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Is our human capacity for sensory experience the "gold standard" by which all other species should be measured? Such a view would falsely assume that we share the same sensory capabilities as other creatures. Many animals can see light spectra that we cannot, hear lower and/or higher sounds, produce and detect electrical fields, navigate by the earth's magnetic field, and perceive time far more acutely than we can. These sensory abilities do not necessarily have relevance to experiencing pleasure, but they do suggest realms of pleasure for animals that we as humans can only imagine.

For too long scientists have denied the existence of positive sensory experiences in other species because we cannot know for certain what another being feels. But in the absence of compelling evidence to the contrary, it is more reasonable to assume that other creatures, who share so much in common with us through our shared evolutionary origins, do, in fact, experience pleasure. We cannot feel the hummingbird's response to a trumpet flower's nectar, the dog's anticipation of chasing a ball, or the turtle's experience of basking in the sun, but we can imagine those feelings based on our own experiences of similar situations. What we can observe in animals, combined with our capacity to empathize from our own experience, leaves little doubt that the animal kingdom is a rich repository of pleasure. And as we grow to accept and acknowledge the pleasure that attends animals' lives, evidence for it will proliferate, for we are more likely to find something when we are looking for it.

See also Emotions—*Emotions and Affective Experiences*
Emotions—*Emotions and Cognition*
Play—*Social Play Behavior and Social Morality*

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Jonathan Balcombe

Empathy

The term *empathy* means that you *feel* the emotion of another individual as a result of witnessing their emotional state, or thinking about their emotional state. Because most of the literature on empathy focuses on examples of distress, we will talk about empathy with respect to distress, keeping in mind that, in theory, empathy can apply to any emotion, including joy and happiness. When you have empathy for another individual in distress, you feel the distress of the other person and you may have a desire to help them.

Empathy is very similar to *sympathy* and sometimes people use the term sympathy for such cases. However, colloquially, and in the modern scientific literature, empathy differs from sympathy because with sympathy you feel *sorry for* the other individual, but you do not feel the same emotion as they feel. There are opposing cases where you feel the other individual's emotion so strongly that you yourself become distressed and need to be soothed, and thus you cannot help the other individual. When this happens, it is called *emotional contagion*. In empathy, you feel the emotion of the other, but you remain aware that the other individual is the one in distress, and you can focus on their state.

Many people believe that animals other than humans do not experience empathy and sympathy. This is primarily because people believe that empathy results from a high-level thinking process where you imagine what it must be like to be in the situation of the other individual, and then you make inferences about how the other individual must feel. If this is how empathy is achieved, then it would be a high-level cognitive process that requires a large information-processing capacity, and many animals may not have such a capacity. When one individual has conscious thoughts about the state of another and makes mental models of the other's feelings and needs, it is called *cognitive empathy*. Research suggests that cognitive empathy may not exist in creatures other than humans and possibly apes. But most research indicates that the ability to feel the state of another and to try to help the other is an innate and automatic process that does not require conscious thought and exists across species.

Charles Darwin himself expressed in *The Descent of Man* such a 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. In his *Introduction to Social Psychology* (1908/1923), William McDougall also 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. Empirical research supports their view, revealing empathy to be a phenomenon that exists to varying degrees in nonhuman species including rodents, dogs, monkeys, dolphins, and apes. For example, in experiments with human children by Carolyn Zahn-Waxler and colleagues, a mother feigns distress and a researcher observes the reaction of the children. Oftentimes, the family dog also displays consolatory behaviors toward the feigning mother. Both rats and pigeons in the laboratory display a profound emotional response to the suffering of a conspecific (an animal of the same species) and act to terminate the stress. 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 cases of empathy in animals, consider the following anecdotal example from Frans de Waal's book *Bonobo: The Forgotten Ape*.

> Kidogo, a 21 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 the 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.
>
> 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. Caretaker 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.
>
> 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. (p. 157)

Where Does Empathy Come From?

How can animals experience empathy to varying degrees? What does it mean to have some degree of empathy? At the root, empathy results from the way that the nervous system is designed. When you perceive an action or an emotion, you activate the part of your brain that you yourself use to generate that action or emotion. This is called the *perception–action* design of the nervous system. You can see that this is true if you think of an extreme case. Think about when you watch a very intense sports event or when you see someone in a movie who is very upset. You can become so involved in the action that you actually make their gestures for them. You jerk your own arm as the goalie stretches to catch the ball, and you frown and start to cry as the main character experiences a tragedy. The sight of their actions stimulated the action in your own brain so strongly that you actually generated an action potential that traveled down your spinal column to stimulate the muscles. These are called *ideo-motor actions*. In less extreme cases, when you attend to the actions and emotions of another, you still activate these parts of your brain, but to a lesser degree. Thus, you feel the emotion of the other, and you understand what it is like to be them, but you do not necessarily show any outward sign of this.

