2006). In fact, behavioral copying ("aping") is pronounced in all of the primates. Social facilitation experiments show that satiated primates begin eating again when they see others eat (Addessi & Visalberghi 2001, Dindo & de Waal 2006), scratch themselves when others scratch themselves (Nakayama 2004), and show neonatal imitation similar to that of human infants (Bard 2006, Ferrari et al. 2006). Novel behavior is copied, too, at least by the apes. Examples are juveniles imitating the peculiar walk of others (de Waal 1998 [1982], Köhler 1925) as well as successful do-as-I-do experiments with human models (Custance et al. 1995, Myowa-Yamakoshi & Matsuzawa 1999).

Bodily similarity—such as with members of the same gender and species—likely enhances shared representation and identification, which has been proposed as the basis of true imitation (de Waal 1998, 2001), such as seen in the apes (Horner & Whiten 2005). The tendency of nonhuman primates to copy each other is as spontaneous as the empathic response. Thus, mirror neurons fire automatically to observed actions, even intentions (Fogassi et al. 2005), and monkeys require no extrinsic rewards to copy each other's behavior (Bonnie & de Waal 2006).

In accordance with the PAM (Preston & de Waal 2002a), the motivational structure of both imitation and empathy therefore includes (*a*) shared representations; (*b*) identification with others based on physical similarity, shared experience, and social closeness; and

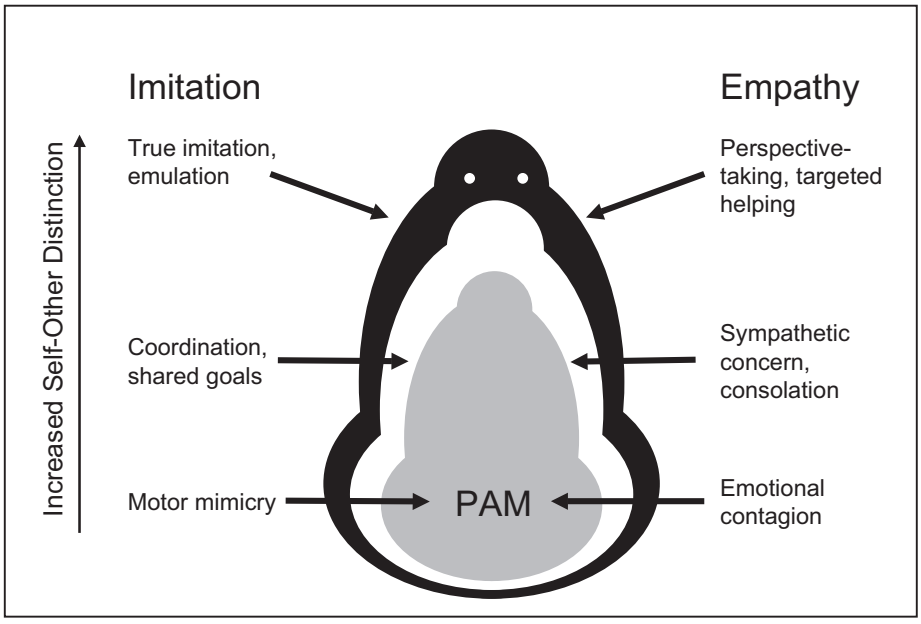

Figure 2

The Russian doll model of empathy and imitation. Empathy (*right*) induces a similar emotional state in the subject and the object, with at its core the perception-action mechanism (PAM). The doll's outer layers, such as sympathetic concern and perspective-taking, build upon this hard-wired socio-affective basis. Sharing the same mechanism, the doll's imitation side (*left*) correlates with the empathy side. Here, the PAM underlies motor mimicry, coordination, shared goals, and true imitation. Even though the doll's outer layers depend on prefrontal functioning and an increasing self-other distinction, these outer layers remain connected to its inner core.

(*c*) automaticity and spontaneity. All of this applies to the core mechanism, not necessarily to the more complex outer layers of the Russian doll model, which develop in interaction with the environment.

FROM EMPATHY TO ALTRUISM

Not all altruistic behavior requires empathy. When animals alert others to an outside threat, work together for immediate self-reward, or vocally attract others to discovered food, biologists may speak of altruism or cooperation, but this behavior is unlikely to be motivated by empathy with the beneficiary.

Emotional Contagion

Self-centered vicarious arousal, known as personal distress, represents the oldest kind of empathy. A good example seems the intensified pain response of mice seeing other mice in pain (Langford et al. 2006). Emotional contagion may lead individuals frightened by the alarm of others to hide or flee, a mother distressed by her offspring's distress to reassure both herself and her offspring by warming or nursing them, or inhibit an individual from inflicting pain upon another because of the vicarious negative arousal induced by the other's distress calls. Thus, simple empathic reactions may benefit both the actor and individuals close to them.

Behavioral copying, too, often produces adaptive outcomes. Imagine a group of animals in which every member was to eat, sleep, forage, or play independently: This would be impossible for nomadic animals, such as primates. Being in sync is often a matter of life or death (Boinski & Garber 2000).

Sympathetic Concern

Directed altruism requires the addition of other-orientation to emotional activation. In nonhuman primates, the most common empathy-based concern for others is defense against aggression. Exceptional urgency and extreme motivation are required because the reaction needs to be swift and actors may face bodily danger when assisting others against an attacker. For example, when a female reacts to the screams of her closest associate by defending her against a dominant male, she takes enormous risk on behalf of the other. She may very well be injured. What other than high emotional arousal can reasonably explain such bravery? Note the following description of two long-time chimpanzee friends in a zoo colony: "Not only do they often act together against attackers, but 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 1998 [1982], p. 67).

