Altruistic Behavior in Primates

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Abstract: Prosocial behavior is a key component of human interaction, and its evolutionary origins are particularly interesting for scientists due to its immediate cost to the actor. Current literature on primate prosocial behavior reflects conflicting or incomplete evidence for varying hypotheses, such as reciprocity, kin theory, cooperative breeding, and inequity, leaving the evolutionary foundation for this behavior poorly understood. This review paper explores the various proximate and ultimate factors influencing primate prosocial behavior and synthesizes an overarching hypothesis that functions to connect the current fragmented state of the literature. It proposes that ecology supports kin selection, leading to an increase in cooperative breeding or reciprocal behaviors, which thus increases overall social tolerance. Proximate mechanisms, such as underlying neuronal response and situational equity, reinforce these behaviors, leading to the altruistic behavior displayed in some primates today.
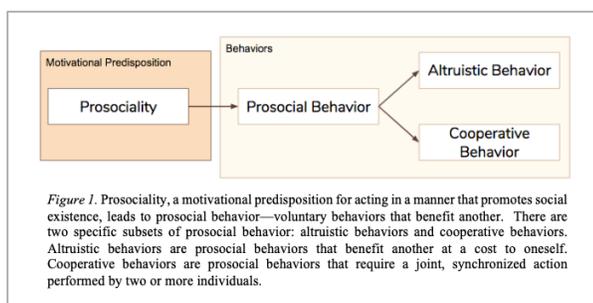
Introduction

Helping behavior is particularly puzzling for scientists because it involves the action of one individual benefitting another, potentially at the cost to oneself. There are several forms of helping behavior that are necessary to define in order to further understand the phenomenon (see Figure 1). Prosocial behavior is used as an overarching term for helping behavior, simply defined as voluntary behaviors that benefit another (Marshall-Pescini, Dale, Quervel-Chaumette, & Range, 2016). Altruistic behavior, a specific subset of prosocial behaviors, refers to actions that benefit another at a cost to oneself (Silk, 2012). Cooperative behaviors are a subset of prosocial behaviors that require joint action of two or more individuals (Brosnan & de Waal, 2002). Overall, prosocial, altruistic, and cooperative behaviors are an exhibition of prosociality—the motivational predisposition for acting in a manner that promotes social existence (Burkart, Fehr, Efferson, & van Schaik, 2007).

Altruistic behavior is typically cited as a defining characteristic of the human species. Humans exhibit exceptional acts of altruism in many facets of life, such as feeding and paying for offspring until they reach adulthood, caring for non-kin individuals, dividing labor, donating to charity, and contributing to conservation efforts. The evolution of altruism garners particular attention since it is hard to understand from a fitness standpoint, given its immediate cost to the actor. An investigation of altruistic behavior in humanity's closest relatives across the primate order will hopefully shed some light on the behavior demonstrated in ourselves.

Non-human primates demonstrate altruistic behavior in the wild, however, to a lesser extent than that exhibited by humans. Evidence shows most primates frequently engage in allogrooming, many demonstrate mutual group support (such as territory patrol and defense from predators), some share food provisions, and some demonstrate allomaternal care, in which individuals who are not the breeding parents of an infant help raise the infant (Goosen, 1981; Koenig, 2017; Muller & Mitani, 2005). However, these behaviors are not uniform across the order, nor consistent from the wild to the laboratory. For example, human's closest

Figure 1. Prosociality, a motivational predisposition for acting in a manner that promotes social existence, leads to prosocial behavior—voluntary behaviors that benefit another. There are two specific subsets of prosocial behavior: altruistic behaviors and cooperative behaviors. Altruistic behaviors are prosocial behaviors that benefit another at a cost to oneself. Cooperative behaviors are prosocial behaviors that require a joint, synchronized action performed by two or more individuals.

living relative, the chimpanzee (*Pan troglodytes*) demonstrates cooperative behaviors in the wild and captivity, however, more often than not fails to demonstrate prosocial behavior in laboratory setups (Silk & House, 2011). By contrast, the more distantly related common marmoset (*Callithrix jacchus*) exhibits consistent prosocial preference both in the wild and in laboratory experiments (Burkart et al., 2007). Such interspecific differences have been used to propose several hypotheses for the basis of altruistic behavior, which are broken down into proximate and ultimate influences.