The perception–action design of the nervous system is not a recent development in evolution reserved solely for humans; on the contrary, it seems that all chordates have aspects of a perception–action design, and that this is extremely important for survival. For example, if an animal that lives in a group 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, birds and monkeys. Given this mechanism, danger is more likely to be detected even though each individual spends less time on vigilance. This "more eyes" phenomenon allows greater investment in activities that promote reproductive success, such as feeding and finding mates.

The spread of positive emotions, such as excitement, is also representative of this perception–action design of the nervous system. Wild dogs, for example, are described as nosing, licking, squeaking, and jumping at each other before the onset of a hunting expedition. Flocks of geese flap their wings and hop up and down on the ground before flying off. 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 spreads to reach all individuals in the area, thereby maximizing the success of the effort. These examples demonstrate the importance of the perception–action design of the nervous system for coordinating group activities that are crucial for escape from predation, for foraging, hunting, and mass migrations—all of which directly affect the reproductive success of the individual.

Alarm and vicarious excitement are very basic forms of empathy, more akin to emotional contagion. These basic forms of empathy were the first to evolve and are the first to appear in development in primates. For example, Frans de Waal describes a scene from his observations of rhesus macaques (*Macaca mulatta*) where 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. Emotional contagion is also thought to be the first stage of empathic response in humans, exemplified when infants in a nursery cry in response to other infants' cries, and one-year-old children seek comfort after witnessing the injury of another.

Extensive research from primates indicates that the mother–offspring relationship is crucial for proper development of empathy. In the mother–offspring relationship, the fact that the infant can feel the state of the mother allows the infant to learn about the world simply by watching how the mother reacts to things. In experiments by Susan Mineka and colleagues, infant monkeys learn to fear snakes just from one instance of seeing the mother react fearfully to a snake. In a similar experiment designed by Joseph Campos and colleagues, infant humans look to the reaction of their mother before deciding whether or not to crawl off of a potentially dangerous cliff.

It is also adaptive that the mother can feel the state of the infant because it allows the mother to provide proper care for the infant. The fact that the infant receives immediate and appropriate responses to its needs does two things.

1. The infant does not need to throw a loud, disruptive, and physiologically stressful tantrum (that may draw unwanted attention from group members and predators) to communicate its needs.
2. The infant develops the ability to regulate its own emotions so that it can eventually soothe itself and change moods as necessary without help from the mother.

Data from animals and humans indicate that this emotional learning is necessary for the development of empathy since an individual that cannot regulate its own emotions will become overly distressed from perceiving distress in another, and will not be able to help the other.

Thus, the perception–action design of the nervous system is very adaptive. It allows group-living animals to coordinate their activities, and in the mother–offspring bond it stimulates mothers to take appropriate action for their infants, and it allows infants to develop emotional regulation abilities and to learn about the environment by watching others.

How is it that empathy is extended beyond the mother–infant relationship? Caregiving in the parent and offspring relationship results when the infant requests care using distress signs, and the mother soothes the infant by satisfying the infant's needs. These same cues, once set up in infancy, can also be used to generate empathy outside of this relationship. 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 & Aureli, 1996). In his book, *Love and Hate* (1971/1974) Irenäus 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. The following data from nonhuman animals attest to the fact that displays of distress in one individual evoke distress and helping in unrelated adult subjects.

Evidence for Empathy in Nonprimates

Russell Church, in 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 reward. In the beginning of Church's experiment, all subjects showed fear when they observed an adjacent rat being shocked (the fear was measured with a decrease in bar pressing, thought to be a behavioral indication of fear). Although this response was much greater if the observing animal previously experienced a shock paired to that of the other animal, even subjects who had previously experienced shock without the conditioned pairing showed fear when the adjacent rat was shocked. This experiment was replicated with pigeons. The fact that animals showed distress without having a shock paired to that of the other animal indicates that rats and pigeons are sensitive to the state of the other. This is further supported by the following study, which investigated the potential for altruism in albino rats.

In 1962, George Rice and Priscilla Gainer 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 toward the suspended rat. Notice that the behavioral response of fear is traditionally represented by a *decrease* in bar pressing. 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 for their own safety.

Further discounting the role of fear in producing the "altruistic" response, in a subsequent experiment by George Rice in 1964, 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." 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. The behavioral descriptions indicate that only the subjects in the shock experiment were overly stressed by the sight of the other 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. It also provides further support for the idea that the development of emotion regulation abilities is important for empathic responding, even in rats.

These data provide compelling nonprimate evidence for the perception–action link between individuals and its role in producing empathic or altruistic behavior. Faced with the mild distress of a live animal, rats and pigeons react as if the object affects them emotionally 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, because the extent to which rats and pigeons understand the impact of their own behavior on others remains unknown. Also, learning 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 past experience. There exists vast support for the effect of previous experience with the distress situation or distressed individual.