When Kagan (2000) argued against animal empathy by claiming that a chimpanzee would never jump into a lake to save another, Flack & de Waal (2000) replied with a quote from Goodall (1990, p. 213): "In some zoos, chimpanzees are kept on man-made islands, surrounded by water-filed moats . . . Chimpanzees cannot swim and, unless they are rescued, will drown if they fall into deep water. Despite this, individuals have sometimes made heroic efforts to save companions from drowning—and were sometimes successful. One adult male lost his life as he tried to rescue a small infant whose incompetent mother had allowed it to fall into the water."

To explain such behavior on the basis of expected return-benefits makes a huge cognitive leap by injecting ultimate goals into proximate decision-making (see Introduction, above). Admittedly, chimpanzees may deliberately engage in grooming as a way of gaining future return-favors (de Waal 1998 [1982], 1997b; Koyama et al. 2006), but grooming is a low-cost service. It is hard to imagine that the chimpanzee's extreme hydrophobia could be overcome by a cognitive gamble on future returns. A male who jumps in the water must have an overwhelming immediate motivation, which probably only emotional engagement can produce.

Fortunately, with regard to primate altruism, we do not need to rely on qualitative accounts as there exists ample systematic data, such as a rich literature on support in aggressive contexts (Harcourt & de Waal 1992), cooperation (Kappeler & van Schaik 2006), and food-sharing (Feistner & Mcgrew 1989). Although some have argued that food-sharing may not be truly altruistic because it is subject to social pressure (Gilby 2006), the problem with this view is that top-ranking individuals (who have no trouble resisting pressure) are among the most generous (de Waal 1989), and sharing occurs even when individuals are separated by bars, hence insulated from pressure (de Waal 1997c, Nissen & Crawford 1932). Rather, the begging and distress signals typical of food beggars hint at a mediating role of empathy.

In short, empathy may motivate directed altruism in primates as often visible in the similarity of facial expressions and vocalizations of both altruists and beneficiaries. Empathy is the only mechanism capable of providing a unitary motivational explanation for a wide variety of situations in which assistance is dispensed according to need. Perhaps confusingly, the mechanism is relatively autonomous in both animals and humans. Thus, empathy often reaches beyond its original evolutionary context, such as when people send money to distant tsunami victims, when primates bestow care on unrelated juvenile orphans (Thierry & Anderson 1986), or when a bonobo tries to rescue an injured bird (de Waal 1997a).

Empathic Perspective-Taking

Evidence for altruism based on empathic perspective-taking mostly consists of striking

anecdotes, which are admittedly open to multiple interpretations. However, anecdotes have traditionally provided productive starting points for research (debated between Kummer et al. 1990 and de Waal 1991).

Targeted helping has been described for cetaceans since the ancient Greeks. Dolphins are said to save companions by biting through harpoon lines or by hauling them out of nets in which they were entangled. Dolphins also support sick companions near the surface to keep them from drowning, and stay close to females in labor. Whales tend to interpose themselves between a hunter's boat and an injured conspecific, or capsize the boat (Caldwell & Caldwell 1966, Connor & Norris 1982).

Elephants are known to reassure distressed companions (Payne 1998, Poole 1996) and to support or lift up others too weak to stand (Hamilton-Douglas et al. 2006, Joubert 1991). Moss (1988, p. 73) offers a typical description of a young female, Tina, shot by a poacher: "Teresia and Trista became frantic and knelt down and tried to lift her up. They worked their tusks under her back and under her head. At one point they succeeded in lifting her into a sitting position but her body flopped back down. Her family tried everything to rouse her, kicking and tusking her, and Tallulah even went off and collected a trunkful of grass and tried to stuff it into her mouth."

For great apes, there exist literally hundreds of qualitative accounts of targeted helping, of which I cite just two striking examples:

Example 1:

> During one winter at the Arnhem Zoo, before releasing the chimps, the keepers hosed out all rubber tires in the enclosure and hung them on a horizontal log. One day, Krom was interested in a tire in which water had stayed behind. Unfortunately, this particular tire was at the end of the row, with six or more heavy tires in front of it. Krom pulled and pulled at the one she wanted but couldn't remove it. She worked in vain for over ten minutes, ignored by everyone, except Jakie, a seven-year-old Krom had taken care of as a juvenile.
>
> Immediately after Krom gave up and walked away, Jakie approached the scene. Without hesitation he pushed the tires one by one off the log, beginning with the front one, followed by the second, and so on, as any sensible chimp would. When he reached the last tire, he carefully removed it so that no water was lost, carrying it straight to his aunt, placing it upright in front of her. Krom accepted his present without any acknowledgment, and was already scooping up water with her hand when Jakie left (de Waal 1996, p. 83).

Example 2:

> The two-meter-deep moat in front of the old bonobo enclosure at the San Diego Zoo had been drained for cleaning. After having scrubbed the moat and released the apes, the keepers went to turn on the valve to refill it with water when all of a sudden the old male, Kakowet, came to their window, screaming and frantically waving his arms so as to catch their attention. After so many years, he was familiar with the cleaning routine. As it turned out, several young bonobos had entered the dry moat but were unable to get out. The keepers provided a ladder. All bonobos got out except for the smallest one, who was pulled up by Kakowet himself (de Waal 1997a, p. 34).

Because it is almost impossible, and probably unethical, to create situations in the laboratory in which primates experience intense fear or distress, there is a scarcity of experiments on costly altruism of the kind described above. More often, experiments 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 food for both itself and another by manipulating part B of the same apparatus. Colman et al. (1969) found 1 out of 4 tested macaques to be consistently other-regarding, yet two recent replications failed to find the same tendency in chimpanzees (Jensen et al. 2006, Silk et al. 2005). This has led authors to conclude that other-regarding preferences may be uniquely human. It is impossible to prove the null hypothesis, however. Given the overwhelming observational evidence for spontaneous helping and cooperation among primates, it seems only a matter of time until other-regarding preferences will be experimentally confirmed.

