THE COMMUNICATION OF EMOTIONS AND THE POSSIBILITY OF

EMPATHY IN ANIMALS

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The possibility of nonhuman animals having empathy and sympathy has thus far received little attention in behavioral biology. This is due in part to the portrayal of the natural world as a field of combat rather than a place of social connectedness. Some prominent contemporary evolutionists, such as Williams (1989) and Dawkins (1976), still follow T. H. Huxley (1894), seeing no room within the evolutionary realm for morality and kindness. According to Huxley, such tendencies could have come into being only secondarily, as a cultural innovation of the human species. According to many contemporary psychologists and neuroscientists, "true empathy" is a cognitive innovation more akin to perspective taking (imagining yourself in the physical or mental place of another) (e.g. Povinelli et al. 1992a and b, Thompson, 1987, Ungerer et al. 1990). This characterization limits "true empathy" to those who can pass high level cognitive tests, usually humans above a certain age.

Interestingly, Darwin (1871) himself expressed in The Descent of Man a much more united view, partly inspired by moral philosophers such as Adam Smith and David Hume. Darwin saw morality, including one of its pillars – sympathy – as a natural tendency; a viewpoint that is now all but forgotten but highly relevant to the present discussion (Flack & de Waal, 2000). Empirical research on animals

supports Darwin's view, revealing empathy to be a phylogenetically continuous phenomenon that exists to varying degrees in non-human species.

In experiments designed to elicit distress in children, the family dog often displays consolatory behaviors towards the human feigning distress (Zahn-Waxler et al. 1984). Both rats and pigeons in the laboratory display a profound emotional response to the suffering of a conspecific and act to terminate the stress manipulation. Monkeys react similarly in experimental distress situations, even starving themselves to prevent a conspecific from being shocked in their presence. There are many striking examples of empathy in apes. Much research has empirically demonstrated the existence of consolation in chimpanzees, whereby one animal will act to soothe the distress of another.

To whet the appetite for the existence of empathy in apes, consider the following anecdotal example from de Waal's (1997b) *Bonobo: The Forgotten Ape*:

> "Kidogo, a twenty-one year old bonobo [*Pan paniscus*] at the Milwaukee County Zoo suffers from a serious heart condition. He is feeble, lacking the normal stamina and self-confidence of a grown male. When first moved to Milwaukee Zoo, the keepers' shifting commands in the unfamiliar building thoroughly confused him. He failed to understand where to go when people urged him to move from one place to another.
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> Other apes in the group would step in, however. They would approach Kidogo, take him by the hand, and lead him in the right direction. Care-taker and animal trainer Barbara Bell observed many instances of spontaneous assistance, and learned to call upon other bonobos to move Kidogo. If lost, Kidogo would utter distress calls, whereupon others would calm him down, or act as his guide. One of his main helpers was the highest-ranking male, Lody. These observations of bonobo males walking hand-in-hand dispel the notion that they are unsupportive of each other.
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> Only one bonobo tried to take advantage of Kidogo's condition. Murph, a five-year-old male, often teased Kidogo, who lacked the assertiveness to stop the youngster. Lody, however, sometimes interfered by grabbing the juvenile by an ankle when he was about to start his annoying games, or by going over to Kidogo to put a protective arm around him" (de Waal 1997b:157).

Macaque monkeys also show a high degree of tolerance and helping towards handicapped group members, attesting to a high degree of social attachment. Azalea, a rhesus macaque (Macaca mulatta) who lived in a socially-housed group, had autosomal trisomy (de Waal et al. 1996). As a result of her

disorder, Azalea had motor defects and delays in developing social behavior. She had a high dependency on her mother and kin and poorly defined dominance relationships. Despite these physical and social defects in a group of highly structured, aggressive animals, Azalea was tolerated and accepted in the group. Up until her death at age 32 months, Azalea was not peripheralized from the group and there were no signs of aggressive rejection by other group members. A wild female Japanese macaque (M. fuscata) named Mozu had congenitally deformed lower portions of her legs and arms. Despite her related difficulties with locomotion, foraging and care of young, Mozu was an integrated member of her group and had five offspring who lived to reproduce (de Waal 1996b).

Given that many animals are emotionally affected by the distress of another, and sometimes show appropriate helping responses, we regard empathy as a general class of behavior that exists across species, to different degrees of complexity. As a general class, empathy relies on the fact that conspecifics are emotionally interlinked. The emotional state of one individual has the potential to elicit a similar state in nearby individuals. This emotional linkage has been present in primitive forms through much of the evolutionary history of chordates in the form of alarm and vicarious arousal. This basic linkage was then augmented by enhanced cognitive and emotional abilities through evolution and extended ontogeny (development of the individual), allowing individuals to experience empathy in the absence of releasing stimuli, towards more distant individuals, and without being overwhelmed by personal distress. These additions increase the likelihood of empathy and helping, and allow for more and more complex forms of empathy, like those characteristic of the mother-infant bond and of highly cooperative animals, such as wolves, dolphins and primates.

WHAT IS EMPATHY?

Across and within disciplines, scientists use the term empathy differently (for reviews see Eisenberg and Lennon 1983, Hornblow 1980, Wispé 1986). Some definitions hinge on psycho-

physiological aspects, some stress evolutionary emergence, and others developmental emergence. Usually, definitions are operationalized to support a specific research agenda rather than a broad theoretical perspective. For the purpose of clarity, working definitions are provided here for emotional contagion, empathy, and sympathy that are generally consistent with the definitions employed by current researchers (e.g. Eisenberg and Strayer 1987, Hoffman 1982, O'Connell 1995, Wispé 1986).

