Is Human Prosocial Behavior Unique?:

Insights and New Questions from Non-Human Primates

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Chapter Summary: In this chapter, we discuss recent experimental work providing insight into the ways in which other primate species' prosocial preferences are similar to and different from our own.

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Abstract

Recent positive neuroscience research suggests that brain regions associated with rewarding outcomes are activated not only when rewarding events happen to us, but also when rewarding events happen to other people. Intriguingly, some of the neural areas implicated in the representation of these vicarious rewards are shared with a variety of other mammalian species, raising questions about the evolutionary origins of human prosociality. In this chapter, we discuss the recent experimental work we've conducted as part of our Positive Neuroscience project exploring whether our closest living relatives — the non-human primates — also show human-like patterns of prosocial preferences. We first provide an overview of work by a number of different primate research teams showing that other primate species do behave prosocially in some contexts. For instance, primates will help other individuals achieve their goals in some simple situations and will opt for outcomes that provide food rewards to a partner as well as to themselves. However, our project's studies and those of other research teams have demonstrated that these prosocial preferences seem to be relatively fragile compared to the more robust prosocial preferences observed in humans. Additionally, experimental work has shown that some prosocial motivations may be uniquely human. Specifically, there is no good evidence that other primates engage in third party punishment or that they are averse to cases of advantageous inequity. We conclude by suggesting that future neuroscientific work should look more critically at how and why primates may fail take into account others' preferences in these situations.

Keywords: non-human primates, other-regarding preferences, prosociality, inequity aversion, third party punishment

For centuries, thinkers from a number of disciplines have assumed that human psychology is— at its core— deeply selfish. Economists using models of utility maximization and rational choice have long assumed that people are inherently self-interested and thus should spend most of their time maximizing their own personal wealth and resources. Evolutionary biologists have long held a similar assumption, presuming that humans and other organisms are built to maximize their own selfish reproductive needs. Under this view, human psychology should be largely concerned with accumulating goods associated with survival and reproduction. Although the idea that human beings are deeply self-interested fits squarely with both economic and biological theory, this assumption contradicts most people's experience with actual human interactions. Indeed, across all cultures, people are shockingly *less* self-interested than economic and evolutionary models seem to assume. People regularly behave in ways that systematically violate their own self-interest. Many of these deviations from self-interest involve cases in which people forego a personal payoff in order to do nice things for others. From pausing to hold the elevator for a stranger to donating money to help disaster victims, we humans engage in a number of behaviors that reduce our own welfare in order to benefit others. Such widespread prosocial acts have lead social scientists to argue that humans possess what have come to be known as *other-regarding preferences*, namely preferences for maximizing other people's welfare in addition to our own.

Why do people prefer to sacrifice their own wealth and time in order to benefit others' welfare? Recent research in the field of positive psychology suggests a provocative yet remarkably intuitive answer: *we're nice to others because it feels good*. A growing body of empirical evidence suggests that prosocial actions are intrinsically rewarding (Andreoni, 1990; Lyubomirsky, King, and Diener, 2005; Seligman, 2002). People feel a sense of satisfaction when

others experience positive outcomes (Singer and Fehr, 2005) and report more positive wellbeing after engaging in prosocial actions such as giving to charity or volunteering (e.g., Thoits and Hewitt, 2001). Indeed, recent empirical work suggests that spending money on others increases one's personal wellbeing more than spending money on oneself does (Dunn, Aknin, and Norton, 2008). Taken together, this work suggests that we humans may prefer taking costs to make others feel good because doing so has the counterintuitive effect of making us feel good too.