EMPATHY AS EVOLVED PROXIMATE MECHANISM OF DIRECTED ALTRUISM

A Russian doll is a satisfying plaything for the biologist since every outer layer encompasses an older, inner one. This is relevant to the origin of empathy: All prosocial behavior, even when dependent on prefrontal functioning, probably has PAM-based emotion sharing at its core (Preston & de Waal 2002a). Without this emotional component, it is hard to see why we or other animals would care.

Humans have so little control over empathic activation that they regularly shield themselves from it, e.g., by covering their eyes when in a movie something gruesome is about to happen. This is because they have already identified with the on-screen characters. One way to cognitively control empathy is to inhibit such identification. How self-imposed filters and contextual appraisal modulate the brain's empathic response remains a major unresolved issue (de Vignemont & Singer 2006). Sometimes, empathy appears wholly absent. For example, chimpanzees are capable of brutally killing each other (de Waal 1998 [1982], Wrangham & Peterson 1996), hence must be capable of suppressing empathic activation in relation to conspecifics, which has led Goodall (1986, p. 532) to call their victims "dechimpized." (It is important to note, though, that a species' occasional violence by no means argues against it having empathic capacities—if so, human empathy would be the first to be denied.)

The PAM model predicts that the greater the similarity or familiarity of the subject and object, the more their representations will agree, hence the more accurate their state-matching. Generally, the empathic response is amplified by similarity, familiarity, social closeness, and positive experience with the other (Table 1 in Preston & de Waal 2002a). In human studies, subjects empathize with a confederate's pleasure or distress if they perceive the relationship as cooperative, yet show an antipathic response (i.e., distress at seeing the other's pleasure or pleasure at seeing the other's distress) if they perceive the relationship as competitive (Lanzetta & Englis 1989, Zillmann & Cantor 1977). These effects of previous experience have recently been confirmed by functional magnetic resonance imaging: Seeing the pain of a cooperative confederate activates pain-related brain areas, but seeing the pain of an unfair confederate activates reward-related brain areas, at least in men (Singer et al. 2006).

Relationship effects are also known for rodents, in which emotional contagion is measurable between cagemates but not between strangers (Langford et al. 2006). In monkeys, empathic responses to another's fear or pain are enhanced by familiarity between subject and object (Masserman et al. 1964, Miller at al. 1959). Thus, the empathy mechanism is biased the way evolutionary theory would predict. Empathy is (*a*) activated in relation to those with whom one has a close or positive relationship, and (*b*) suppressed, or even turned into Schadenfreude, in relation to strangers and defectors. The latter, retaliatory aspect corresponds with well-documented chimpanzee behavior: These apes not only

reciprocate favors within positive relationships, but also take revenge upon those who have previously acted against them (de Waal & Luttrell 1988).

A common way in which mutually beneficial exchanges are achieved is through investment in long-term bonds to which both parties contribute. This reciprocity mechanism is commonplace in nonhuman primates (de Waal & Brosnan 2006) and has been suggested for human relations as well. Individual interests may be served by partnerships (e.g., marriages, friendships) that create a long-lasting communal "fitness interdependence" mediated by mutual empathy. Within these relationships, partners do not necessarily keep careful track of who did what for whom (Clark & Mills 1979), and derive psychological and health benefits not only from receiving but also from giving support (Brown & Brown 2006).

If altruism is produced by mechanisms, such as empathy and bonding, that produce emotional identification with the other, one may well ask if helping another does not boil down to helping oneself. It does, but as Smith (1759) argued, this is no reason to call empathy-based altruism selfish. A truly selfish individual would have no trouble walking away from another in need, whereas empathic engagement hooks one into the other's situation. Since the mechanism delivers intrinsic rewards exclusively via the other, it is genuinely other-oriented (Wispé 1991). At the same time, it is futile to try to extract the self from the process. There simply is no satisfactory answer to the question of how altruistic is altruism (debated among Batson et al. 1997, Cialdini et al. 1997, Hornstein 1991, Krebs 1991). This is, in fact, the beauty of the empathy-altruism connection: The mechanism works so well because it gives individuals an emotional stake in the welfare of others.

CONCLUSION

More than three decades ago, biologists deliberately removed the altruism from altruism. There is now increasing evidence that the brain is hardwired for social connection, and that the same empathy mechanism proposed to underlie human altruism (Batson 1991) may underlie the directed altruism of other animals. Empathy could well provide the main motivation making individuals who have exchanged benefits in the past to continue doing so in the future. Instead of assuming learned expectations or calculations about future benefits, this approach emphasizes a spontaneous altruistic impulse and a mediating role of the emotions. It is summarized in the five conclusions below:

1. An evolutionarily parsimonious account (cf. de Waal 1999) of directed altruism assumes similar motivational processes in humans and other animals.
2. Empathy, broadly defined, is a phylogenetically ancient capacity.
3. Without the emotional engagement brought about by empathy, it is unclear what could motivate the extremely costly helping behavior occasionally observed in social animals.
4. Consistent with kin selection and reciprocal altruism theory, empathy favors familiar individuals and previous cooperators, and is biased against previous defectors.
5. Combined with perspective-taking abilities, empathy's motivational autonomy opens the door to intentionally altruistic altruism in a few large-brained species.