Emotional contagion refers to an emotional state in an observer (hereafter, "the subject") as a direct result of perceiving the emotional state of another (hereafter, "the object"). The level of emotion in the subject is generally high and self-focused. Emotional contagion includes the spreading of all forms of emotion from one individual to another (e.g. the spreading of joy or distress through a crowd). For the purpose of the present chapter, we will focus on the contagion of distress, as most research in the field deals with this aspect. With respect to humans, the contagion of distress is also referred to as "personal distress" (e.g. Batson et al. 1987, Eisenberg et al. 1990, 1996, 1998). The two terms will be used interchangeably here. **Empathy** refers to situations in which the subject has a similar emotional state to an object as a result of the perception of the object's situation or predicament. In contrast to emotional contagion, the distinction between self and other is maintained, and the emotional state remains object-focused rather than self-focused. This may or may not result in succorant or prosocial actions to alleviate the distress of the object. Because empathy is a shared-state phenomenon, the definition usually implies some degree of "state matching". State matching is a broad term that implies some concordance between the subjective states of individuals, including physical, psychological, and cognitive components. However, because empathy is more a process than a result, an incidence can still qualify as empathy even if the subject's beliefs about the object are incorrect or their states do not exactly match. **Cognitive empathy** refers to a shared state that is arrived at through more cognitive means, as when the distress of the object is displaced spatially or temporally, the situation of distress is unfamiliar, or the object of distress is unfamiliar. **Sympathy** refers to a state in which the subject feels "sorry for" the object as a

result of perceiving the distress of the object; this may or may not result in succorant or prosocial actions to alleviate the distress. Sympathy, does not automatically imply an accurate representation of the other's state of mind or a matching emotional response, but it usually implies that any distress related to the perception of the other's situation is object-focused (as opposed to self-focused). Authors from before the 1950's generally use the word "sympathy" for what we refer to here as "empathy," and some contemporary authors use "empathy" for what we call "sympathy."

The general class of empathy behavior includes any phenomenon whereby the subject comes to perceive or understand the state of the object through a shared-state mechanism. This includes emotional contagion, empathy and cognitive empathy. Because we view empathy as a general class of behavior, one that exists across species to different degrees, the word will be applied below to cases that fall outside of more rigid definitions. For example, in many cases of animal empathy, the subject is agitated or distressed by the object's distress, and acts to eliminate the stressor or soothe the object. Because of the subject's arousal, many people construe these as cases of emotional contagion and suggest that the subject's motivation to help is purely selfish. Such determinations are mistaken for multiple reasons. One cannot make a strict demarcation between emotional contagion and empathy, especially one that relegates the former to animals and the latter to humans. Because empathy evolved from emotional contagion, the two share much of their proximate mechanism and thus exist on a continuum. In each situation, the subject feels a unique degree of arousal, distinction from the object, and motivation to help. Moreover, empathy is by definition a shared state phenomenon. As such, one cannot experience it without to some extent feeling the distress of another. In which case, any act that reduces the distress of the object can be seen as partially selfish. The selfish versus altruistic distinction is especially irrelevant if one takes an evolutionary perspective, since this larger context can construe any behavior that promotes reproductive success as partially selfish.

To illustrate these principles, consider an human adult who witnesses a terrible car accident. This subject may see the victims crying and injured, the cars shattered. This may elicit some shared emotional state of distress. The subject may elaborate further on the distress, thinking about what it would be like if their car was destroyed, if they or their children were injured, etc. All of this may lead to great distress in the subject. Despite the high level of distress, the subject may still have an awareness that he/she is not the one who was injured and helping may occur *both* because it would helps the object and because it soothes personal distress. Thus, personal distress can co-exist with an understanding of the subject-object distinction and there is great difficulty separating selfish from altruistic motivations. This ambiguity is a result of the continuous nature of empathy; in accordance, the term will be used flexibly in this chapter to connote any type of understanding that is arrived at by participating in the state of another organism or object.

The following sections will elaborate on the evolution of empathy from the emotional linkage of individuals. It will establish why is it adaptive for individuals to be emotionally linked, especially the role this linkage plays in group living, the mother-infant bond, and interactions between conspecifics. Experimental evidence for empathy in rodents, monkeys and apes will be provided. This is followed by a discussion of cognitive empathy and empathy disorders as they speak to the recent evolutionary changes in empathy and the proximate mechanism.

GROUP LIVING AND EMPATHY

It is to the advantage of members of any cooperative, social species to be emotionally affected by the distress of a conspecific. Emotional contagion is the most basic expression of this emotional linkage or "physiological linkage" (to use a term from Levenson and Reuf 1992, see also Brothers, 1989, Plutchik 1987). McDougall anticipated current evolutionary ideas of empathy when he stated that

empathy must exist in all group-living animals, or those with the "gregariousness instinct", because these animals are innately affected by the emotions of others (McDougall 1908/1923).

Early in individual development this emotional linkage is seen as the mere spreading of emotion, without any necessary facilitation of behavior. For example, in rhesus macaques, a severely distressed infant will often cause other infants to approach, embrace, mount or even pile on top of the victim. These macaque scenes seem to result from the spread of distress to the other infants who then seek contact to soothe their own emotional arousal (de Waal 1989). Emotional contagion is also thought to be the first stage of empathic responding in humans, exemplified when infants in a nursery cry in response to other infants' cries (Sagi and Hoffman 1976) and one year-old children seek comfort after witnessing the injury of another (Hoffman 1990, Zahn-Waxler et al. 1992).

Juvenile and adult members of all group-living species also show emotional contagion behaviors that facilitate group movements that are important for survival. For example, if one group member sees something dangerous, usually a predator, an alarm call is given and in most cases the group collectively moves away from the source of danger. Thus, the alarm of one individual alarms others. This phenomenon is well-documented for many species, including ground squirrels (e.g. Sherman 1977), birds (e.g. Powell 1974) and monkeys (e.g. Cheney and Seyfarth 1985). Given this mechanism, danger is more likely to be detected even though each individual spends less time on vigilance (Kenward 1978, Powell 1974). The "more eyes" phenomenon allows greater investment in activities that promote reproductive success, such as feeding and finding mates.