Proximate influences immediately influence an outcome behavior, such as underlying cognitive mechanisms or psychological traits and motivations (Marshall-Pescini et al., 2016). One proximate influence referenced in the literature is empathy, defined as the capacity to be affected by and share the emotional state observed in another (de Waal, Leimgruber, & Greenberg, 2008). It is hypothesized elicited empathy in a situation increases incidences of prosocial behavior in response. Another influence considered in the literature is increased social tolerance, which is the level to which individuals behave civilly towards conspecifics. Individuals with high social tolerance placed in a given moment are expected to be more likely to behave prosocially. A third quality that seems to immediately affect prosocial tendencies is inequity, characterized by unequal reward distributions between two individuals in which one receives more of an item or an item of greater worth than another individual. It is believed in an unequal situation in which the recipient would receive a greater reward than the donor, there is a decrease in the likelihood of prosocial action by the donor (Silk & House, 2011).

Comparatively, ultimate influences explain why a trait evolved. These factors increase fitness in the long term. Kin selection is studied as an ultimate influence for altruistic behavior because performing helping behaviors towards those related to the helper will increase the fitness of those with the individual's genes, thus increasing the overall likelihood of the perpetuation of the helper's genes (Marshall-Pescini et al., 2016). Reciprocity also functions as an ultimate influence, where altruistic behaviors towards those individuals likely to reciprocate will increase fitness of the donor in the long term (Jaeggi & Gurven, 2013).

The present review will evaluate the literature on altruistic behavior based upon the proximate and ultimate influences believed to play a role in its exhibition. Observation of behavior in the wild will be considered; however, the paper's focus will be on controlled laboratory studies which truly address the motivation behind a prosocial behavior independent of confounding factors in the wild.

Proximate Influences
Mechanisms Behind Empathy

One mechanism underlying empathy in both humans and non-human primates is "state-matching," which elicits similar emotions in an observer to those displayed by another. This mechanism was first discovered in macaques (*Macaca mulatta*) when researchers observed that the same neurons fire within a specific area of the premotor cortex both when the monkey performs an action and when another individual performs a similar action (Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Neurons of this nature are termed "mirror neurons," and evidence for mirror neurons has since been shown in numerous human studies as well. An experiment utilizing functional magnetic resonance imaging in which individuals either observed or emulated a facial expression showed similar activity in both scenarios within particular structures of the brain associated with emotion (Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003).

Studies show oxytocin plays an important role in empathy as well. A study investigated oxytocin's role in helping behavior utilizing the Dictator Game—a behavioral economic game in which a "proposer" subject has the opportunity to allocate any proportion of an endowment to a recipient (Camerer & Thaler, 1995). Endowments are in the form of cash or currency that can be exchanged for cash, and standard setup involves this exchange occurring anonymously in order to control for any reputational outcomes for a proposer or for reciprocity effects. In a Dictator Game with an experimental group that received 40 IU oxytocin, results showed individuals with increased oxytocin are more likely to allocate money more generously (Zak, Stanton, & Ahmadi, 2007). Those in the oxytocin group were 80% more generous, and thus altruistic, than those in the placebo group (Zak et al., 2007). Several

other studies utilizing similar experimental design corroborate the role of both oxytocin and mirror neurons as biological underpinnings for empathy and thus prosocial behavior (Barraza & Zak, 2009; Batson, 2014; De Waal, 2007; de Waal & Suchak, 2010; Jazayari, Ballesta, & Duhamel, 2017; Piliavin & Charng, 1990; Schino & Aureli, 2009).

Social Tolerance and Cooperative Breeding

Social tolerance is increased in species who follow a cooperative breeding mechanism, which in turn increases the incidence of prosocial behavior within those species. Social tolerance is a trait seen in varying levels within species, exhibited by behaviors such as territory sharing, food sharing, or reception of those of different beliefs or race in humans. Cooperative breeding, also known as allomaternal care, is a mechanism in which individuals who are not the breeding parents of an infant help raise the infant. Cooperative breeding depends upon behaviors characteristic of social tolerance, such as food sharing and infant assistance, in order to function. As expected, evidence shows social tolerance is higher in cooperatively breeding species (Burkart & van Schaik, 2010). Social tolerance has since been hypothesized as a proximate mechanism for the basis of prosocial behavior (Marshall-Pescini et al., 2016). In order to investigate this claim, scientists have turned to laboratory setups testing for prosociality in both cooperatively breeding and non-cooperatively breeding primates, since comparing the results between these two groups is a means to examine the influence of social tolerance.