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LITERATURE CITED

Acebo C, Thoman EB. 1995. Role of infant crying in the early mother-infant dialogue. *Physiol. Behav.* 57:541–47

Addessi E, Visalberghi E. 2001. Social facilitation of eating novel food in tufted capuchin monkeys (*Cebus apella*): input provided by group members and responses affected in the observer. *Anim. Cogn.* 4:297–303

Adolphs R, Cahill L, Schul R, Babinsky R. 1997. Impaired declarative memory for emotional material following bilateral amygdala damage in humans. *Learn. Mem.* 4:291–300

Adolphs R, Damasio H, Tranel D, Cooper G, Damasio AR. 2000. A role for somatosensory cortices in the visual recognition of emotion as revealed by three-dimensional lesion mapping. *J. Neurosci.* 20:2683–90

Adolphs R, Tranel D, Damasio H, Damasio AR. 1994. Impaired recognition of emotion in facial expressions following bilateral damage to the human amygdala. *Nature* 372:669–72

Anderson JR, Gallup GG. 1999. Self-recognition in nonhuman primates: past and future challenges. In *Animal Models of Human Emotion and Cognition*, ed. M Haug, RE Whalen, pp. 175–94. Washington, DC: APA Books

Anderson JR, Myowa-Yamakoshi M, Matsuzawa T. 2004. Contagious yawning in chimpanzees. *Proc. R. Soc. Lond. B* (Suppl.)271:S468–70

Bard KA. 2007. Neonatal imitation in chimpanzees (*Pan troglodytes*) tested with two paradigms. *Anim. Cogn.* 10:233–42

Batson CD. 1991. *The Altruism Question: Toward a Social-Psychological Answer*. Hillsdale, NJ: Erlbaum

Batson CD, Sager K, Garst E, Kang M, Rubchinsky K, Dawson K. 1997. Is empathy-induced helping due to self-other merging? *J. Person. Soc. Psychol.* 73:495–509

Bischof-Köhler D. 1988. Über den Zusammenhang von Empathie und der Fähigkeit sich im Spiegel zu erkennen. *Schw. Z. Psychol.* 47:147–59

Bischof-Köhler D. 1991. The development of empathy in infants. In *Infant Development: Perspectives from German-Speaking Countries*, ed. M Lamb, M Keller, pp. 245–73. Hillsdale, NJ: Erlbaum

Boesch C. 1992. New elements of a theory of mind in wild chimpanzees. *Behav. Brain Sci.* 15:149–50

Boinski S, Garber PA. 2000. *On the Move: How and Why Animals Travel in Groups.* Chicago: Univ. Chicago Press

Bonnie KE, de Waal FBM. 2007. Copying without rewards: socially influenced foraging decisions among brown capuchin monkeys. *Anim. Cogn.* DOI: 10.1007/s10071-006-0069-9

Bowlby J. 1958. The nature of the child's tie to his mother. *Int. J. Psychoanal.* 39:350–73

Bräuer J, Call J, Tomasello M. 2005. All great ape species follow gaze to distant locations and around barriers. *J. Comp. Psychol.* 119:145–54

Brown SL, Brown RM. 2006. Selective investment theory: recasting the functional significance of close relationships. *Psychol. Inq.* 17:1–29

Bugnyar T, Heinrich B. 2005. Food-storing ravens differentiate between knowledgeable and ignorant competitors. *Proc. Roy. Soc. Lond. B* 272:1641–46

Caldwell MC, Caldwell DK. 1966. Epimeletic (care-giving) behavior in Cetacea. In *Whales, Dolphins, and Porpoises*, ed. KS Norris, pp. 755–89. Berkeley: Univ. Calif. Press

Carr L, Iacoboni M, Dubeau MC, Mazziotta JC, Lenzi GL. 2003. Neural mechanisms of empathy in humans: a relay from neural systems for imitation to limbic areas. *Proc. Natl. Acad. Sci. USA* 100:5497–502

Charman T. 2002. Understanding the imitation deficit in autism may lead to a more specific model of autism as an empathy disorder. *Behav. Brain Sci.* 25:29–30

Charman T, Swettenham J, Baron-Cohen S, Cox A, Baird G, Drew A. 1997. Infants with autism: an investigation of empathy, pretend play, joint attention, and imitation. *Dev. Psychol.* 33:781–89

Chartrand TL, Bargh JA. 1999. The chameleon effect: the perception-behavior link and social interaction. *J. Personal. Soc. Psychol.* 76:893–910

Church RM. 1959. Emotional reactions of rats to the pain of others. *J. Comp. Physiol. Psychol.* 52:132–34

Cialdini RB, Brown SL, Lewis BP, Luce CL, Neuberg SL. 1997. Reinterpreting the empathy-altruism relationship: when one into one equals oneness. *J. Personal. Soc. Psychol.* 73:481–94

Clark MS, Mills J. 1979. Interpersonal attraction in exchange and communal relationships. *J. Personal. Soc. Psychol.* 37:12–24

Colman AD, Liebold KE, Boren JJ. 1969. A method for studying altruism in monkeys. *Psychol. Record* 19:401–5

Connor RC, Norris KS. 1982. Are dolphins reciprocal altruists? *Am. Natural.* 119:358–72

Cordoni G, Palagi E, Borgognini TS. 2004. Reconciliation and consolation in captive Western gorillas. *Int. J. Primatol.* 27:1365–82

Custance DM, Whiten A, Bard KA. 1995. Can young chimpanzees imitate arbitrary actions? Hayes and Hayes 1952 revisited. *Behaviour* 132:835–59

Damasio AR. 1994. *Descartes' Error: Emotion, Reason, and the Human Brain.* New York: Putnam

Darwin C. 1982 [1871]. *The Descent of Man, and Selection in Relation to Sex.* Princeton, NJ: Princeton Univ. Press