The vicariousness of positive emotions, such as excitement, is also representative of this innate emotional linkage between individuals. Wild dogs, for example, are described as nosing, licking, squeaking and jumping at each other before the onset of a hunting expedition (van Lawick and Lawick-Goodall 1971). Sled dogs similarly jump up and down, barking and whining, before the beginning of a

mushing drive. In these situations, the energy is concentrated in time and intensity, but reaches all individuals in the area, thereby maximizing the success of the effort.

The previous examples demonstrate the importance of the emotional linkage between group-living individuals in coordinating group movements. Such coordination is crucial for escape from predation, foraging, hunting, and mass-migrations – all of which directly affect the reproductive success of the individual.

MOTHER-OFFSPRING EMPATHY

Dyadic relationships are also characterized by an emotional or physiological linkage between individuals. The mother-offspring relationship offers the most basic example of this capacity (as noted by others, including Darwin 1872/1988, McDougall 1908/1923 and Plutchik 1987).

Effects of the mother on the infant

Offspring are behaviorally and physiologically affected by the emotional state of their care-givers. For example, infant monkeys are aroused by the perception of fear in their mothers in the presence of a snake. These infants learn to fear snakes without the need for a more costly direct experience (Mineka, et al. 1984, Mineka and Cook 1988, Mineka and Cook 1993). Similarly, normally-developing human infants social reference to their mothers when approaching a visual cliff, to determine whether or not to cross (Sorce et al. 1985). Twenty-month-old infants with autism, who are impaired in empathic processes, do not attempt to engage the attention of an adult in response to an ambiguous object or situation (Charman et al. 1997). In the normal case, the emotion of the mother is perceived and adaptively incorporated into future decisions by the offspring without necessitating the same level of response by the subject (as in alarm) or previous experience by the subject (as required by conditioning models, e.g. Allport 1924, Church 1959).

Beyond these examples of learning, the infant's emotion regulation processes are regulated by continuous and coordinated emotional and physical contact between the mother and infant (e.g. Brazelton et al. 1974, Deboer 1979, Gable 1992, Levine 1990, Stern 1974, 1977). Infants and their caretakers are thought to use their emotional expressions to reinforce positive affect, transform negative affect and allow for breaks when arousal is too high (Tronick 1989). Such responsiveness by the caregiver is also thought to organize the child's behavior (Campos 1983) and understanding of self, creating a sense of security and efficacy (e.g. Bell and Ainsworth 1972).

A lack of coordinated activity between caregiver and infant is thought to contribute to behavioral problems associated with an inability to assess and control emotions, such as tantrums, poor impulse control, and risk-taking (Tronick 1989). Rhesus macaques raised without their mothers lack the normal, adaptive relationship between behavior and neurochemistry in response to stress (Kraemer and Clarke 1996). They are also impaired at sending and receiving emotional expressions to normally-developing conspecifics in an affect communication paradigm (described below, Miller et al. 1967). Human infants with autism may also be impaired with respect to the coordination of activity with their caregiver. They are less likely than normal children to smile in response to smiles from their mother and are less likely to combine eye contact with smiles (Dawson et al. 1990, Kasari et al. 1990).

The ability to engage emotionally in the social environment, while still regulating emotional arousal, is crucial for appropriate empathetic responding throughout life (Eisenberg et al. 1998, Gurthrie et al. 1997; Ungerer, 1990). Data from animals and humans indicate that those who cannot regulate personal distress are less likely to be sympathetic or help the object and more likely to direct helping towards themselves (Batson et al. 1987, Doherty 1997, Eisenberg et al. 1994, 1998, Eisenberg and Okun 1996, Rice 1964).

Effects of the infant on the mother

Eibl-Eibesfelt postulates that the evolution of parental care in birds and mammals created not only actions by the parent to care for the offspring, but concurrent actions by the offspring to request such care (1970/1974). Similarly, interactional views of development postulate that the infant directs the mother's behavior as much as the mother directs the infant's (Bell 1968, 1971, Bell and Ainsworth 1972, Brazelton et al. 1974, Osofsky 1971, Wiesenfeld and Klorman 1978, Yarrow et al. 1971). It is thought that infants modify the affective and behavioral responses of their caregivers through smiling and crying. Such behaviors can signal the infant's state, and thus provide the impetus for attention and action by the caregiver (Acebo and Thoman 1995, Bowlby 1958). Illustrating the importance of this mechanism, a female chimpanzee at a zoo lost a succession of infants despite intense positive interest because she was deaf and did not correct positional problems (such as sitting on the infant, or holding it the wrong way) in response to soft distress calls (de Waal 1982).

Contagious distress from offspring to parent can also act as an unconditioned stimulus. This allows situational variables that precede the distress to act as conditioned stimuli, teaching parents to act before a stressful display erupts. This learning can result from direct experience with the offspring or can be indirectly applied from personal experience. For example, multiparous antelope cows, in agreement with data from many captive and wild ungulate species, anticipate the needs of their calves and approach them for nursing before the calves have emitted a response (Murdock et al. 1983). The parents (indirectly, though inclusive fitness) and the offspring (directly) benefit because the offspring's needs are satisfied without the cost of a stressful display. Such predictive empathy can also eliminate the unwanted attention from group members and predators caused by a displaying infant.

Therefore, taking advantage of the physiological linkage between individuals is a successful and low-risk way to facilitate the mother-offspring bond. It simultaneously allows infants to develop emotional regulation abilities and adaptively learn about the environment. It stimulates mothers to take

action for the infant when appropriate and facilitates discrimination of the type of care needed. The emotional linkage between individuals thus fulfills many of the goals of extended care-giving simultaneously, proximately, and without the need for explicit instruction or a long history of conditioning.