Cooperatively breeding species consistently demonstrate prosocial tendencies when tested in the paradigm known as the Prosocial Choice Test (PCT) (Figure 2). The PCT follows a general setup in which a donor chooses between two options: a 0/1 prosocial option that delivers a reward to a recipient and nothing to the donor, and a 0/0 neutral option that delivers no rewards. This reward distribution is recommended over a 1/1 and 0/1 test—in which both the donor and recipient receive rewards in the 1/1 distribution and the donor alone receives a reward in the 0/1 distribution—because primates demonstrate a preference for larger numbers of rewards, which would be a confounding drive for an individual to choose the 1/1 distribution (Uher
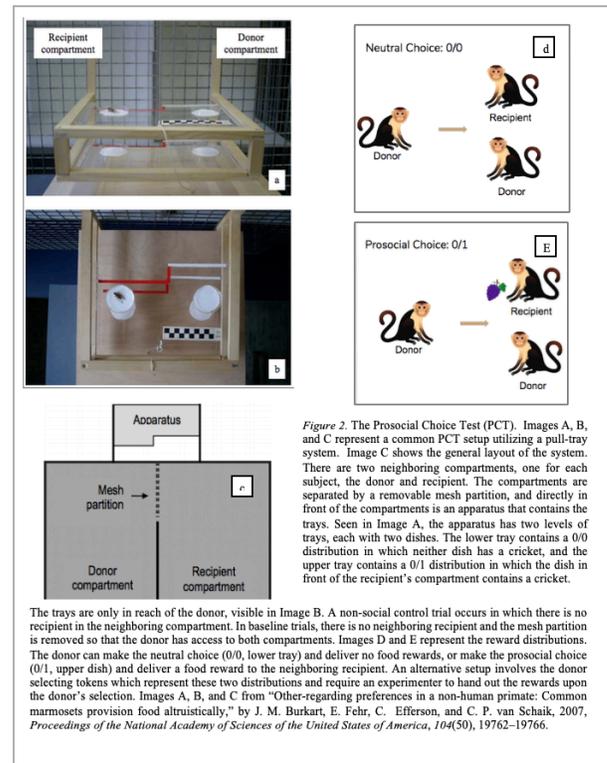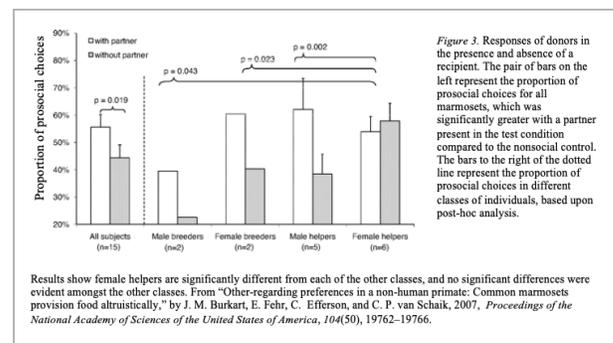
Figure 2. The Prosocial Choice Test (PCT). Images A, B, and C represent a common PCT setup utilizing a pull-tray system. Image C shows the general layout of the system. There are two neighboring compartments, one for each subject, the donor and recipient. The compartments are separated by a removable mesh partition, and directly in front of the compartments is an apparatus that contains the trays. Seen in Image A, the apparatus has two levels of trays, each with two dishes. The lower tray contains a 0/0 distribution in which neither dish has a cricket, and the upper tray contains a 0/1 distribution in which the dish in front of the recipient's compartment contains a cricket. The trays are only in reach of the donor, visible in Image B. A non-social control trial occurs in which there is no recipient in the neighboring compartment. In baseline trials, there is no neighboring recipient and the mesh partition is removed so that the donor has access to both compartments. Images D and E represent the reward distributions. The donor can make the neutral choice (0/0, lower tray) and deliver no food rewards, or make the prosocial choice (0/1, upper dish) and deliver a food reward to the neighboring recipient. An alternative setup involves the donor selecting tokens which represent these two distributions and require an experimenter to hand out the rewards upon the donor's selection. Images A, B, and C from "Other-regarding preferences in a non-human primate: Common marmosets provision food altruistically," by J. M. Burkart, E. Fehr, C. Efferson, and C. P. van Schaik, 2007, *Proceedings of the National Academy of Sciences of the United States of America, 104*(50), 19762–19766.

