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Abstract

Darwin offered an evolutionary perspective on the origins of human morality, suggesting that humans share a biological foundation with nonhuman primates. This paper reviews the current literature on moral and prosocial behaviors of nonhuman primates, specifically examining whether nonhuman primates exhibit behaviors that are typical of empathy and fairness. The literature documents that nonhuman primates exhibit empathetic behaviors regarding emotional contagion and sympathetic concern. There is also evidence that nonhuman primates have a sense of fairness, seen in their reciprocal behaviors and aversion to inequity. Taken together, this suggests that there are evolutionary roots of morality, lending empirical support to Darwin's theory.

Keywords: morality, evolution, primates, empathy, fairness, Darwin

Human morality has puzzled some of the world's greatest minds for millennia, with differing perspectives and potential large-scale social implications. Whereas Aristotle argued that moral behavior resulted from a wise application of virtue to a specific circumstance (Irwin, 2000), Bentham (1781) took a utilitarian stance toward morality, claiming the best action is the one that maximizes well-being for the most people possible. Still today, differences in values often precipitate turbulent political debates and fuel legislative decision making. With differing perspectives on morality, opposing ideologies easily develop, and it becomes difficult to agree on universal codes of proper behavior. Understanding the origins of morality may help humanity to unify on a global scale, disregarding cultural differences and leading toward a brighter future with less suffering due to ideological conflict.

Darwin (1871) offered a biological perspective on the origins of morality. He thought prosocial behavior and reciprocity—empathy and fairness—were adaptations that ensured greater survival and reproductive success in social animals. Given that humans are socially intricate creatures, Darwin theorized that human morality emerged because of the species' need for group cooperation. If Darwin's hypothesis on the origin of morality was correct, then one should be able to empirically investigate and observe the behaviors of humankind's closest relatives, nonhuman primates, to test whether they display any behaviors akin to what might be considered "moral."

Because morality is a complex topic, the scope of this paper is limited to the fundamental moral behaviors necessary for basic cooperation, given that Darwin (1871) suggested cooperation as the fundamental precursor to moral behavior. The moral foundations theory (MFT) posits that the preeminent pillars of morality are care and fairness (Graham et al., 2013). This means if any two or more individuals are to cooperate morally—that is, without any unnecessary suffering—they must act mutually caring and fair to a sufficient degree. The concept of care is central to empathy, or the ability to feel what others feel and respond appropriately. Fairness implicates ideas of equality. In the present review, MFT is utilized as a conceptual framework to analyze the displays of empathy (i.e., care)

and fairness observed in nonhuman primates. If Darwin was correct in his analysis of the development of human morality as a survival mechanism, then the literature should present evidence of such in nonhuman primates, given the common ancestor and phylogeny. The emergence of human morality can be understood from an evolutionary perspective, showing that primates' need for cooperation has led to the development of empathetic and fair behaviors.

Necessary Cooperation as a Precursor to Moral Behaviors

The core assumption in Darwin's theory on the origins of morality is the necessity of social cooperation for survival. For the propagation of the species, animals require at least minimal social interaction when they mate. However, social interactions among nonhuman primates take on a much broader and richer repertoire of behaviors than simply mating. Most nonhuman primates travel in troops, forage together, sleep near each other, and spend most of their lives embedded within a complex social network (Swedell, 2012). Researchers have documented how chimpanzees will cooperatively and systematically stalk and hunt prey, showing their adept ability to cooperate (Butynski, 1982; Nishida, Uehara, & Nyundo, 1979; Takahata, Hasegawa, & Nishida, 1984). Researchers have observed even more intricate cooperative behaviors, such as lower-ranking chimpanzees uniting to defeat a common enemy higher in the dominance hierarchy (Gilby et al., 2013). These interdependent interactions allow for the development of significant social bonds, evidenced in the formation of troops that exhibit ingroup and outgroup biases (Campbell & de Waal, 2011). These social bonds are maintained through cooperation, and monkeys with stronger social bonds have more reproductive success (Schülke, Bhagavatula, Vigilant, & Ostner, 2010; Silk et al., 2009; Silk et al., 2010). Clearly the need for cooperation is a key factor in understanding primate behavior.

Not only do most monkeys and apes rely on the social group for success in reproduction, protection, and obtaining food, but psychologists have also demonstrated that the altricial infant is unable to fully recuperate social competence after extensive periods of isolation (Harlow, Dodsworth, & Harlow, 1965). Rhesus

monkey infants that were socially isolated for six or more months were unable to thrive when reintegrated into the group. Because of their lack of typical socialization, they were unable to navigate the social atmosphere, had severe anxious reactions to novel stimuli, exhibited cognitive deficits, and displayed atypical social behavior (Harlow, Dodsworth, & Harlow, 1965). This suggests not only that social cooperation is beneficial to primate survival, but also that the primate cannot thrive without socialization. Because most nonhuman primates evidently need each other, this emphasis on social cooperation has enabled the development of a rudimentary capacity for socioemotional competence. This socioemotional competence is seen in behaviors of empathy and fairness—the beginnings of morality.