EMPATHY OUTSIDE THE PARENT-OFFSPRING RELATIONSHIP

Empathy may be phylogenetically and ontogenetically based in the emotional linkage between individuals, especially mothers and offspring. But empathy is thought to be more generally exercised across the lifespan in many mammals. How could empathy be extended outside of the mother-infant relationship? Empathy between parent and offspring is described as primarily the result of innate releasing stimuli. Such releasing effects, once in place, can also guide the extension of empathy towards non-offspring. A distressed chimpanzee, for example, who has just lost a major battle will "pout, whimper, yelp, beg with outstretched hand, or impatiently shake both hands" in order to solicit the consolatory contact of others (de Waal 1996a). Eibl-Eibesfeldt argues that the infantile releasers of caregiving are used throughout adult human life, such as the use of a high-pitched voice or "baby names" between lovers (1970/1974). The following data from nonhuman animals attest to the fact that displays of distress by an object evoke distress in unrelated adult subjects.

Experimental evidence for empathy in rodents

Church (1959) first established that rats were affected by the emotional state of conspecifics while testing to see if the pain reaction of a conspecific could be used as a conditioned stimulus for a subject. According to his conditioning model, if the distress of the object is followed by a painful stimulus to the subject, then the subject will be conditioned to fear the pain reaction of the object. This

was thought to be a possible mechanism for altruism, as subjects would learn to help others in the absence of any obvious, immediate reward (Allport 1924, Church 1959). In the beginning of Church's experiment, all subjects decreased bar pressing when an adjacent rat was shocked even before having experienced any paired shock to themselves. Decreased bar pressing in these experiments is the dependent measure, thought to be a behavioral indication of fear (Estes and Skinner 1941). The decreased pressing response rapidly adapted, with subjects returning to baseline levels after repeated trials. However, as predicted, when subjects were additionally pre-trained with their own shock paired to that of the adjacent animal, and then presented with a shock to the object only, their bar pressing greatly decreased for the entire ten-day duration of the experiment. Even subjects who had previously experienced shock without the conditioned pairing decreased bar pressing when the adjacent rat was shocked. This experiment was replicated with pigeons (Watanabe and Ono 1986).

The effect from training the subject with shock paired to the object proves that an individual can be conditioned to fear distress in others. The source of distress in nature is often relevant to all of the animals in an area. Thus, life experience may condition individuals to fear the distress of others in a similar way as achieved in the experiment. However, such conditioning is the result of the general design of the nervous system and need not be the only mechanism for empathy. The fact that animals showed distress without having a paired shock indicates that rats and pigeons are emotionally linked to their conspecifics. This is further supported by the following study, which investigated the potential for altruism in albino rats.

Rice and Gainer (1962) presented a rat with the sight of another rat being suspended just off the floor by a hoist. Bar pressing by the subject lowered the stimulus animal onto the floor and thus terminated its distress responses (wriggling of the body, distress vocalizations). Subjects in this experiment increased their bar pressing to the sight of the suspended animal, thus displaying what the authors referred to as an "altruistic response", operationally defined as a behavior that reduces the

distress of another. The interpretation was bolstered by behavioral data as the subjects spent the duration of each trial in a location close to and oriented towards the suspended rat. Notice that the behavioral response of fear is traditionally represented by a *decrease* in bar pressing (Church 1959, Estes and Skinner 1941). Thus, the subjects in this experiment were likely aroused by the sight of the object (in the form of emotional contagion), but were not pressing the bar out of fear.

Further discounting the role of fear in producing the "altruistic" response, in a subsequent experiment the rat subjects witnessed delivery of electric shocks to the object. Rather than pressing the bar to eliminate the shock of the object, the subjects "typically retreated to the corner of their box farthest from the distressed, squeaking, and dancing animal and crouched there, motionless, for the greater part of this condition" (Rice 1964:167). Noting the interference of fear with bar pressing in this study, Rice concluded that the increase in bar presses in the original "suspended distress" study was not the result of distress in the subject (as hypothesized by Lavery and Foley 1963). The behavioral descriptions indicate that the subjects only in the later experiment were overly stressed by the sight of the stimulus animal receiving shocks and were thus unable to surpass their own distress to act altruistically. This is consistent with many findings in the human literature, which show that an overly distressed subject is less likely to respond with empathy or sympathy (referenced above). It also provides further support for the idea that the development of emotion regulation abilities is important for empathic responding (above), even in rats.

Lavery and Foley (1963) tried to prove that the rat altruism findings were not altruistic, but rather represented the fear of the subjects and the desire to eliminate the disturbing stimulus. They used recordings of rat squeaks as the stimulus, rather than a live conspecific, and compared the rate of bar pressing to the stimulus of white noise. The stimulus was extinguished if the subject pressed the bar. The animals pressed the bar more during the white noise than during the rat squeaks. The authors concluded that the white noise was more noxious, causing the increased bar pressing and that the low response rate

to actual rat squeaks indicated a low level of empathy. While a recorded loop of squeaks may seem equivalent to live distress calls to a human researcher, it is unlikely to be perceived as a natural stimulus, especially after multiple iterations. It is equivalent to the recorded loop of screams one might hear coming from a haunted house, the response to which rapidly habituates. The experiment supports the idea that a single mode of affect does not have the same effect as the rich, multi-modal cues of a live animal (e.g. Partan and Marler 1999, Preston and Jacobs, in preparation).