& Call, 2008). A nonsocial control condition, with no neighboring recipient, ensures prosocial choices are due to the presence of a conspecific. Options are typically selected by the donor using a token system or by pulling a tray containing the rewards into reach of the recipient. The prosocial behavior of common marmosets, a cooperatively breeding species who thus have increased social tolerance, was studied utilizing a tray-pulling setup of the PCT (Burkart et al., 2007). Displayed in Figure 3, the proportion of prosocial choices of the donors in the test condition was significantly greater than the proportion in the control condition. Thus, this cooperatively breeding species demonstrated prosociality. Further analysis was performed by partitioning the subject pool by

Figure 3. Responses of donors in the presence and absence of a recipient. The pair of bars on the left represent the proportion of prosocial choices for all marmosets, which was significantly greater with a partner present in the test condition compared to the nonsocial control. The bars to the right of the dotted line represent the proportion of prosocial choices in different classes of individuals, based upon post-hoc analysis.

Results show female helpers are significantly different from each of the other classes, and no significant differences were evident amongst the other classes. From "Other-regarding preferences in a non-human primate: Common marmosets provision food altruistically," by J. M. Burkart, E. Fehr, C. Efferson, and C. P. van Schaik, 2007, *Proceedings of the National Academy of Sciences of the United States of America, 104*(50), 19762–19766.

sex and social role. It was discovered that female and male breeders as well as male helpers made the prosocial choice preferentially, but female helpers showed no preference. These results are consistent with naturalistic observations demonstrating female helpers have a minimized role in allomaternal care, rarely engaging in infant carrying, which suggests a lower social tolerance (Burkart et al., 2007). The researchers of this study were particularly deliberate in their methodology and analysis, considering—and rejecting—the following alternative explanation proposed by critics: the subjects do not truly understand their role in the experiment and the consequences of their choices in terms of who benefits, thus discounting prosociality as a motivation for their behavior. However, the study included both a baseline pre-test and post-test in which the donors had access to the neighboring cage and thus could retrieve the food reward. These baseline tests demonstrated a significant preference for the prosocial choice when the monkey could collect the reward compared to the nonsocial control condition in which they could not access the neighboring cage and there was no recipient (Burkart et al., 2007). These results support the monkeys' grasp of the consequences of their actions.

Similar significant results for a prosocial tendency have been demonstrated in another cooperatively breeding species, the cotton top tamarin (*Saguinus oedipus*) (Cronin, Schroeder, & Snowdon, 2010; Hauser, Chen, Chen, & Chuang, 2003). Furthermore, capuchin monkeys (*Cebus apella*), which follow an intermediate degree of cooperative breeding, also show a preference for the prosocial option in the laboratory (Burkart & van Schaik, 2010; de Waal et al., 2008). This intermediate breeding system likely requires an increased social tolerance, though lesser than that in fully cooperatively breeding species.

