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Review Article

Empathy in Nonhumans: A Brief Overview

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Abstract

We present a brief overview of the study of empathy in nonhumans. We begin with a historical perspective that focuses on early ideas about empathy developed by Peter Kropotkin and Adam Smith. From there we discuss the origin and evolution of the multiple layers of empathy – emotional contagion sympathetic concern, and empathetic perspective-taking – casting that discussion within the "Russian doll model" of empathy developed by de Waal. For each layer we provide examples from the animal behavior literature.

INTRODUCTION

The history of the study of empathy in nonhumans has parallels with work on tool use, deception, strategic behavior, and many other cognitively sophisticated behaviors in nonhumans. We assume a complex behavior (or a suite of behaviors) to be uniquely human, and consequently, little research explores the phenomenon in nonhumans. But, eventually someone stumbles upon an example of the cognitively sophisticated behavior in question in nonhumans. Once that example makes its way into the literature, people begin to realize what Darwin and others have long recognized: that many complex behaviors are found, albeit in different and sometimes more rudimentary forms, across the animal kingdom. Soon researchers are proposing that we redefine the behavior in question. For example, tool use does not necessarily involve crafting wheels or gears (a definition that almost guarantees it will be seen only in humans): it simply means shaping an object to serve some function. Stripping a branch bare, so it can be used to probe a termite mound, is creating a tool. How common tool use, or empathy, or whatever the behavior in question is, and in what ways it might differ across species, then become empirical questions, rather than philosophical ones, about our supposed human uniqueness.

We provide a brief overview of the study of empathy in nonhumans, a behavior, that, like tool use, was assumed to be something humans, and only humans, were capable of. We adopt de Waal and Preston's (*1*) definition of empathy "as emotional and mental sensitivity to another's state, from being affected by and sharing in this state to assessing the reasons for it and adopting the other's point of view," and begin with a historical perspective on this behavior. From there, we segue into more modern studies of empathy in nonhumans.

HISTORICAL PERSPECTIVE ON PROSOCIAL BEHAVIOR AND EMPATHY IN NONHUMANS

Darwin's colleague, Thomas Henry Huxley, described animal behavior in a way that left little room for empathy: "From the point of view

of the moralist, the animal world is on about the same level as the gladiator's show," Huxley wrote (*2*). "The creatures are fairly well treated, and set to fight; whereby the strongest, the swiftest and the cunningest live to fight another day. The spectator has no need to turn his thumb down, as no quarter is given" (*2*).

Huxley argued, that with the exception of interactions between genetic relatives, natural selection should rarely, if ever, favor prosocial behavior. And most western scientists of the day agreed with him. But a Russian scientist/anarchist/prince named Peter Kropotkin, who had spent five years studying natural history in Siberia, thought otherwise. Kropotkin hypothesized that natural selection could, and often did, favor prosocial behaviors – what he referred to as mutual aid. In time, Kropotkin proposed his "law of mutual aid" wherein mutual aid was of "the greatest importance for the maintenance of life, the preservation of each species and its further evolution" (*3*). In his book *Mutual Aid: A Factor in Evolution*, Kropotkin provides example after example of prosocial behavior in insects, in birds, and in mammals, including primates, who "display the greatest solicitude for their wounded, and do not abandon a wounded comrade during a retreat till they have ascertained that it is dead and that they are helpless to restore it to life" (*3*).

Kropotkin was not satisfied demonstrating mutual aid in nonhumans and casting it in an evolutionary framework, he also wanted to understand it from a proximate perspective. In real time, what caused animals to dispense mutual aid? Here is where empathy enters the picture, but Kropotkin's initial sortie into nonhuman empathy came through an unexpected source: the work of economist/political scientist Adam Smith.

Though Kropotkin the anarchist/proto-socialist knew Smith's famous 1776 book, *An Inquiry into the Nature and Causes of the Wealth of Nations* well (*4*), it was another one of Smith's books that would provide him his theory for the proximate causation of mutual aid in animals. Many years earlier, in 1759, Smith published *The Theory of Moral Sentiments* (*5*), a book Kropotkin thought "far superior to the work of his [Smith's] old age upon political economy." In *The Theory of Moral Sentiments*, Smith proposed that empathy was the key to *human* goodness. We put ourselves in the position of the other and assume they feel what we would feel in their situation, and so we sometimes help others who are in discomfort or pain. In Smith's words, this empathy was a human universal: "How selfish soever man may be supposed there are evidently some principles in his nature, which interest him in the fortune of others … of this kind is pity or compassion, the emotion which we feel for the misery of others, when we either see it, or are made to conceive it in a very lively manner. The greatest ruffian, the most hardened violator of the laws of society, is not altogether without it" (*5*).