In the last few years, research in the field of positive neuroscience has gained better insight into why being nice to others feels so good— actions that benefit others seem to recruit some of the same neural systems as actions that benefit the self (Fehr and Camerer, 2007; Zaki and Mitchell, this volume). In a landmark paper, Moll et al. (2006) observed that making charitable monetary donations seemed to activate mesolimbic reward systems, the same regions that are activated when people experience selfishly rewarding events like winning money (Knutson, Adams, Fong, and Hommer, 2001; O'Doherty, Kringelbach, Rolls, Hornak, and Andrews, 2001) or eating delicious food (O'Doherty, Deichmann, Critchley, and Dolan, 2002; for similar results see Harbaugh, Mayr, and Burghart, 2007; Zaki and Mitchell, 2011). Similarly, work in positive neuroscience has revealed that when paying a cost to punish norm violators, participants recruit neural areas associated with anticipated monetary rewards, even though the participants' own money is being lost rather than gained (de Quervain et al., 2004). Finally, Tabibnia, Satpute, and Lieberman (2008) observed that reward regions responded more to gaining a monetary payoff when that payoff represented a fair share of an allotment than when it represented an unfair offer. In this way, our tendency to prefer prosocial behaviors to purely selfish behaviors may be mediated by the neural regions that represent reward contingencies. Specifically, these regions may respond more strongly when we engage in acts that help others

compared to those that help only ourselves. Furthermore, these positive neuroscience studies suggest that this preference is rooted in some pretty basic neurocircuitry— the neural regions that represent reward contingencies across a variety of mammalian species. Our ancient mammalian reward systems may thus be wired to respond when rewarding events happen to others (see also Chang, Winecoff, and Platt, 2011).

1. The Evolutionary Origins of Social Preferences?

The fact that human prosocial preferences are encoded in reward circuitry that's evolutionarily ancient raises an important question about the evolution of these preferences: if human other-regarding preferences rely on relatively evolutionarily ancient neural circuitry, then is it possible that similar social preferences exist in our distant evolutionary relatives as well? Are humans the only species that cares about others' rewards? Or do our close evolutionary relatives— the extant non-human primates (hereafter, just primates)— show similar other-regarding preferences?

Our goal in this chapter is to explore these questions about the evolutionary origins of human prosociality. Specifically, we will review what primate researchers have learned in the last decade about the other-regarding preferences of our closest living relatives. Just as social scientists have developed empirical techniques for tapping into human social preferences, so too have primate researchers established empirical methods for testing such preferences in other primate species. Although these empirical tasks have given primate cognition researchers new insights into primates' tendencies to help and donate resources to others, they have also given rise to some controversy about what— if any— other regarding tendencies primates actually possess (see reviews in de Waal, 2008; Silk and House, 2012; Warneken and Tomasello, 2009).

Here, we review primates' performance in these experimental tasks, pointing out areas where there are still open questions in the field. After reviewing this new body of work on primates' prosocial preferences, we will argue that results from our own positive neuroscience project as well as results from other labs have demonstrated two clear cases where primates' social preferences may differ markedly from those of our own species. We'll then discuss what these two differences mean for future studies investigating the neural mechanisms underlying human social behavior.

2. Exploring the Nature of Primate Social Preferences

Human prosociality is undoubtedly unique in many respects— no other species runs marathons to raise money for charities, engages in formal pedagogical instruction, and works to preserve the environment for strangers in future generations. Nevertheless, despite obvious differences, it is clear that primates naturally act in ways that benefit others in some contexts (see review in de Waal, 2008). One often-cited naturalistic example of primates' concern for others occurs in the aftermath of aggression. Primates from a variety of species will perform friendly behaviors towards another individual who was just part of a conflict (Aureli, Cords, and van Schaik, 2002). In one of the first studies of these post-aggression behaviors, de Waal and van Roosmalen (1979) observed that chimpanzees who had recently engaged in a fight would increase social contact with one another after the altercation, often grooming, embracing, or kissing each other shortly thereafter. This type of post-conflict reunion, referred to as reconciliation, has now been documented in many different primate species (for a review see Aureli et al., 2002). Some primates, specifically great apes, also engage in third party consolation, in which individuals who were merely bystanders to the original aggressive situation seek out victims in order to give their support (e.g., Cordoni, Palagi, and Tarli, 2006; de

Waal and Roosmalen 1979; Palagi, Cordoni, Borgognini, and Tarli, 2006). Such behaviors have been interpreted as evidence for a prosocial motivation to console victims of aggression (de Waal, 2008).