Dawkins R. 1976. *The Selfish Gene.* Oxford, UK: Oxford Univ. Press

Deacon TW. 1997. *The Symbolic Species: The Co-Evolution of Language and the Brain.* New York: Norton

Decety J, Chaminade T. 2003a. Neural correlates of feeling sympathy. *Neuropsychology* 41:127–38

Decety J, Chaminade T. 2003b. When the self represents the other: a new cognitive neuroscience view on psychological identification. *Conscious Cogn.* 12:577–96

Decety J, Grèzes J. 2006. The power of simulation: imagining one's own and other's behavior. *Brain Res.* 1079:4–14

Decety J, Jackson PL. 2006. A social-neuroscience perspective on empathy. *Curr. Dir. Psychol. Sci.* 15:54–58

de Gelder B, Snyder J, Greve D, Gerard G, Hadjikhani N. 2004. Fear fosters flight: a mechanism for fear contagion when perceiving emotion expressed by a whole body. *Proc. Natl. Acad. Sci. USA* 101:16701–6

de Vignemont F, Singer T. 2006. The empathic brain: how, when and why? *Trends Cogn. Sci.* 10:435–41

de Waal FBM. 1989. Food sharing and reciprocal obligations among chimpanzees. *J. Hum. Evol.* 18:433–59

de Waal FBM. 1991. Complementary methods and convergent evidence in the study of primate social cognition. *Behaviour* 118:297–320

de Waal FBM. 1996. *Good Natured: The Origins of Right and Wrong in Humans and Other Animals.* Cambridge, MA: Harvard Univ. Press

de Waal FBM. 1997a. *Bonobo: The Forgotten Ape.* Berkeley: Univ. Calif. Press

de Waal FBM. 1997b. The chimpanzee's service economy: food for grooming. *Evol. Hum. Behav.* 18:375–86

de Waal FBM. 1997c. Food-transfers through mesh in brown capuchins. *J. Comp. Psychol.* 111:370–78

de Waal FBM. 1998 [1982]. *Chimpanzee Politics: Power and Sex Among Apes.* Baltimore, MD: Johns Hopkins Univ. Press

de Waal FBM. 1998. No imitation without identification. *Behav. Brain Sci.* 21:689

de Waal FBM. 1999. Anthropomorphism and anthropodenial: consistency in our thinking about humans and other animals. *Philos. Topics* 27:255–80

de Waal FBM. 2001. *The Ape and the Sushi Master.* New York: Basic Books

de Waal FBM. 2003. On the possibility of animal empathy. In *Feelings & Emotions: The Amsterdam Symposium*, ed. T Manstead, N Frijda, A Fischer, pp. 379–99. Cambridge, UK: Cambridge Univ. Press

de Waal FBM. 2005. *Our Inner Ape.* New York: Riverhead

de Waal FBM, Aureli F. 1996. Consolation, reconciliation, and a possible cognitive difference between macaque and chimpanzee. In *Reaching into Thought: The Minds of the Great Apes*, ed. AE Russon, KA Bard, ST Parker, pp. 80–110. Cambridge, UK: Cambridge Univ. Press

de Waal FBM, Brosnan SF. 2006. Simple and complex reciprocity in primates. In *Cooperation in Primates and Humans: Mechanisms and Evolution*, ed. PM Kappeler, CP van Schaik, pp. 85–105. Berlin: Springer

de Waal FBM, Davis JM. 2003. Capuchin cognitive ecology: cooperation based on projected returns. *Neuropsychology* 41:221–28

de Waal FBM, Dindo M, Freeman CA, Hall M. 2005. The monkey in the mirror: hardly a stranger. *Proc. Natl. Acad. Sci. USA* 102:11140–47

de Waal FBM, Luttrell LM. 1988. Mechanisms of social reciprocity in three primate species: symmetrical relationship characteristics or cognition? *Ethol. Sociobiol.* 9:101–18

de Waal FBM, van Roosmalen A. 1979. Reconciliation and consolation among chimpanzees. *Behav. Ecol. Sociobiol.* 5:55–66

di Pellegrino G, Fadiga L, Fogassi L, Gallese V, Rizzolatti G. 1992. Understanding motor events: a neurophysiological study. *Exp. Brain Res.* 91:176–80

Dimberg U. 1982. Facial reactions to facial expressions. *Psychophysiology* 19:643–47

Dimberg U. 1990. Facial electromyographic reactions and autonomic activity to auditory stimuli. *Biol. Psychol.* 31:137–47

Dimberg U, Thunberg M, Elmehed K. 2000. Unconscious facial reactions to emotional facial expressions. *Psychol. Sci.* 11:86–89

Dindo M, de Waal FBM. 2006. Partner effects on food consumption in brown capuchin monkeys. *Am. J. Primatol.* 69:1–9

Dittus WPJ, Ratnayeke SM. 1989. Individual and social behavioral responses to injury in wild toque macaques (*Macaca sinica*). *Int. J. Primatol.* 10:215–34

Dugatkin L. 1997. *Cooperation Among Animals: An Evolutionary Perspective.* New York: Oxford Univ. Press

Dugatkin L. 2006. *The Altruism Equation: Seven Scientists Search for the Origin of Goodness*. Princeton, NJ: Princeton Univ. Press

Eibl-Eibesfeldt I. 1974 [1971]. *Love and Hate*. New York: Schocken

Eisenberg N. 2000. Empathy and sympathy. In *Handbook of Emotion*, ed. M Lewis, JM Haviland-Jones, pp. 677–91. New York: Guilford. 2nd ed.