Evidence for Empathy in Monkeys

Macaque monkeys show a high degree of tolerance and helping toward handicapped group members, attesting to the fact that they perceive the different abilities of other individuals, and take these into account when interacting with them. Azalea, a rhesus macaque who lived in a socially-housed group, had a genetic disorder, autosomal trisomy. 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. Azalea was tolerated and accepted in the group despite her physical and social defects, even though rhesus macaques are typically highly structured and aggressive. 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.

Few experimental studies have been conducted on empathy in nonhuman primates, and most of those occurred in the 1950s and 60s. The most extensive inquiry comes from the Department of Clinical Science in Pittsburgh. John Murphy, Robert Miller and Arthur Mirsky were the first to show that the emotion of one monkey could act as the conditioned stimulus for another. This interanimal conditioning provided a springboard for a long and successful investigation into the communication of affect between rhesus monkeys.

In one experiment in 1958, subjects were trained until they understood that they could terminate a shock to themselves by pressing a bar in their chamber. After this, the experimenters instead delivered the shock to another monkey, in the presence of the subject, but it was still the subject that could terminate the shock by pressing the bar. Seventy-one percent of the time on the first day the subjects would press the bar to terminate the shock to the other animal. The other monkey quickly learned that the shock came after conditioned stimulus of a change in lighting and "began to leap and run around whenever its compartment was illuminated." Seventy-three percent of the bar presses by the subject occurred to this distress in the other monkey, before the shock was even administered. In addition, the subjects displayed "piloerection, urination, defecation and excited behavior" at the sight of the distressed other monkey. While this shows that the monkey subjects did not want to observe the distress of a live conspecific, in subsequent experiments, the monkey subjects did not respond to the sight of an albino rat being shocked or to a monkey-like puppet thrashing around. The response could be reinstated using pictures of monkeys, especially pictures of familiar monkeys showing fear, but this response was less strong and less clear than to the live stimulus animals. The familiarity response is expected given that it would be most adaptive to help individuals that are close to you or that you are related to. There is also empirical support for this bias toward familiarity in the human literature from subjects of all ages, infants to undergraduates.

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 stimuli.

A similar task tried to condition subjects to respond to the positive emotion of other monkeys by associating the emotion with the delivery of food. This version of the task was less successful than the distressing version. Heart rate data from the same experiment revealed that when the task was successful, the subject monkey and the other monkey had similar trends in their heart rates. These results confirm the proposed basis for empathy in emotional contagion and the perception–action link. They further attest to the fact that circumstances involving risk and distress are more emotionally salient to the subjects. The emotion literature in general has been much more successful in finding the biological basis of negative emotions than positive. This makes sense given that the failure to detect danger can be deadly, which has a much greater impact on 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. 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 light stimulus. Subsequently, one of the two chains was reprogrammed to also deliver a shock to the other monkey in view of the subject. Thus, the subject would have to witness the shock of the other monkey in order to receive the food reward for that chain. In the second set of experiments, 10 out of 15 subjects displayed a preference for the nonshock 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 other monkey. These subjects 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.

Familiarity effects are also seen in cognitive empathy experiments with monkeys. Although the monkeys in these experiments were unable use perspective-taking information to switch roles with their partners, subjects who were housed together performed better than unfamiliar individuals, and familiar subjects shared more food with their partners after the experiment. In a later experiment, pairs of macaque monkeys that were trained to cooperate for food showed a dramatic increase in their tendency to get along. These data support the role of familiarity in facilitating communication and cooperation, further supporting theoretical models and empirical evidence for empathy and altruism.

The above experiments suggest that monkeys will act to avoid witnessing the distress of a conspecific. 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 emotion and intention. Further, subject's responses were facilitated by their familiarity with the particular distress situation. Given that these monkey species are often characterized 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.

Evidence for Empathy in Apes

In a content analysis of over 2,000 anecdotal reports of nonhuman primate empathy, Sanjida O'Connell counted the frequency of three types of empathy: *emotional* (understanding another's emotion—closest to the definition used here), *concordance* (understanding nonemotional states—similar to cognitive empathy) and *extended* (acts of helping tailored to the other's needs). Chimpanzees exhibited all three types of empathy. Examples where one chimpanzee displayed an understanding of the emotion of another (excitement, grief/sadness/frustration, and fear) were extremely common, with most outcomes resulting in the subject comforting the chimpanzee in distress. Chimpanzees appeared to comprehend the emotions, attitudes, and situations of another individual and even endangered their own lives to save conspecifics in danger. In one case, reported by Jane Goodall, an adult male chimpanzee died trying to rescue an infant who had fallen over the electric fence into a moat on the other side. 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 toward handicapped individuals mentioned above).