These cases of consolation suggest that primates are— at least in some cases— motivated to act in ways that make other conspecifics feel better. Unfortunately, although such naturalistic cases provide compelling hints that primates are concerned with other individuals' outcomes, it is rather tricky to compare such naturalistic behaviors with the sorts of measures used to test other-regarding preferences in humans. For this reason, primate researchers have recently begun developing experimental tests of primates' other-regarding tendencies that match tasks developed for humans (for a review of such human tasks, see Camerer, 2003). The goal of these new experimental approaches is to both advance our understanding of the cognitive factors that promote and hinder the expression of prosociality across primates and to address the question of whether such preferences in primates are similar to the other-regarding preferences observed in humans.

3. Do Primates Show Other-Regarding Preferences in Experimental Tasks?

3.1 Primate Instrumental Helping Tasks. One experimental task developed to test primates' prosocial preferences involves setting up cases in which primate participants have the opportunity to help another recipient reach a particular goal (e.g., Barnes, Hill, Langer, Martinez, and Santos, 2008; Drayton and Santos, in preparation; Skerry, Sheskin, and Santos, 2011; Warneken and Tomasello, 2006; Warneken, Hare, Melis, Hanus, and Tomasello, 2007; Yamamoto, Humle, and Tanaka, 2012). In one classic study, Warneken and Tomasello (2006) presented chimpanzees with situations in which a human experimenter appeared to have trouble achieving a certain goal, such as trying to get an out-of-reach object. Even though the

chimpanzees were never rewarded for helping, they tended to help the human achieve their goal at relatively high rates. Capuchin monkeys in our own lab also show high rates of helping human experimenters on this task, at least in cases in which they are given a reward for helping (Barnes et al., 2008). Finally, chimpanzees and bonobos are willing to help a conspecific obtain out-of-reach food items by unlocking a door that leads to the desired food (Hare and Kwetuenda, 2010; Warneken et al., 2007). In these helping studies, primates often (though not always, see Skerry et al., 2011) are willing to take small costs to perform actions that help others complete their goals.

3.2 Primate Donation Games. In an attempt to better compare primates' other-regarding preferences with those of adult humans tested on experimental economic tasks, primate cognition researchers have also developed a set of experimental "donation" methods in which primate subjects have the option to donate food to another conspecific. In a typical study (e.g., Silk et al., 2005), the actor primate can pull one of two tools: one gives him and a recipient a desirable piece of food, whereas the other gives the actor the same desirable piece of food but a smaller piece of food (or no food) to the recipient. Note that in this set-up, the actor's own reward does not differ between the two choices, and thus a preference for one choice over the other can be interpreted as reflecting a desire for giving the partner a specific outcome. Primate actors can therefore do one of three things: they can choose to give the recipient the generous option, they can be mean and give the recipient the less valued option, or they can act totally indifferent to the other individual's rewards and just choose randomly.

The logic of this donation task is pretty straightforward, but the pattern of primates' performance on this task has been anything but. When researchers tested chimpanzees on this task, they were surprised to learn that chimpanzees didn't seem to care about other individuals'

payoffs (Jensen, Hare, Call, and Tomasello, 2006; Silk et al., 2005; Vonk et al., 2008);

chimpanzees who have now been tested across a number of labs tend to perform at chance on

this task, failing to show any preference for the recipient's payoff (although see Horner, Carter,

Suchak, and de Waal (2011) for at least one study showing generous performance in

chimpanzees on a similar choice task). Although this pattern of indifferent performance in

chimpanzees is mirrored in some other primate species, such as cotton-top tamarin monkeys

(Cronin, Schroeder, Rothwell, Silk, and Snowdon, 2009; Stevens, 2010), several other primate

species show more generous performance on donation tasks (Burkhart, Fehr, Efferson, and van