Across the literature, non-cooperative breeders (or independent breeders) typically demonstrate a lack of prosociality in laboratory experiments. The chimpanzee shows no preference for the prosocial option when studied utilizing various methodologies (Brosnan et al., 2009; Jensen, Hare, Call, & Tomasello, 2006; Vonk et al., 2008; Yamamoto & Tanaka, 2010). Notably, Horner, Carter, Suchak, and de Waal (2011) demonstrated a significant preference for the prosocial option amongst chimpanzees utilizing a setup of the PCT with token exchange. The researchers posit this discrepancy is due to prior flaws in methodology. Horner et al. (2011) placed chimpanzees in close proximity (<1m) without glass barriers and attempted to eliminate any location biases that could form when allowing the subject to explore both the donor and recipient compartments. However, the study by Brosnan et al. (2009), which failed to demonstrate a prosocial tendency, did not include a glass barrier, nor conditioning that would lead towards location biases. Furthermore, the chimpanzees' understanding of the experimental setup was ensured prior to testing (Brosnan et al., 2009). In the study by Jensen et al. (2006) which also exhibited no prosocial preference, a second experimental setup eliminated any possible location biases and ensured experimental understanding, and although the chimpanzees were in separate rooms, the recipients were clearly visible and recognized by the donors. However, following this methodology, it is possible results were due to an aversion towards inequity.
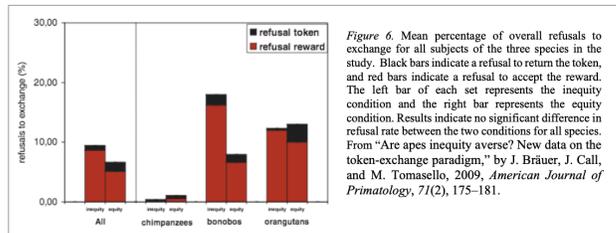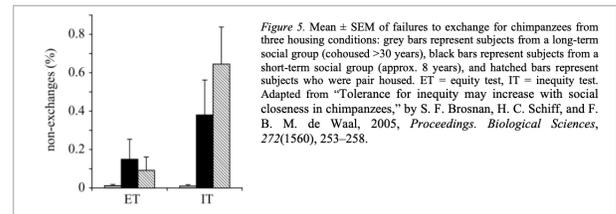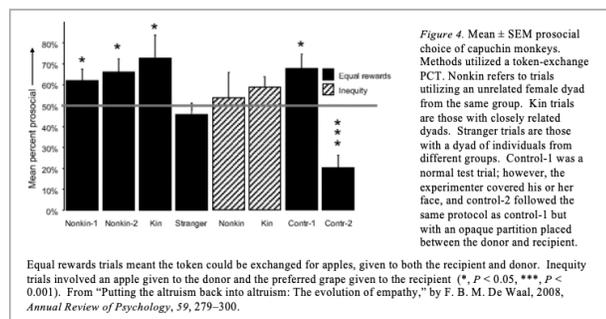
Inequity

Studies show primates are inequity averse, and thus less likely to engage in an altruistic act when the act results in an unequal distribution of rewards. Inequity comes in two forms: disadvantageous inequity, in which a partner receives a greater reward than a focus individual, and advantageous inequity, in which the focus individual receives a greater reward than his or her partner. This inequity aversion (IA) has structural roots in the brains of both human and nonhuman primates. Humans with lesions on the ventromedial and orbitofrontal subdivisions of the prefrontal cortex, which evidence shows play a role in social behavior, demonstrate an abnormal, decreased aversion to social inequity (Jazayari et al., 2017). This unusual behavior suggests the lesions disrupt the normal human processing of reward outcomes. A study on macaque monkeys demonstrated ventral striatal neurons were sensitive to reward inequity; specific striatal neurons fired during advantageous inequity, and another subset of striatal neurons fired during disadvantageous inequity (Báez-Mendoza, van Coeverden, & Schultz, 2016). This evidence demonstrates monkeys recognize differing reward

distributions at the neuronal level, and several studies investigate the behavioral consequences of these distributions.

For nonhuman primates, inequity aversion is studied in the laboratory utilizing a modified token PCT in which one token delivers a reward to the donor (the "selfish choice"), and a different token delivers a reward to both individuals but the reward to the recipient is of greater value than that to the donor (the "prosocial choice"). Following this methodology, significant results showed capuchin monkeys were more inclined to act prosocially when presented with equal rewards compared to conditions containing inequity (Figure 4; de Waal et al., 2008). Preference of the prosocial option in the inequity conditions did not significantly exceed chance, unlike the equal rewards conditions. However, prosocial choice was significantly greater in the inequity conditions compared to the control condition in which the donor was unable to see the neighboring recipient conspecific.

Inequity aversion is also studied utilizing a test paradigm in which an individual is given a token that can be exchanged for a reward, and depending on the token, it is exchanged for either a less desirable or equally desirable reward compared to that given to a neighboring conspecific. The number of exchange refusals, in which the subject either refuses to give the token in exchange for the reward or the subject refuses the reward upon exchange, are measured per trial. Utilizing this methodology, researchers found chimpanzees demonstrated a significantly greater percentage of exchange refusals when receiving a reward of less desirable quality, thus demonstrating an aversion to inequity (Figure 5; Brosnan, Schiff, & de Waal, 2005). However, upon replication of this study, researchers failed to reproduce these findings in chimpanzees, bonobos, and orangutans, rather

Figure 5. Mean ± SEM of failures to exchange for chimpanzees from three housing conditions: grey bars represent subjects from a long-term social group (cohoused >30 years), black bars represent subjects from a short-term social group (approx. 8 years), and hatched bars represent subjects who were pair housed. ET = equity test, IT = inequity test. Adapted from "Tolerance for inequity may increase with social closeness in chimpanzees," by S. F. Brosnan, H. C. Schiff, and F. B. M. de Waal, 2005, *Proceedings. Biological Sciences*, *272*(1560), 253–258.