Empathy

MFT considers care to be the first fundamental social rule among societies (Graham et al., 2013). For the purpose of this paper, the term empathy will be used instead of care, in accordance with the developmental model proposed by de Waal (2008). Regarding the development and emergence of empathy, the literature suggests that it be analyzed in at least two sequential stages (de Waal, 2008). The first stage, which the organism must develop before reaching the other, is emotional contagion. The second stage, which envelops and builds on emotional contagion, is sympathetic concern. Together, the two constructs produce a mechanism that can explain the bulk of empathetic phenomena as the organism senses how others feel and modifies its own behavior in response (de Waal, 2008).

Emotional contagion is the organism's capacity to match or sense the state of arousal in another. Researchers consider this empathetic reaction to be largely reflexive as it does not require advanced cognitive processing and is present in most mammals (de Waal, 2008). In one study, rhesus macaques displayed emotional contagion as they acted significantly more avoidant in response to pictures of fearful conspecifics—members of the same species—rather than calm ones (Miller, Murphy, & Mirsky, 1959). Researchers also examined how contagious yawning might exemplify the activation of the emotional contagion mechanism in apes as they noticed that chimpanzees yawn when they see familiar chimpanzees yawn but not with unfamiliar

chimpanzees or other species (Campbell & de Waal, 2014; de Waal, 2009). This display of emotional contagion suggests that nonhuman primates exhibit one of the fundamental requirements of empathy.

If the organism can adeptly match the state of arousal in others, then the next layer in the empathetic mechanism available for development is *sympathetic concern*. Sympathetic concern occurs when the animal recognizes the emotion in another and intentionally attempts to address it (de Waal, 2008). Sympathetic concern is different from emotional contagion in that it is a cognitive evaluation of another's emotions, whereas emotional contagion is largely instinctive. Sympathetic concern drives the animal to engage in prosocial behavior towards another.

Examples of sympathetic concern in nonhuman primates are present in evidence showing how they deliberately act to terminate distress in others. For instance, in an experiment with rhesus macaques, researchers taught them to pull on one of two chains for food (one of the chains always released greater quantities of food). After the monkeys were taught, the researchers later adjusted the chains so that pulling the chain with the larger reward delivered a shock to a nearby monkey. After seeing the nearby monkey get shocked, two-thirds chose the non-shock chain, although it released less food, and the remaining one-third quit pulling the chains for five to 12 days—suggesting they might rather go hungry than shock their conspecifics (Masserman, Wechkin, & Terris, 1964). This shows that these monkeys are capable of sympathetic concern toward their peers.

These prosocial behaviors are not limited to unrealistic artificial laboratory settings either. Chimpanzees and bonobos, our closest genetic relatives, exhibit reconciliatory and consoling behaviors after either witnessing or experiencing physical conflicts and fights with other apes in the troop (Clay & de Waal, 2013; de Waal & van Roosmalen, 1979). Reconciliation occurs when two former opponents engage in affiliative body contact after conflict. These bodily contact behaviors are precipitated by an outstretched hand inviting the other back and followed by embracing, kissing, grooming, and submissive vocalizations. Reconciliation serves an important function in

maintaining long-term social cohesion as it reduces the state of arousal in the opponents (de Waal & van Roosmalen, 1979). Similarly, consolation occurs when a third-party bystander approaches the distressed victim post-conflict and administers the same arousal-reducing behaviors seen in reconciliation (Romero, Castellanos, & de Waal, 2010). These behaviors suggest that chimps and bonobos possess complex socioemotional cognition, can identify conspecifics that are suffering, and, as researchers speculate, deliberately act to ameliorate others' distress for the longevity of the social group. The evidence of both emotional contagion and sympathetic concern displayed in nonhuman primate behavior engenders a plausible model of empathetic behavior (de Waal, 2008). This points toward an evolutionary origin of human empathy and a fundamental aspect of human morality.

Fairness

The second foundational aspect upon which moral systems function is fairness (Graham et al, 2013). Fairness is the moral concept that individuals within the group should be treated equally and without discrimination. Although there exists some degree of cultural variation, there is evidence for a universal sense of human fairness (Henrich, 2000; Henrich et al., 2001). This universality of fairness suggests a possible biological foundation and may therefore be present to some degree among nonhuman primates as well. As primates have evolved to require cooperation for survival, they might have developed behaviors which display the emergent and fundamental qualities of fairness. Researchers have studied and documented fairness along two different dimensions: reciprocity and aversion to inequity.