After reading *The Theory of Moral Sentiments* Kropotkin came to think that empathy was the key to a proximate understanding of mutual aid in animals. Smith was right about empathy in humans, Kropotkin argued: the only shortcoming of *The Theory of Moral Sentiments* was that it did not extend this theory of empathy far enough. "Adam Smith's only mistake," Kropotkin wrote, "was not to have understood that this same feeling of sympathy in its habitual stage exists among animals as well as among men" (*6*). Empathy – what Kropotkin here called sympathy – was the proximate key to animal, as well as human, mutual aid.

When Kropotkin proposed this theory toward the end of the nineteenth century, no one was doing experiments, let alone controlled experiments, on empathy in nonhumans. Over the last few decades that has begun to change.

CONTEMPORARY WORK ON EMPATHY IN NONHUMANS

Eleanor, an African elephant (*Loxodonta Africana*) matriarch, was dying. She was already in poor health and when she took a hard fall, it was Grace, an unrelated matriarch of another herd, who came running to her aid within minutes (*7*). Grace, with her raised tail and secretions streaming from her temporal lobes, was showing stereotypical signs of distress in African elephants (*8, 9*). Even after Grace's own family had left the area, she stayed with Eleanor and continuously tried to help her to her feet by lifting with her tusks. It was, as Douglas-Hamilton recounts (*7*), a heart-wrenching scene with "Grace appear[ing] very stressed, vocalizing, and continuing to nudge and push Eleanor with her tusks." Other examples similar to this type of helping behavior have been documented in elephants (*10 ,11 ,12*), but are they instances of empathy? To answer that question, let's first look at one theory for the evolution of empathy and next how animal behaviorists and evolutionary biologists have examined empathy in nonhumans.

EVOLUTION OF EMPATHY

One hypothesis for the origin and evolution of empathy is that it dates back to birds and very early mammals (*13*). Natural selection, the argument goes, initially favored the development of emotional understanding in the context of parental care, where young offspring use distress calls and body language to encourage parents to respond appropriately to their needs (*14–16*). After the empathetic ability to recognize and respond to the emotions of others was established in parent-offspring interactions, it was co-opted to other social contexts. Then, over time, natural selection fine-tuned the expression of empathy such that, depending on the ecology and life history of the species in question, it might be modulated by extrinsic factors, including similarity between recipient

and donor (*17*), prior social relationships (*18*), temperament (*19*), prior emotional state (*20, 21*), and cognitive complexity (*13*).

THE MULTIPLE LAYERS OF EMPATHY

As a conceptual framework for studying empathy, de Waal proposed the "Russian doll model:" like a Russian nesting doll, empathy has multiple layers, each scaffolded on the layers within (*13*).

The Innermost Layer/The Core: Emotional Contagion

At the innermost layer of the Russian doll, called the core, empathy manifests as simple responses to another's affective state, such as mirroring via motor mimicry (*e.g.*, contagious yawning) and emotional contagion via state-matching, both of which are facilitated by what is called the perception-action model (PAM). The PAM proposes that the nervous system has evolved in a way such that it maps the emotional state of others onto the neural, experiential and mental representations of those states in self (*1, 17*).

Emotional contagion occurs when an observer matches the emotional state of another, as, for example, when observing another in distress elicits personal distress in the observer (*22–24*). That distress could alter the emotional state of the observer and promote behavior that helps the individual in distress, much like intense begging displays by offspring result in provisioning by parents (*25*).

Some of the earliest studies of this sort of empathy involved examining the response of rats to a distressed conspecific (*20, 26, 27*). In one famous study (*20*), Church found that rats that had been trained to press a lever to receive food, decreased their rate of lever-pushing when it caused another rat, in an adjacent arena, to receive an electric shock. The frequency of lever-pushing decreased further when the foraging rat had previously experienced an electric shock itself, suggesting that the change in behavior in the foraging rate was induced by the perception of another individual in distress, and that this was magnified by prior experience with the source of distress. Masserman *et al.* (*28*) found similar results in rhesus macaques (*Macaca mulatta*): even when individuals were hungry, one third of the monkeys chose a chain-pulling option that provided them less food, *if* the alternative option, associated with a greater food payoff, resulted in a nearby conspecific receiving an electrical shock.