These data provide compelling non-primate evidence for the physiological linkage between individuals and the expression of altruistic behavior. Faced with the mild distress of a live animal, with all of the relevant cues, albino rats and pigeons react as if the object emotionally affects them and take measures to eliminate the distress of the object. This is not to say that these reactions necessarily involve an intention to help the other: the reactions rely on state-matching and are functionally altruistic, but the extent to which rats and pigeons understand the impact of their own behavior on others remains unknown. Also, learning in the form of past experience played a crucial role in the duration of the subjects' responses, illustrating that emotional contagion is not simply an innate response, but is affected by experience in development. There exists vast support for the effect of previous experience with the distress situation or distressed individual (e.g. Batson et al. 1981, Feshbach and Roe 1968, Gruen and Mendelsohn 1986).

Experimental evidence for empathy in monkeys

Few experimental studies have been conducted on empathy in nonhuman primates, and most of those few occurred in the 1950s and 60s. The most extensive inquiry comes from the Department of Clinical Science in Pittsburgh. Murphy, Miller and Mirsky (1955) were the first to show that a conspecific could act as the conditioned stimulus (CS) for rhesus monkeys. Inter-animal conditioning

provided a spring-board for a long and successful investigation into the communication of affect between rhesus monkeys.

In one series of experiments, subjects were trained to avoid shock by pressing a bar in response to the sight of a conspecific. The subject and the stimulus animal were in different chambers. When a light went on in the adjacent chamber, the stimulus animal became visible and the subject would have to press the bar to avoid or terminate shock to himself. After extinction to this paradigm, a series of trials delivered the shock instead to the stimulus animal (now the object) just after the lighting changed (Mirsky et al. 1958). Thus, the sight of the object was now associated with shock to the object only, but the subject had exclusive access to the bar that terminated the shock. The subjects responded 71 percent of the time on the first day to the sight of the object in distress from the shock. The object quickly conditioned to the change in lighting as a conditioned stimulus (CS) that preceded the unconditioned stimulus (UCS). As a result, the object "began to leap and run around whenever its compartment was illuminated" (Mirsky 1958:437). Seventy-three percent of the bar presses by the subject occurred to this agitation in the object, before the administration of the shock. In addition, the subject displayed "piloerection, urination, defecation and excited behavior" to the sight of the distressed object (1958:437).

In manipulation checks, the conditioned monkeys did not respond to the sight of an albino rat being shocked or a monkey-like puppet thrashing around in the stimulus room. Avoidance learning in a subsequent study could be reinstated using pictures of monkeys, but the response was less strong and less clear than to the live stimulus animals. (Miller et al. 1959a and b). The conditioned animals responded the strongest to pictures of familiar monkeys showing fear. The familiarity response is expected given that empathy and altruism are theoretically thought to be biased towards kin and then familiar individuals (Trivers 1971). There is also empirical support for this bias toward familiarity in the

human literature from subjects of all ages, infants to undergraduates (e.g. Cialdini et al. 1997, Macdonald and Silverman 1978, Stinson and Ickes 1992, Zahn-Waxler and Radke-Yarrow 1982).

Thus, similar to the findings with rats and pigeons, after learning the consequences of shock, these monkeys were aroused by the sight of a conspecific in distress, acted to eliminate the suffering of the stimulus animal, but were less responsive to artificial or unfamiliar (but similar) stimuli.

A similar task tried to condition subjects to respond to the positive affect of objects, by associating the affect with the delivery of food to the subjects. This version of the task was less successful in conditioning animals than the aversive version (Miller et al. 1966). This was due to a failure of reception by the conditioned animal, and not to a lack of expressiveness by the stimulus animals. Importantly, heart rate data from the same experiment revealed that the responder and stimulus animals that were successful in communicating affect had matching heart rate data. These results confirm the proposed basis for empathy in emotional contagion and physiological linkage. They further attest to the fact that circumstances involving risk are more emotionally salient. Indeed, the emotion literature in general has been much more successful in finding the biological substrates for processing negative than positive emotions (e.g. Adolphs et al. 1994, 1995, Ekman et al. 1983). The preponderance of circuits for processing negative emotions makes sense given that the failure to detect danger can have lethal consequences, dealing the most harmful blow to an individual's potential for reproductive success.

In a similar series of studies done at Northwestern University Medical School, monkeys were found to refrain from bar pressing to obtain a reward if it caused another monkey to receive a shock (Wetchkin et al. 1964). In these experiments, the animals were first trained to pull one of two chains for the delivery of food, depending on the color of the conditioned light stimulus. Subsequently, one of the two chains was re-programmed to also deliver a shock to the object in view of the subject. Thus, the subject would have to witness the shock of the object in order to receive the conditioned food-reward for that chain. In the second set of experiments (Masserman et al. 1964), 10 out of 15 subjects displayed a

preference for the non-shock chain in testing even though this resulted in half as many food rewards. Of the remaining 5 subjects, one stopped pulling the chains altogether for 5 days and another for 12 days after witnessing the shock of the object. These monkeys were literally starving themselves to keep a conspecific from being shocked. In agreement with the rat findings, starvation was induced more by visual than auditory communication, was more likely to appear in animals that had previously experienced shock themselves, and was enhanced by familiarity with the shocked individual (Masserman et al. 1964).

Familiarity effects are also seen in cognitive empathy experiments involving monkeys in role reversal tasks (Mason and Hollis 1962). Although the monkeys in these experiments were unable use perspective-taking information to switch roles with their partner, subjects who were housed together performed better than unfamiliar individuals and familiar subjects increased food-sharing with their partners after the experiment. In a later experiment, macaque pairs that were trained to cooperate for food similarly showed a dramatic increase in their conciliatory tendency (Cords and Thurnheer 1993). These data support the role of familiarity in facilitating communication and cooperation, further supporting theoretical models and empirical evidence for empathy and altruism (cited above).