According to evolutionary biology, organisms likely exhibit prosocial behaviors towards others because they expect a future favor in return—a phenomenon known as reciprocity. Reciprocity meets the criteria for an elementary sense of fairness (i.e., “you scratch my back and I’ll scratch yours”), and reciprocal exchanges among nonhuman primates have been well documented. Researchers found that vervet monkeys preferentially gave more attention in their calls to previous grooming partners and that long-tailed macaques offered more

support during conflicts to those that had recently groomed them (Hemelrijk, 1994; Seyfarth, & Cheney, 1984). Brosnan and de Waal (2002) also found that brown capuchins and chimpanzees shared significantly more food with those that had shared food with them in the past or had previously groomed them. Moreover, a modified version of the ultimatum game was administered to chimpanzees and human children. In the game, one individual chose between two tokens that could be exchanged for rewards with their partner's cooperation. A green token gave both participants equal rewards, but a red token gave more rewards to the chooser than to the partner. Researchers found that chimpanzees and human children responded to this task like typical human adults—that is, they favored the prosocial option if their partner's cooperation was required (Proctor, Williamson, de Waal, & Brosnan, 2013). This suggests that the sense of human fairness depends on cooperation and may have deep evolutionary roots.

Theoreticians propose that during the evolution of cooperation it was advantageous for primates to compare their rewards to those of others within the troop (Brosnan & de Waal, 2003). This development of comparison may have ensured that each member was receiving enough resources for survival and resulted in a natural tendency to avoid situations which produce severely unequal outcomes. Researchers found evidence for this natural aversion to inequity among brown capuchins (Brosnan & de Waal, 2003). In this study, two capuchins were caged side-by-side and assigned the simple task of giving a pebble to the researcher. Upon completion of the task, researchers rewarded each monkey with either cucumbers or grapes. The monkey that received the less-preferred cucumbers, when noticing the other monkey had received the preferable grapes, rejected the inequality and refused to continue participating in the exchanges. This evidence lends further support to a sense of fairness present among nonhuman primates and may help explain the universal human sense of basic fairness.

Summary

Having reviewed the extant literature, there appears to be substantial evidence for Darwin's proposition that the need for

social cooperation among primates likely spurred the development of prosocial and moral behaviors. The evidence for the importance of primate sociality can be found in a hallmark study on social deprivation in which infant monkeys isolated for six or more months were unable to recover in social or cognitive competence (Harlow, Dodsworth, & Harlow, 1965). This deep-seated biological drive for sociality and cooperation has likely engendered the evolution of prosocial behaviors. These prosocial behaviors may resemble prototypes of basic human morality, according to the criteria of MFT.

The prosocial behaviors of nonhuman primates reviewed here have met at least two fundamental moral criteria: empathy and fairness. Nonhuman primates exhibited empathy in how they identified emotional arousal in facial expressions of peers, voluntarily avoided food at the expense of conspecifics, and practiced reconciliation and consolation behaviors. Fairness has been observed in how they preferentially helped those that had helped them in the past, favored the prosocial option while playing the ultimatum game in the condition of necessary cooperation, and exhibited aversion to inequity when unequal rewards were distributed.

Discussion

Although nonhuman primates seem to be capable of certain forms of empathy and fairness, research in different species that attempts to generalize to humans must be interpreted within ethological context, understanding the discrepancies between nonhuman and human primates. For instance, many nonhuman primates live in strict social hierarchies whereas human societies tend to be more flexible. Strict hierarchies are, by definition, intrinsically unequal and unfair to some degree, which could propose translational problems for interpreting studies on fairness in nonhuman primates. Likewise, notwithstanding the biological similarities, humans possess more advanced neural and cortical structures, offering greater complexity in emotion processing, empathy, and moral reasoning. Despite these limitations, the evidence presented in this review remains robust in a general evolutionary sense, given that the findings were supported across many different species of nonhuman primates.

Several areas concerning the degree of moral development in nonhuman primates remain unstudied. One direction for future

research lies in exploring whether they are capable of perspective taking. *Perspective taking* is the third layer of the empathetic mechanism proposed by de Waal (2008), but there is a dearth in the literature assessing if nonhuman primates can attain this degree of socioemotional competence. Moreover, the scope of this paper focused on only two of the five moral foundations posited by MFT. The other three foundations—loyalty, authority, and sanctity—remain for further synthesis. Future research might effectively orient towards identifying how nonhuman primates navigate these other moral concepts in addition to replicating results across multiple species.

Nonetheless, the literature demonstrates that nonhuman primates engage in cooperative, empathetic, and fair behaviors toward one another. Using MFT as a conceptual framework, these empathetic and fair behaviors may qualify as the two most elementary pillars upon which moral systems stand. Understanding this evidence from an evolutionary perspective suggests that several aspects of human morality have a plausible biological foundation.

Although the varying forms of human morality may still be shrouded in mystery and subject to endless philosophical debate, the evidence reviewed here elucidates a part of what makes humans moral creatures. There seems to be something within the inherent biological nature that predisposes people to be good—or at least to perform prosocial behaviors. The senses of empathy and fairness have biological roots deep enough that they travel back through the phylogenetic tree and are manifested in nonhuman primates. If basic morality has biological roots, then there should be some universally shared ground on which opposing human ideologies can agree. Considering the biological origins of human morality may help destructive nations and cultures reconnect with a shared language common to all: empathy and fairness.

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