Middle Layer: Sympathetic Concern

Sympathetic concern, the next level of empathy in the Russian doll model, also involves behavioral contagion, but now the observer attempts to understand the situation experienced by another, and then engages in other-oriented behavior. One type of sympathetic concern is consolation behavior, where a bystander makes affiliative contact with and offers reassurance to a distressed individual. For example, chimpanzees (*Pan troglodytes*) sometimes embrace an individual after it has been attacked by a third party (*29, 30*). Such consolation has been shown to reduce stress in the victim of the attack (*31, 32*). Despite an obvious benefit accrued by the consoler, and, indeed, in the face of possible retaliation by the aggressor against the consoler, this behavior has been documented in both wild and captive chimpanzees, as well as bonobos (*Pan paniscus*) and stump-tailed macaques (*Macaca arctoides*; *17, 29–34*).

Consolation behavior is not restricted to primates, and has also been found in dogs (*Canis lupus familiaris*; *35*), rooks (*Corvus frugilegus*; *36)*, prairie voles (*Microtus ochrogaster*; *37*), and possibly African elephants (recall the story of Grace and Eleanor, also Bates *et al.*; *38*). Plotnik and de Waal (*39*) studied consolation behavior in female Asian elephants (*Elephas maximus*). Distress was caused by aggression, separation from a group, accident, etc., and distressed animals emitted numerous vocalizations (trumpets, roars and rumbles) and displayed postural changes (*e.g*, ears forward, tail erect). Compared to controls, bystanders who observed another elephant in distress emitted more affiliative vocalizations and touched the distressed individual significantly more often.

Outermost Layer: Empathetic Perspective-Taking

Empathetic perspective-taking, the outer layer in the Russian doll model, involves recognizing and responding to the emotional states of others, while maintaining self-other differentiation. Empathetic perspective-taking requires the observer to recognize that her own emotional state and needs are separate from those of another. This type of empathy can motivate targeted helping behavior, defined as "help and care based on a cognitive appreciation of [another's] *specific* need or situation" (*13*). Evolution of the prefrontal cortex likely facilitated self-recognition and imagination, which are thought to greatly facilitate empathetic perspective-taking, and thus, targeted helping behavior (*16*). In part, due to ethical constraints, controlled studies of targeted helping are relatively rare and often anecdotal. For example, Hart *et al.* (*39*) reviewed instances of reported targeted helping behavior in elephants by both kin and non-kin to help lift injured individuals, rescue calves from holes, and protect individuals after being darted by park rangers. Targeted helping may also play a role in understanding instances when dolphins help injured conspecifics to the water surface.

One of the better sets of controlled studies of targeted helping has been done using rats (*18, 41, 42*). Rats were housed in pairs for two weeks before experimental trials began. In each pair, one individual was selected as the 'free' rat and the other the 'trapped' rat, and distress was

elicited by confining the trapped rat in a restrainer with a door that could only be opened from the outside by the free rat. The free rats not only learned to open the door, releasing the trapped rat, but did so more often than when the restrainer was empty or contained a toy rat. The free rats also continued to open the restraining door even when doing so resulted in their cage-mates' being released into another enclosure, which suggests it was indeed targeted helping, rather than motivation for social contact, that elicited door opening. In a follow-up study, Bartal *et al*. (*42*) found that rats were just as likely to release a familiar conspecific as they were to release an unfamiliar conspecific, as long as the unfamiliar conspecific was of their strain. But when rats were raised from birth with individuals from another strain, they helped unfamiliar individuals of their fostered strain significantly more often than strangers of their own strain.

If free rats were engaged in targeted helping, then if the state of the free rats were experimentally manipulated, it should affect their door-opening behavior. Bartal *et al*. (*18*) compared a group of free rats treated with midazolam, a common antianxiety medication, with a control group, and found a significant decrease in door-opening behavior when the restrainer contained a cage-mate, but not when the restrainer housed food: shared emotional representation (lessened by the midazolam) was necessary to motivate targeted helping behavior.

CLOSING THOUGHTS

Although ideas about empathy in nonhumans have been around since the time of Darwin, it is only in the last few decades that animal behaviorists, including those in both biology and psychology, have been developing a conceptual framework for understanding different types of empathy and how they are related. Both experimental and observational work to date on emotional contagion, sympathy, and targeted helping suggest that empathy is more common in nonhumans than once thought. Future behavioral work, paired with work on the neurobiology, endocrinology, and molecular genetics of empathy, will, no doubt, further our understanding of this fascinating behavior.

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