Emery NJ, Clayton NS. 2001. Effects of experience and social context on prospective caching strategies by scrub jays. *Nature* 414:443–46

Fehr E, Fischbacher U. 2003. The nature of human altruism. *Nature* 425:785–91

Feistner ATC, McGrew WC. 1989. Food-sharing in primates: a critical review. In *Perspectives in Primate Biology*, Vol. 3, ed. PK Seth, S Seth, pp. 21–36. New Delhi: Today Tomorrow's

Ferrari PF, Visalbergi E, Paukner A, Gogassi L, Ruggiero A, Suomi SJ. 2006. Neonatal imitation in rhesus macaques. *PLOS Biol.* 4:1501–8

Flack JC, de Waal FBM. 2000. Being nice is not a building block of morality: response to commentary discussion. *J. Consc. Stud.* 7:67–77

Fogassi L, Ferrari PF, Chersi F, Gesierich B, Rozzi S, et al. 2005. Parietal lobe: from action organization to intention understanding. *Science* 308:662–67

Fuentes A, Malone N, Sanz C, Matheson M, Vaughan L. 2002. Conflict and postconflict behavior in a small group of chimpanzees. *Primates* 43:223–35

Fujisawa KK, Kutsukake N, Hasegawa T. 2006. Peacemaking and consolation in Japanese preschoolers witnessing peer aggression. *J. Comp. Psychol.* 120:48–57

Gallup GG. 1982. Self-awareness and the emergence of mind in primates. *Am. J. Primatol.* 2:237–48

Gallup GG. 1983. Toward a comparative psychology of mind. In *Animal Cognition and Behavior*, ed. RL Mellgren, pp. 473–510. New York: North-Holland

Gilby IC. 2006. Meat sharing among the Gombe chimpanzees: harassment and reciprocal exchange. *Anim. Behav.* 71:953–63

Goodall J. 1986. *The Chimpanzees of Gombe: Patterns of Behavior.* Cambridge, MA: Belknap

Goodall J. 1990. *Through a Window: My Thirty Years with the Chimpanzees of Gombe.* Boston, MA: Houghton Mifflin

Hamilton WD. 1964. The genetical evolution of social behaviour I and II. *J. Theor. Biol.* 7:1–52

Hamilton-Douglas I, Bhalla S, Wittemyer G, Vollrath F. 2006. Behavioural reactions of elephants towards a dying and deceased matriarch. *Appl. Anim. Behav. Sci.* 100:87–102

Harcourt AH, de Waal FBM. 1992. *Coalitions and Alliances in Humans and Other Animals.* Oxford, UK: Oxford Univ. Press

Hare B, Call J, Tomasello M. 2001. Do chimpanzees know what conspecifics know? *Anim. Behav.* 61:139–51

Hare B, Call J, Tomasello M. 2006. Chimpanzees deceive a human competitor by hiding. *Cognition* 101:495–514

Hatfield E, Cacioppo JT, Rapson RL. 1993. Emotional contagion. *Curr. Dir. Psychol. Sci.* 2:96–99

Hauser MD. 2000. *Wild Minds: What Animals Really Think.* New York: Holt

Hirata S. 2006. Tactical deception and understanding of others in chimpanzees. In *Cognitive Development in Chimpanzees*, ed. T Matsuzawa, M Tomanaga, M Tanaka, pp. 265–76. Tokyo: Springer Verlag

Hoffman ML. 1975. Developmental synthesis of affect and cognition and its implications for altruistic motivation. *Dev. Psychol.* 11:607–22

Hoffman ML. 1981a. Is altruism part of human nature? *J. Personal. Soc. Psychol.* 40:121–37

Hoffman ML. 1981b. Perspectives on the difference between understanding people and understanding things: the role of affect. In *Social Cognitive Development*, ed. JH Flavell, L Ross, pp. 67–81. Cambridge, UK: Cambridge Univ. Press

Hoffman ML. 1982. Development of prosocial motivation: empathy and guilt. In *The Development of Prosocial Behavior*, ed. N Eisenberg, pp. 281–338. New York: Academic

Horner V, Whiten A. 2005. Causal knowledge and imitation/emulation switching in chimpanzees and children. *Anim. Cogn.* 8:164–81

Hornstein HA. 1991. Empathic distress and altruism: still inseparable. *Psychol. Inq.* 2:133–35

Jensen K, Hare B, Call J, Tomasello M. 2006. What's in it for me? Self-regard precludes altruism and spite in chimpanzees. *Proc. R. Soc. Lond. B Biol. Sci.* 273:1013–21

Johnson DB. 1992. Altruistic behavior and the development of the self in infants. *Merrill-Palmer Q. Behav. Dev.* 28:379–88