Consolation is a primary example of empathy in chimpanzees. Consolation, as first defined by Frans de Waal & Angeline van Roosmalen, occurs when a bystander approaches a recipient of aggression, shortly after a fight. De Waal describes in *Chimpanzee Politics: Power and Sex among Apes* (1982) 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."

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. Thus, in consolation, there is no direct benefit for the consoler. One can say that in consolation, the consoling individual has become distressed from the sight of the victim and seeks comfort for his or her own feelings (which would be emotional contagion, but not empathy). 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 approach the other.

The tendency to console seems to be unique to apes and humans: It has not been found in any monkey species despite intensive efforts to find it. The reports on chimpanzees are far from anecdotal. De Waal & van Roosmalen based their conclusion on an analysis of hundreds observations, and a recent study by de Waal & Filippo Aureli includes an even larger sample.

There is also sporadic anecdotal evidence for cognitive empathy in chimpanzees. There is the example of Kidogo from the beginning of this entry. In another case from de Waal's *Good Natured*, a male chimpanzee saw a female struggling with a technical problem and waited until she had left the scene to solve it and bring her the item she was after. In another case, Kuni, a bonobo female at the Twycross Zoo in England, tried to "help" a bird:

> 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.

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 nonhuman empathy, the rescue of a 3-year-old boy at the Brookfield Zoo, on August 16, 1996. The child, who had fallen 6 meters (20 ft) 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, 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.

In sum, data currently exist for cases of subjects appearing distressed, but consoling the object (emotional contagion), and for cases where the subject consoles the object, but does not appear to be distressed (empathy or sympathy). Anecdotes such as the ones above, with Kidogo the bonobo or Kumi the chimpanzee, point to the existence of cognitive empathy, but without being able to know what these animals were feeling or thinking at the time, it is hard to make a firm conclusion. The data on consolation, the striking anecdotes of cognitive empathy, and other data on cognitive perspective-taking abilities in apes suggest 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 actually similar to human consolation.

Cognitive Empathy

Only humans and the great apes, together classified as the Hominoids, have been cited as evincing cognitive empathy (also known as *perspective-taking*). The above reports on consolation behavior provide the only systematic data indicating a substantial, perhaps radical difference between the way chimpanzees 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 experiment developed by Daniel 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. If one subject could successfully do the other's task just from watching, he was considered to have empathy. Chimpanzees but not monkeys succeeded in the task, further suggesting that apes can use perspective-taking to gain knowledge. In a similar experiment by William Mason & J. Hollis, monkeys were also unsuccessful in learning the role of their partner in a communication experiment.

Experiments from human development and from evolution suggest that cognitive empathy evolved at the same time or in the same species as many other social–cognitive capabilities. Some suggest that cognitive empathy was made possible by the evolution of other abilities such as perspective-taking. Others suggest the opposite, that empathy is a prerequisite for perspective-taking! While this debate is a long way from being resolved, it is true that the quality of empathy has changed along with other cognitive abilities in recent evolutionary history, starting well before the appearance of our species. This change correlates with a disproportionate increase in the prefrontal cortex in recent primate evolutionary history.

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 individuals to acquire motor skills and social skills easily. It is hoped that once we fully understand how empathy evolved and how the nervous system accomplishes empathy, it will be easier for people to see how empathy is rooted in more basic processes such as emotional contagion and that we share this ability with many other species.

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Stephanie D. Preston

Exploratory Behavior
Inquisitiveness in Animals

Peter Marler and William J. Hamilton III in *Mechanisms of Animal Behavior* started their chapter on exploration and play with the following statement: "Animals spend much of their time in motor activity, the function of which is often difficult to identify." (1966, p. 159). Twenty-eight years later, H. Keller, K. Schneider & B. Henderson (1994) wrote in the foreword to their collective book: "... we have not attempted to arrive at a definition of curiosity and exploratory behavior upon which every contributor to this volume would agree. Given the state of the art in research and theory on curiosity and exploratory behavior, we thought to attempt to do so would be counterproductive." (1994, p. 3).

Some present-day textbooks on animal behavior even fail to include that form of behavior in the index. Does that mean that the subject itself is unimportant and uninteresting? Apparently not. It is commonly agreed that, among the so-called higher animals, exploration is the principal form of behavior and may be analyzed together with other behavioral forms (Keller, Schneider & Henderson, 1994). However, in comparison with such activities as feeding, caring for young, nesting or attracting mates, exploratory behaviors prove to be much more difficult to analyze in terms of their adaptive value. This is because exploratory behaviors:

- include elements of other forms of behavior;
- are triggered by a variety of stimuli (it is impossible to pinpoint key stimuli or specific releasers);