Figure 6. Mean percentage of overall refusals to exchange for all subjects of the three species in the study. Black bars indicate a refusal to return the token, and red bars indicate a refusal to accept the reward. The left bar of each set represents the inequity condition and the right bar represents the equity condition. Results indicate no significant difference in refusal rate between the two conditions for all species. From "Are apes inequity averse? New data on the token-exchange paradigm," by J. Bräuer, J. Call, and M. Tomasello, 2009, *American Journal of Primatology*, *71*(2), 175–181.

finding no significant aversion to inequity (see Figure 6; Bräuer, Call, & Tomasello, 2009). Bräuer et al. (2009) made a slight procedural change in order to reduce confounds from the methodology by Brosnan et al. (2005), which may explain the difference in results. Brosnan et al. (2005) explicitly held up the more favorable food (grapes) to the primates before each control trial, which may have created an expectation that the subjects would receive a grape during the control, leading them to be more likely to exchange during the control compared to the test trials. While replicating, Bräuer et al. (2009) did not explicitly hold up the grape each time, although all rewards were visible at all times.

Mixed results for primate inequity aversion may be affected by closeness of the recipient. In humans, results of economic behavioral games such as the Dictator Game suggest individuals have a strong preference for equitable outcomes (Silk & House, 2011). However, humans tend to respond differently to inequity when the other recipient is closely related. Each of the nonhuman primate studies mentioned in this section found the same trend, where level of relation to the partner appeared to play a slight role in the number of prosocial choices by the donor. This confounding factor is known as kin selection and is discussed in detail in the next section.

Ultimate Influences
Kin Selection

Kin selection is studied in the laboratory using PCT paradigms in which the recipients vary in relatedness to the donors. If the kin selection hypothesis is correct, results should indicate

Figure 4. Mean ± SEM prosocial choice of capuchin monkeys. Methods utilized a token-exchange PCT. Nonkin refers to trials utilizing an unrelated female dyad from the same group. Kin trials are those with closely related dyads. Stranger trials are those with a dyad of individuals from different groups. Control-1 was a normal test trial; however, the experimenter covered his or her face, and control-2 followed the same protocol as control-1 but with an opaque partition placed between the donor and recipient.

Equal rewards trials meant the token could be exchanged for apples, given to both the recipient and donor. Inequity trials involved an apple given to the donor and the preferred grape given to the recipient (*, *P* < 0.05, ***, *P* < 0.001). From "Putting the altruism back into altruism: The evolution of empathy," by F. B. M. De Waal, 2008, *Annual Review of Psychology*, *59*, 279–300.

significant prosocial choice for recipients who are related to the donor and no bias for the prosocial choice in trials with a stranger.

The role of kin selection on capuchin monkey prosocial behavior was investigated by performing multiple PCT trials with recipients of varying relatedness (de Waal et al., 2008). Results demonstrated prosocial tendencies increased with social closeness, being lowest towards strangers and highest towards kin (see Figure 4). All test conditions with equal rewards resulted in a significant preference for the prosocial option, greater than that due to chance, except for the trial with strangers (de Waal et al., 2008). Similarly, when studying the influence of inequity on chimpanzees, results showed a significant correlation to relatedness (Brosnan et al., 2005). Measuring the amount of exchange refusals during trials with unequal rewards, the researchers found individuals from a long-term social group (housed together for more than 30 years) almost never refused an exchange, while those from short-term or unrelated groups showed significant aversion to disadvantageous inequity with a much greater proportion of refusals (Figure 5; Brosnan et al., 2005).