Joubert D. 1991. Elephant wake. *Natl. Geogr.* 179:39–42
Kagan J. 2000. Human morality is distinctive. *J. Consc. Stud.* 7:46–48
Kappeler PM, van Schaik CP. 2006. *Cooperation in Primates and Humans: Mechanisms and Evolution*. Berlin: Springer
Köhler W. 1925. *The Mentality of Apes.* New York: Vintage
Koski SE, Sterck EHM. 2007. Triadic post-conflict affiliation in captive chimpanzees: does consolation console? *Anim. Behav.* 73:133–42
Koyama NF, Caws C, Aureli F. 2006. Interchange of grooming and agonistic support in chimpanzees. *Int. J. Primatol.* 27:1293–309
Krebs DL. 1991. Altruism and egoism: a false dichotomy? *Psychol. Inq.* 2:137–9
Kummer H, Dasser V, Hoyningen-Huene P. 1990. Exploring primate social cognition: some critical remarks. *Behaviour* 112:84–98
Kuroshima H, Fujita K, Adachi I, Iwata K, Fuyuki A. 2003. A capuchin monkey (*Cebus apella*) recognizes when people do and do not know the location of food. *Anim. Cogn.* 6:283–91
Kutsukake N, Castles DL. 2004. Reconciliation and postconflict third-party affiliation among wild chimpanzees in the Mahale Mountains, Tanzania. *Primates* 45:157–65
Ladygina-Kohts NN. 2001 [1935]. *Infant Chimpanzee and Human Child: A Classic 1935 Comparative Study of Ape Emotions and Intelligence*, ed. FBM de Waal. New York: Oxford Univ. Press
Langford DJ, Crager SE, Shehzad Z, Smith SB, Sotocinal SG, et al. 2006. Social modulation of pain as evidence for empathy in mice. *Science* 312:1967–70
Lanzetta JT, Englis BG. 1989. Expectations of cooperation and competition and their effects on observers' vicarious emotional responses. *J. Personal. Soc. Psychol.* 56:543–54
Levenson RW, Reuf AM. 1992. Empathy: a physiological substrate. *J. Personal. Soc. Psychol.* 63:234–46
Lewis M. 2002. Empathy requires the development of the self. *Behav. Brain Sci.* 25:42
Lewis M, Brooks-Gunn J. 1979. *Social Cognition and the Acquisition of Self.* New York: Plenum
Lipps T. 1903. Einfühlung, innere Nachahmung und Organempfindung. *Arch. für die gesamte Psychol.* 1:465–519
MacLean PD. 1985. Brain evolution relating to family, play, and the separation call. *Arch. Gen. Psychiatry* 42:405–17
Mallavarapu S, Stoinski TS, Bloomsmith MA, Maple TL. 2006. Postconflict behavior in captive western lowland gorillas (*Gorilla gorilla gorilla*). *Am. J. Primatol.* 68:789–801
Masserman J, Wechkin MS, Terris W. 1964. Altruistic behavior in rhesus monkeys. *Am. J. Psychiatry* 121:584–85
Mayr E. 1961. Cause and effect in biology. *Science* 134:1501–6
Melis A, Hare B, Tomasello M. 2006. Engineering cooperation in chimpanzees: tolerance constraints on cooperation. *Anim. Behav.* 72:275–86
Menzel EW. 1974. A group of young chimpanzees in a one-acre field. In *Behavior of Non-human Primates*, Vol. 5, ed. AM Schrier, F Stollnitz, pp. 83–153. New York: Academic
Miller RE, Murphy JV, Mirsky IA. 1959. Relevance of facial expression and posture as cues in communication of affect between monkeys. *Arch. Gen. Psychiatry* 1:480–88
Moss C. 1988. *Elephant Memories: Thirteen Years in the Life of an Elephant Family.* New York: Fawcett Columbine
Myowa-Yamakoshi G, Matsuzawa T. 1999. Factors influencing imitation of manipulatory actions in chimpanzees. *J. Comp. Psychol.* 113:128–36
Nakayama K. 2004. Observing conspecifics scratching induces a contagion of scratching in Japanese monkeys (*Macaca fuscata*). *J. Comp. Psychol.* 118:20–24

Nissen H, Crawford M. 1932. A preliminary study of food-sharing behavior in young chimpanzees. *J. Comp. Psychol.* 22:383–419

O'Connell SM. 1995. Empathy in chimpanzees: evidence for theory of mind? *Primates* 36:397–410

Palagi E, Cordoni G, Borgognini Tarli S. 2006. Possible roles of consolation in captive chimpanzees (*Pan troglodytes*). *Am. J. Phys. Anthrop.* 129:105–11

Palagi E, Paoli T, Borgognini Tarli S. 2004. Reconciliation and consolation in captive bonobos (*Pan paniscus*). *Am. J. Primatol.* 62:15–30

Panksepp J. 1998. *Affective Neuroscience: The Foundations of Human and Animal Emotions.* New York: Oxford Univ. Press

Parr LA. 2001. Cognitive and physiological markers of emotional awareness in chimpanzees, *Pan troglodytes*. *Anim. Cogn.* 4:223–29

Parr LA, Hopkins WD. 2001. Brain temperature asymmetries and emotional perception in chimpanzees. *Pan troglodytes. Physiol. Behav.* 71:363–71

Parr LA, Waller BM. 2007. The evolution of human emotion. In *Evolution of Nervous Systems: A Comprehensive Reference*, Vol. 4, ed. JA Kaas, pp. 447–72. New York: Academic

Paukner A, Anderson JR. 2006. Video-induced yawning in stumptail macaques (*Macaca arctoides*). *Biol. Lett.* 2:36–38

Payne K. 1998. *Silent Thunder: In the Presence of Elephants*. New York: Penguin

Platek SM, Mohamed FB, Gallup GG. 2005. Contagious yawning and the brain. *Cogn. Brain Res.* 23:448–52

Plomin R, Emde RN, Braungart JM, Campos J, Corley R, et al. 1993. Genetic change and continuity from fourteen to twenty months: The MacArthur Longitudinal Twin Study. *Child Dev.* 64:1354–76

Plotnik J, de Waal FBM, Reiss D. 2006. Self-recognition in an Asian elephant. *Proc. Natl. Acad. Sci. USA* 103:17053–57

Plutchik R. 1987. Evolutionary bases of empathy. In *Empathy and Its Development*, ed. N Eisenberg, J Strayer, pp. 3–46. Cambridge, UK: Cambridge Univ. Press

Poole J. 1996. *Coming of Age with Elephants: A Memoir.* New York: Hyperion

Potegal M. 2000. Post-tantrum affiliation with parents: the ontogeny of reconciliation. In *Natural Conflict Resolution*, ed. F Aureli, FBM de Waal, pp. 253–55. Berkeley: Univ. Calif. Press

Povinelli DJ. 1998. Can animals empathize? Maybe not. *Sci. Am.* **http://geowords.com/lostlinks/b36/7.htm**