The above experiments suggest that nonhuman primates will act to avoid witnessing the distress of a conspecific. Beyond conditioning, subjects in some experiments accepted reductions in food, sometimes to the point of starvation, to avoid participating in or witnessing the distress of the object. Across experiments, familiarity with the stimulus animal affected the ability of animals to communicate affect and intention. Further, subject's responses were facilitated by their familiarity with the particular distress situation. Given that these monkey species are characterized by many as aggressive and of inferior intelligence, they showed remarkable empathic and altruistic responses to the distress of their conspecifics. This is especially notable given the unnatural laboratory conditions in which the studies were done, and the lack of traditional social bonding opportunities for the animals in most cases.

Behavioral data on ape empathy

In a content analysis of over 2,000 anecdotal reports of non-human primate empathy, O'Connell counted the frequency of three types of empathy: emotional (understanding another's emotion – closest to the definition used here), concordance (understanding non-emotional states – similar to cognitive empathy) and extended (acts of helping tailored to the object's needs) (1995). Chimpanzees exhibited all three types of empathy. Understanding the excitement, grief/sadness/frustration and fear of the subject were extremely common, with most outcomes resulting in the subject comforting the object of distress. Chimpanzees appeared to comprehend the emotions, attitude and situation of another individual and even endangered their lives to save conspecifics in danger. In one case, an adult male chimpanzee died trying to rescue an infant who had fallen over the electric fence into a moat on the other side (in O'Connell 1995 from Goodall 1986). Monkey displays of empathy, by contrast, were restricted to mediation of fights, adoption of orphans, and reactions to illness and wounding (as seen in the tolerance towards handicapped individuals mentioned above).

Consolation is a primary example of empathy in chimpanzees (de Waal 1996b).[1] Consolation, as first defined by de Waal and van Roosmalen (1979), occurs when a bystander approaches a recipient of aggression, shortly after a fight. De Waal describes how two adult female chimpanzees in the Arnhem Zoo colony used to console each other after fights: "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." (1982:67).

Consolation involves contact initiation by a previously uninvolved bystander who is assumed to be less distressed, and directs consolatory efforts to the victim rather than to itself (de Waal 1996a and

b). Thus, in consolation there is no direct benefit for the consoler. One can postulate that in consolation, the consoling individual has become distressed from the sight of the victim and seeks comfort for his or her own feelings. However, the consoler often does not show signs of distress, such as facial expressions or vocalizations, and may wait until after the most intense displays of distress have disappeared to initiate its approach (de Waal 1996a and b).

The tendency to console seems to be unique to apes: it has not been found in any monkey species despite intensive efforts to find it (de Waal and Aureli 1996, de Waal 1996a and b). The reports on chimpanzees are far from anecdotal. De Waal and van Roosmalen (1979) based their conclusion on an analysis of hundreds of post-conflict observations, and the recent study by de Waal and Aureli (1996) includes an even larger sample in which the authors sought to test two predictions regarding post-conflict contact provided by third parties. They reasoned that if such contacts serve the alleviation of distress they should occur more with recipients of aggression than with aggressors, and more with recipients of intense than of mild aggression. Comparing third-party contact tendencies with baseline rates, they found statistical support for both predictions. An identical research design with macaques did not reveal these effects.

This data does not stand on its own, however. There is sporadic anecdotal evidence for what de Waal (1996b) calls cognitive empathy, that is, helping actions that seem to derive from an understanding of the other's predicament. Examples concern the way a bonobo male helped another male (see example described in beginning of this chapter), a case of a male chimpanzee who saw a female struggling with a technical problem and waited until she had left the scene to solve it and bring her the item that she was after (de Waal 1996b), and perhaps the most remarkable case of cross-specific empathy, when a bonobo female, Kuni, at the Twycross Zoo, in England, tried to "help" a bird:

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[1] This is equivalent to O'Connor's emotional category of "understanding grief/sadness/frustration" (1995).

"One day, Kuni captured a starling. Out of fear that she might molest the stunned bird, which appeared undamaged, the keeper urged the ape to let it go. Perhaps because of this encouragement, Kuni took the bird outside and gently set it onto its feet, the right way up, where it stayed looking petrified. When it didn't move, she threw it a little, but it just fluttered. Not satisfied, Kuni picked up the starling with one hand and climbed to the highest point of the highest tree where she wrapped her legs around the trunk so that she had both hands free to hold the bird. She then carefully unfolded its wings and spread them wide open, one wing in each hand, before throwing the bird as hard she could towards the barrier of the enclosure. Unfortunately, it fell short and landed onto the bank of the moat where Kuni guarded it for a long time against a curious juvenile. By the end of the day, the bird was gone without a trace or feather. It is assumed that, recovered from its shock, it had flown away" (de Waal 1997b:156).

Such anecdotes hint at underlying cognitive capacities rarely acknowledged in animals other than ourselves. Familiarity with their imaginative understanding and well-developed caring capacities explains why experts of apes acted with little surprise to the most famous case of empathy, the rescue of a 3-year-old boy at the Brookfield Zoo, on August 16th, 1996. The child, who had fallen six meters into the primate exhibit was scooped up and carried to safety by Binti Jua, an 8-year-old female western lowland gorilla. The gorilla sat down on a log in a stream, cradling the boy in her lap, giving him a gentle back-pat before she continued on her way. This act of sympathy touched many hearts, making Binti a celebrity overnight. Whereas some commentators have tried to explain Binti's behavior as the product of training or a confused maternal instinct (Davidson 1996), her behavior fits entirely with everything else we know about apes, which is that they respond comfortingly to individuals in distress. The only significant difference was that in this case the behavior was directed at a member of a different species (de Waal 1997a).

In sum, data currently exist for cases of subjects consoling the object, but appearing distressed; this is traditionally referred to as emotional contagion. There are also cases where the subject consoles the object but does not appear to share in the state of distress; this is traditionally referred to as sympathy. Therefore, behavioral data on consolation alone cannot prove the existence of what is called "true empathy" (e.g. Thompson 1987, Ungerer et al. 1990) or "cognitive empathy" (de Waal 1996b).