However, studies honing in on the motivation behind prosocial behavior fail to support the kin selection hypothesis. In a study on common marmosets, individuals were placed in a PCT and found to show a significant preference for the prosocial option when a recipient was present compared to the nonsocial control (Figure 3; Burkart et al., 2007). In order to eliminate the possibility that the results were due to kin selection, the researchers performed the trials again but with dyads of unrelated individuals. Results once again showed donors pulled the prosocial tray significantly more often with a partner present than when alone (Burkart et al., 2007). Thus, donors show equally strong unsolicited prosocial behavior towards nonkin as kin. The previously mentioned study on chimpanzees, with results indicating a significant preference for the prosocial option utilizing the PCT, also showed no significant difference between kin and nonkin pairs (Horner et al., 2011). Results collectively indicate level of relatedness may play a role in prosocial behavior, but prosocial behavior is not contingent upon kinship.

Reciprocity

Altruistic behaviors may depend on the likelihood of future reciprocity. Long-term observation of individuals in group living in the wild and captivity (emulating natural circumstances) is often used to study reciprocity, as future reciprocal behaviors can be directly observed. Evidence in these observational studies suggests individuals direct their altruistic behaviors towards those conspecifics that reciprocate most (Schino & Aureli, 2009). A review paper investigated the effect of receiving food and/or other commodities on giving food in 32 independent study populations (eight monkey, eight ape, and 16 human populations) (Jaeggi & Gurven, 2013). Results indicated an overall weighted effect size significantly greater than zero for each collective group—monkey, ape, and human—demonstrating greater likelihood of giving food after receiving food. Additionally, there were no significant differences in effect sizes between each group (Jaeggi & Gurven, 2013). These results indicate a significant independent contribution of reciprocity to primate helping behavior across the order. However, in observational studies, there is high possibility for confounding variables; laboratory studies are often used to hone in on the direct motivation behind prosocial behavior in a controlled setting.

A study investigating unsolicited prosociality using the PCT specifically controlled for reciprocity by eliminating the possibility of reciprocity in its design (Burkart et al., 2007). Results showed a significant preference for the prosocial option when paired with a conspecific compared to the nonsocial control (Figure 3). Dyads were tested in only one direction, the donor never begged to receive food in return, no reciprocal exchanges were ever observed, and calculated reciprocity never produced false positive results in other species known for reciprocity during the prosocial test (Burkart et al., 2007). Thus, the results of a prosocial preference were independent of reciprocity. Numerous studies on various different species, such as chimpanzees and cottontop tamarins, indicate the same insignificant results when studying the influence of reciprocity on prosocial choices in the laboratory setting (Cronin et al., 2010; Horner et al., 2011). Because reciprocity seems to play a role in the wild but is not a necessity

for prosocial behavior in the laboratory, it seems it may increase the likelihood of prosocial behavior but is nonessential.
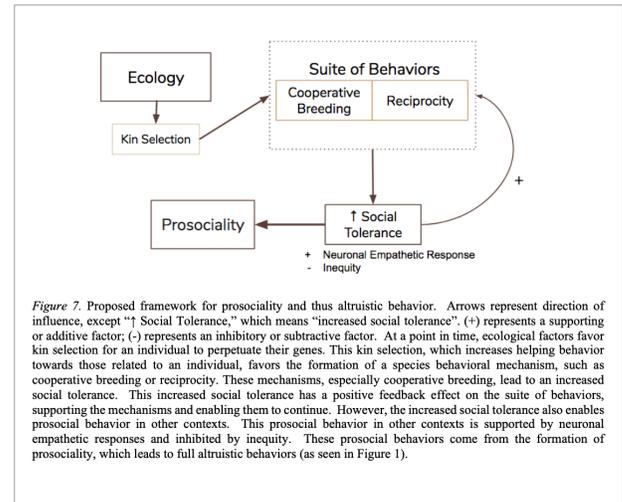
Conclusion

Summary of Results

After assessing the literature in light of various hypotheses thought to play a role in primate prosocial behavior, several general results surface. In terms of the proximate mechanisms, evidence shows mirror neurons and oxytocin underlie empathy in both human and non-human primates. Furthermore, increased social tolerance from cooperative breeding shows a strong correlation to increased prosocial behavior. However, there are some inconsistencies with chimpanzees, who are a non-cooperative breeding species and sometimes demonstrate prosocial behavior in the laboratory, though for the most part they do not. Finally, there is a general trend of aversion to inequity, but it does not prevent prosociality. In terms of the ultimate mechanisms, laboratory results indicate that neither kinship nor reciprocity are necessary for the presence of prosociality. However, there seems to be a trend in relatedness increasing prosocial behavior for kin theory and evidence for reciprocity in the wild.