Preston SD, de Waal FBM. 2002a. Empathy: its ultimate and proximate bases. *Behav. Brain Sci.* 25:1–72

Preston SD, de Waal FBM. 2002b. The communication of emotions and the possibility of empathy in animals. In *Altruistic Love: Science, Philosophy, and Religion in Dialogue*, ed. SG Post, LG Underwood, JP Schloss, WB Hurlbut, pp. 284–308. Oxford, UK: Oxford Univ. Press

Prinz W, Hommel B. 2002. *Common Mechanisms in Perception and Action.* Oxford, UK: Oxford Univ. Press

Reiss D, Marino L. 2001. Mirror self-recognition in the bottlenose dolphin: a case of cognitive convergence. *Proc. Natl. Acad. Sci. USA* 98:5937–42

Rimm-Kaufman SE, Kagan J. 1996. The psychological significance of changes in skin temperature. *Motiv. Emot.* 20:63–78

Rochat P. 2003. Five levels of self-awareness as they unfold early in life. *Consc. Cogn.* 12:717–31

Schino G, Geminiani S, Rosati L, Aureli F. 2004. Behavioral and emotional response of Japanese macaque (*Macaca fuscata*) mothers after their offspring receive an aggression. *J. Comp. Psychol.* 118:340–46
Seed AM, Clayton NS, Emery NJ. 2007. Postconflict third-party affiliation in rooks, *Corvus frugilegus*. *Curr. Biol.* 17:152–58
Shillito DJ, Shumaker RW, Gallup GG, Beck BB. 2005. Understanding visual barriers: evidence for Level 1 perspective taking in an orangutan, *Pongo pygmaeus*. *Anim. Behav.* 69:679–87
Silk JB, Brosnan SF, Vonk J, Henrich J, Povinelli D, et al. 2005. Chimpanzees are indifferent to the welfare of unrelated group members. *Nature* 437:1357–59
Singer T, Seymour B, O'Doherty J, Kaube H, Dolan RJ, Frith CD. 2004. Empathy for pain involves the affective but not sensory components of pain. *Science* 303:1157–62
Singer T, Seymour B, O'Doherty JP, Stephan KE, Dolan RJ, Frith CD. 2006. Empathic neural responses are modulated by the perceived fairness of others. *Nature* 439:466–69
Smith A. 1976 [1759]. *A Theory of Moral Sentiments*, ed. DD Raphael, AL Macfie. Oxford, UK: Clarendon
Sober E, Wilson DS. 1998. *Unto Others: The Evolution and Psychology of Unselfish Behavior*. Cambridge, MA: Harvard Univ. Press
Thierry B, Anderson JR. 1986. Adoption in anthropoid primates. *Int. J. Primatol.* 7:191–216
Tinbergen N. 1963. On aims and methods of ethology. *Z. Tierpsychol.* 20:410–33
Trivers RL. 1971. The evolution of reciprocal altruism. *Q. Rev. Biol.* 46:35–57
Trivers RL. 2002. *Natural Selection and Social Theory*. Oxford, UK: Oxford Univ. Press
van Schaik CP. 2004. *Among Orangutans: Red Apes and the Rise of Human Culture*. Cambridge, MA: Belknap
Virányi Zs, Topál J, Miklósi Á, Csányi V. 2005. A nonverbal test of knowledge attribution: a comparative study on dogs and human infants. *Anim. Cogn.* 9:13–26
Watanabe S, Ono K. 1986. An experimental analysis of "empathic" response: effects of pain reactions of pigeon upon other pigeon's operant behavior. *Behav. Proc.* 13:269–77
Watts DP, Colmenares F, Arnold K. 2000. Redirection, consolation, and male policing: how targets of aggression interact with bystanders. In *Natural Conflict Resolution*, ed. F Aureli, FBM de Waal, pp. 281–301. Berkeley: Univ. Calif. Press
Wechkin S, Masserman JH, Terris W. 1964. Shock to a conspecific as an aversive stimulus. *Psychon. Sci.* 1:47–48
Wicker B, Keysers C, Plailly J, Royet JP, Gallese V, Rizzolatti G. 2003. Both of us disgusted in *my* insula: the common neural basis of seeing and feeling disgust. *Neuron* 40:655–64
Wilson EO. 2005. Kin selection as the key to altruism: its rise and fall. *Social. Res.* 72:159–66
Wispé L. 1991. *The Psychology of Sympathy*. New York: Plenum
Wittig R, Boesch C. 2003. The choice of postconflict interactions in wild chimpanzees (*Pan troglodytes*). *Behaviour* 140:1527–59
Wolpert DM, Ghahramani Z, Flanagan JR. 2001. Perspectives and problems in motor learning. *Trends Cogn. Sci.* 5:487–94
Wrangham RW, Peterson D. 1996. *Demonic Males: Apes and the Evolution of Human Aggression*. Boston, MA: Houghton Mifflin
Yerkes RM. 1925. *Almost Human*. New York: Century
Zahn-Waxler C, Hollenbeck B, Radke-Yarrow M. 1984. The origins of empathy and altruism. In *Advances in Animal Welfare Science*, ed. MW Fox, LD Mickley, pp. 21–39. Washington, DC: Humane Soc. U.S.

Zahn-Waxler C, Radke-Yarrow M. 1990. The origins of empathic concern. *Motiv. Emot.* 14:107–30

Zahn-Waxler C, Radke-Yarrow M, Wagner E, Chapman M. 1992. Development of concern for others. *Dev. Psychol.* 28:126–36

Zillmann D, Cantor JR. 1977. Affective responses to the emotions of a protagonist. *J. Exp. Soc. Psychol.* 13:155–65s

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