Anecdotes such as the ones above, with Kidogo the bonobo or Kumi the chimpanzee, point to the existence of cognitive empathy but also have a great weakness; they are unsuitable for comparing alternative hypotheses. Epistemological problems involved in proving the existence of an internal state pervade ethology and psychology, but these should not impede the development of theoretical ideas and empirical research. On the basis of systematic data on consolation, striking anecdotes of cognitive empathy (for other examples see de Waal 1996b), and data on cognitive perspective-taking abilities in other contexts, we venture to speculate that apes evaluate the emotions and situations of others with a greater understanding than is found in most other animals apart from ourselves. More research is needed, however, to determine the extent to which ape consolation is qualitatively similar to human consolation.

COGNITIVE EMPATHY

Only humans and the great apes, together classified as the Hominoids, have been cited as evincing cognitive empathy (de Waal 1996b). The above reports on consolation behavior provide the only systematic data indicating a substantial, perhaps radical difference between the way chimpanzees and some monkey species respond to distress in others caused by aggressive conflict. This difference seems to fit with the overall higher cognitive level and tendency to take another's perspective of apes relative to monkeys. In a cognitive empathy (i.e. perspective-taking) task developed by Povinelli and colleagues, two animals cooperated to manipulate a lever device to obtain food from opposing sides of an apparatus. Each of the subjects had a different task requirement. Empathy was operationalized as the ability to transfer knowledge of the other subject's role when the roles were reversed. Chimpanzees but not monkeys successfully transferred knowledge in the task, further suggesting that apes can use perspective taking to transfer knowledge (Povinelli et al. 1992a and b, respectively). In a similar experiment, monkeys were again unsuccessful in transferring roles with their partner in a communication paradigm (Mason and Hollis 1962).

Empirical data from development and evolution speak to a correspondence between the emergence of cognitive empathy and the emergence of a whole suite of social-cognitive capabilities. Some suggest that cognitive empathy was made possible by the emergence of other higher cognitive abilities (like perspective-taking). Others suggest that empathy is a prerequisite for the ability to attribute mental states to others (Premack and Woodruff 1978). Short from solving this debate, we can assume that higher cognitive abilities aid social primates in understanding the relationships among individuals, attributing goals and needs to others, predicting others' reactions, and making appropriate decisions (see Byrne and Whiten 1988). It also facilitates optimization of the cost/benefit ratio of helping acts by keeping a record of giving and receiving. Many of these abilities can be accomplished with increases in working memory, long-term memory, behavioral inhibition, and general information processing capacities (Byrne and Whiten 1988, Chance and Mead 1988). All of these abilities are at least partially subserved by the prefrontal cortex (e.g. Fuster 1997, Shiamamura 1996, Thierry 1994), an area in the neocortex, which is known to have expanded disproportionately in recent primate evolutionary history (Finlay and Darlington 1995).

Dealing with empathy per se, increasing long-term and working memory increases the ability of the subject to imagine the state of the object. The subject has access to a larger base of knowledge of the object and its situation and has a larger capacity to hold the information to compare possible outcomes and decide on a course of action. The increase in inhibition associated with prefrontal development also decreases the amount of personal distress that results from thinking about distress situations. Taken together, an increase in prefrontal functions can increase the separation of subject from object and help determine the best course of action, increasing the overall effectiveness of empathy.

<u>EMPATHY DISORDERS</u>

There is neurological evidence to support the importance of the prefrontal cortex for empathy, as also discussed in Hanna Damasio's chapter in this volume. Empathy impairments in sociopathy (also called psychopathy) and autism are thought to be partially due to a disruption in the prefrontal system because both involve deficiencies on tasks requiring inhibition, planning, and attention (Campagna &and Harter 1975, Dawson 1996, Gillberg 1999). By definition, psychopathic individuals are characterized by a lack of emotional responding to the distress of others. Physiological data supports the behavioral findings (e.g. Aniskiewicz. 1979, Blair et al. 1997, House and Milligan 1973, 1976). Children with autism are less physiologically responsive to cues of threat than normally-developing peers, thought to be an indication of their frontal damage (Blair 1999). They also show impaired attention and affect to the distress of an adult as early as 20 months (Charman et al. 1997). Later in childhood, the effects remain on similar tasks (Dawson et al. 1990, Kasari et al. 1990, Loveland and Tunali 1991, Sigman et al. 1992). Children with autism also do not report feeling the same emotion as a protagonist on a videotape (Yirmiya et al. 1992).

Focal prefrontal cortex damage and closed-head injury in adults also result in changes in empathy (reviewed by Eslinger 1998). Patients with early-onset damage to the prefrontal cortex have a syndrome that resembles psychopathy (Anderson et al. 1999). These subjects display little or no empathy or remorse, lack lasting social relationships, and are significantly impaired on moral reasoning, although they perform normally on tasks of intellectual ability. They also fail to produce normal increases in skin conductance in response to the anticipation of losing money in a gambling task, in contrast to subjects with autism. One of the two subjects with early prefrontal damage was a mother marked by "dangerous insensitivity to the infant's needs" (Anderson et al. 1999:1032). The authors propose a mechanism for the disorder whereby brain damage prevents patients from developing knowledge of the emotional aspects required for navigating and understanding social situations.

Psychopathy has recently been found to be a relevant dimension of chimpanzee personality, confirming the view that chimpanzees normally develop sympathetic attitudes. In a detailed study comparing both human subjective impressions of chimpanzee personalities and objective behavioral data, it was found that psychopathy can explain part of the personality variation, as it does in people (Lilienfeld et al. 1999). This paper also reported specific individuals described in the literature as being immune to punishment, lacking in empathy, or prone to unusual deceptiveness and meanness.