Proposed Framework for Prosociality

Based upon these results, these various proximate and ultimate factors may be associated in the manner depicted in Figure 7. At some point in history, there is some specific ecology that favors kin selection in order to increase general fitness of an individual's genes. These pressures then lead to a general system of behavior, whether cooperative breeding or reciprocity, that helps those closely related to or associated with the helper. This suite of behaviors favors the increase of certain traits within the individuals in order to maximize the functionality of the suite of behaviors. This includes an increased social tolerance. By increasing social tolerance, it is easier then to carry out these species' behavioral structures. This general increase in social tolerance may then lead to prosocial behavior in other contexts, outside of cooperative breeding and reciprocity. Because cooperative breeding shows the strongest and most widespread relationship in the laboratory, it is most likely the strongest influence on

Figure 7. Proposed framework for prosociality and thus altruistic behavior. Arrows represent direction of influence, except "↑ Social Tolerance," which means "increased social tolerance". (+) represents a supporting or additive factor; (-) represents an inhibitory or subtractive factor. At a point in time, ecological factors favor kin selection for an individual to perpetuate their genes. This kin selection, which increases helping behavior towards those related to an individual, favors the formation of a species behavioral mechanism, such as cooperative breeding or reciprocity. These mechanisms, especially cooperative breeding, lead to an increased social tolerance. This increased social tolerance has a positive feedback effect on the suite of behaviors, supporting the mechanisms and enabling them to continue. However, the increased social tolerance also enables prosocial behavior in other contexts. This prosocial behavior in other contexts is supported by neuronal empathetic responses and inhibited by inequity. These prosocial behaviors come from the formation of prosociality, which leads to full altruistic behaviors (as seen in Figure 1).

prosocial behavior. Cooperative breeding seems to draw a clear connection to increased social tolerance, whereas this is not clear for reciprocity. Since kin selection and reciprocity show a trend but rarely any significant results, they are most likely contributing factors but not necessary in order to demonstrate prosocial behavior.

The few outlier cases with chimpanzees may be due to an interaction of the other influence factors, like reciprocity, combined with the chimpanzee's higher level of cognitive ability compared to the cooperatively breeding species of monkeys. It is possible this increased cognitive ability enables the chimpanzee to behave more variably, based on learned behaviors and external situational factors, whereas those of lesser cognitive ability follow a certain set of innate behaviors in response to stimulus. Furthermore, it is possible an ancestor of the chimpanzee was once a cooperative breeder, increasing the social tolerance within the species, but since then, this ancestral structure is no longer necessary. This may offer one explanation as to why the increased social tolerance trait is retained within the chimpanzee to some extent.

Outside characteristics of the situation also seem to be contributing factors towards prosociality. Given the mirror neurons within the brain, certain situations elicit varying emotion within an individual, which may also influence the likelihood of a prosocial behavior. Again, the increased cognitive ability of chimpanzees may also increase the weight of this empathetic neuronal response, perhaps influencing their behavior more strongly compared to monkeys.

An additional situational influence is the existence of inequity. Inequity shows a potential trend, but the existence of inequity does not prohibit prosociality, making it only a contributing factor.

Overall, prosociality, and thus altruism, seem to be contingent upon the existence of increased social tolerance and the general mechanisms of empathy. This increased social tolerance is most likely due to cooperative breeding, whether the social structure still stands in the species or fell out of favor at some point in evolution. If not cooperative breeding, it must be some third, unknown structure that is yet observed and studied. The rest of the factors are likely contributing but not necessary towards the existence of prosociality.

Based upon this framework for prosociality, there are a few suggestions for future directions of research. It would be valuable to study other taxa, aside from the primates, in order to see whether other cooperative breeding species also demonstrate prosociality. If the trend transcends the primate order, it would further support this hypothesis. Hand in hand with the study of cooperative breeding in other taxa, it should also be explored whether the individuals have mirror neurons. If the emergence of this neuronal structure coincides with the emergence of prosocial behavior, that also will strengthen the neuronal connection to prosociality. In all, an in-depth phylogenetic analysis is necessary to truly discover what led to human altruism.

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