It seems then, that the quality of empathy (and lack thereof) has changed along with other cognitive abilities in recent phylogenetic history, starting well before the appearance of our species. This change correlates with an increase in the corresponding neural substrates. De Waal (1996b) speaks of "cognitive empathy" to distinguish empathy that relies on perspective-taking from other forms. Yet this does not in any way deny the continuity with more direct forms of state-matching. Cognitive empathy *encompasses* these more emotional processes. If scientists, such as Povinelli (1998) and Hauser (2000), deny the existence of empathy outside the human species, this is because their focus is not on the emotional but the cognitive aspects of the process (as seen in Povinelli et al. 1992a and b). Hence, what they deny in other animals is only cognitive empathy.

But even this position would seem premature given that we have thus far three empirical differences between apes and all other animals, which are: the possession of mirror self-recognition (e.g. Gallup 1982), the occurrence of consolation (de Waal and Aureli 1996), and the presence of special spindle cells in the brain (Nimchinsky et al. 1999). Whereas no one knows if and how these three unique features are related, their co-occurrence does warn at least against drawing a strict mental demarcation line between humans and apes. Indeed, the data reported here, across at least six species, warn against drawing demarcation lines between humans and other animals with respect to emotional aspects of empathy.

TOWARDS A PROXIMATE MODEL FOR EMPATHY

This chapter has described empathy from its roots in the basic emotional linkage between group members, which we may call attachment, to the more complex forms of empathy seen in apes and especially humans. The basis in emotional and social connectedness is crucial to an understanding of empathy and altruism because it creates the bridge between ultimate and proximate explanations, and between phylogeny and ontogeny.

The lack of a proper proximate mechanism for empathy has allowed people to persist in thinking that empathy and altruism are phenomena restricted to humans. Thirty years ago G. W. Allport said it best when he concluded, "the process of *empathy* remains a riddle in social psychology…The nature of the mechanism is not yet understood" (Allport 1968:30 from Wispé 1987). Without a mechanism level description, descriptions of empathy are derived from introspection and as a result may overestimate the cognitive component. For example, Mead (1934) paved the way for a cognitive theory of empathy by stressing the importance of role taking and putting oneself "in the place of" the object. Allport similarly defined empathy as the "imaginative transposing of oneself into the thinking, feeling and acting of another" (Allport 1937 from Wispé 1987). In current experimental paradigms, empathy is sometimes entirely cognitive, without any emotional component whatever (e.g. Povinelli et al. 1992a and b). However, recent findings in neuroscience add empirical support to a lower-level mechanistic explanation of empathy that is at least a century old (Lipps 1903, but see Allport 1924, Becker 1931, and Scheler 1928/1970, for directly opposing views to Lipps). According to this theory (Preston and de Waal, in preparation) the attended perception of another's state, especially an emotional state, involves to differing degrees not only the representation of the other's state in the brain, but a representation through the observer's own substrates of self-initiated behavior. Put more simply, in order to understand another, you must become the other, at least at the level of brain representation.

This "Perception-Action Model" is grounded in the theoretical idea, adopted by many fields over time, that perception and action share a common code of representation in the brain (reviewed by Allport 1987, Prinz 1987, 1992, 1997, Rizzolatti and Arbib 1998). This organization makes sense if, in general, perceptual systems evolved to provide accurate information about the environment in order to appropriately plan and guide movements (Prinz 1992). These common codes are not necessarily restricted to physical movements, but may include abstract, symbolic representations (Prinz 1997). Thus, in the case of emotions, the representations need not just map body postures and facial expressions directly from actor to perceiver; they can map the meanings or goals of the expressions.

The social world of primates is incredibly complex. Monkeys, apes and humans participate in economies of exchange. They groom others in return for resources such as food, protection, or status (literally or metaphorically); they form alliances to protect themselves and to depose dominant individuals; they hide courtship and copulation, and give deceptive calls to access food supplies (for a review see Byrne and Whiten 1988). This complexity requires the primate central nervous system to perceive the facial expressions, body postures, gestures, and voices of others accurately and quickly so that a response can be generated (Brothers 1990). Parsimoniously, the same nervous system link between perception and action that helps us navigate the physical environment helps us to navigate the social environment. Thus, the perception-action link allows for facile motor skill acquisition as well as facile social interaction, as external conditions are accurately perceived and incorporated into the current plan of action. It is hoped that once proximate explanations of empathy are developed further, it will be easier for science to conceive of empathy as a continuous phenomenon that relies on basic processes that evolved from and are shared with many other species.

FINAL COMMENTS

      With regard to altruistic love, the subject of this edited volume, reviewing the animal literature on empathy has borne out some important generalizations. Importantly, these generalizations are supported by the human literature. The basis of empathy in the care-giving bond supports the role of ontogeny in the proper development of the "innate" linkage between individuals. Specifically, continuous contact and coordinated activities are characteristic of a bond that develops a physiologically adaptive response to stress, accurate communication of affect with others and the capacity for empathic responding.

      There were also robust behavioral effects of familiarity with the object of distress and with the distress situation. Both types of familiarity can be subsumed under the general heading of "shared experience". The qualities of group living, under which empathy evolved, provided a shared experience between its members. Individuals were known to each other, and were likely to experience many of the same stressors.

      In today's era of e-mail, commuting, frequent moves, and bedroom communities, the scales are being increasingly tipped against the automatic and accurate perception of others' emotional state, without which empathy is impossible. Fortunately, adjustments can be made in the realms of urban planning, human interface, and the structuring of home and work environments to preserve the social connectedness of our world. Further, because explicit modeling, learning and cognitive perspective-taking can augment empathy, it can thrive despite this less fertile ground with the help of positive role-models and education. All of this requires effort, but the benefits would be profound.

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