Schaik, 2007; de Waal, Leimgruber, Greenberg, 2008; Lakshminarayanan and Santos, 2008;

Takimoto, Kuroshima, and Fujita, 2010). Capuchin monkeys— the species we work with in our

own lab— have consistently performed generously on donation tasks, statistically choosing to

give the best possibly reward to the recipient (de Waal et al., 2008; Lakshminarayanan and

Santos, 2008; Takimoto et al., 2010). However, as our new studies as part of this positive

neuroscience project have revealed, even in capuchins the actual rates of generous donations are

relatively low (e.g., around 60%) and sometimes inconsistent across tasks (see Drayton and

Santos (in preparation) for a case in which capuchins fail to behave generously on a donation

task). Interestingly, there is also evidence that capuchins perform generously only in situations in

which the recipient can see their generous actions. de Waal et al. (2008), for example, found that

actor capuchins selectively chose the mean option when the recipient monkey couldn't easily see

them, suggesting that capuchins care about others' payoffs only in cases where they stand to gain

some reputational benefit (for similar results in human children, see Leimgruber, Shaw, Santos,

and Olson, 2012). Finally, as part of our positive neuroscience project, we've observed that

capuchins' generosity on donation tasks depends a lot on their own recent interactions with

others. Leimgruber et al. (under review) allowed capuchins to first play the role of the recipient on the donation game before acting as the actor in this task (Figure 1). They found that monkeys who received the bad payoff as a recipient were statistically more likely to give the same bad payoff when they played the role of an actor donating to a different monkey; in contrast, when capuchins first received a prosocial payoff, they were reliably more likely to give a generous prosocial reward to a third monkey. These results suggest that monkeys' prosocial behaviors may be more shaped by their recent interactions with other individuals than a general preference to behave prosocially.

[INSERT FIGURE 1 ABOUT HERE]

When all these disparate primate donation tasks findings are considered together, it's somewhat difficult to know what to conclude about primate's prosocial motivations. Even when primates do show generous performance on these tasks, their performance is relatively fragile at best. From this set of findings, it seems that most primate species lack a consistent human-like motive to be generous across all donation situations, which is particularly surprising since being nice involves no cost during this set-up.

3.3 Conclusions from Primate Experimental Economic Tasks. The experimental studies of primates' prosocial motivations to date reveal a somewhat complicated pattern of performance in experimental donation and helping tasks. On the one hand, some primates tested in instrumental helping tasks are motivated to take small costs to help other individuals complete their goals (see also Warneken and Tomasello, 2009). On the other hand, primates show relatively inconsistent prosociality when tested in food donation tasks, with few species showing consistently prosocial patterns across all studies (see Silk and House, 2012). In this way, primates do demonstrate some

prosocial behaviors but fail to exhibit the sort of consistency regularly observed in the human species (e.g., Camerer and Thaler, 1995).

4. Two Potentially Human Unique Social Motivations

Primates' inconsistent performance on the experimental tasks reviewed above makes it somewhat difficult to develop strong conclusions about the extent to which primates' prosocial preferences match the ones observed in the human species. However, more recent work using related experimental tasks has begun to suggest that primates may lack two salient aspects of human prosocial preferences.

4.1 Uniquely human third party punishment. The first domain in which primate preferences seem to differ from those of humans involves third party situations. As both experimental and real world examples attest, human prosocial behaviors often extend beyond cases of direct actions towards a recipient. Humans regularly take costly actions on behalf of unrelated individuals— we like to punish individuals who have behaved unfairly toward anonymous third parties (e.g., Fehr and Fischbacher, 2004) and to reward those who have done nice things to others we don't know (e.g., Almenberg, Dreber, Apicella, and Rand, 2010). Importantly, we are willing to prosocially reward and punish third party individuals even in cases when we ourselves were not directly affected by these individuals' behaviors. In this way, humans seem to regularly engage in costly behaviors purely on behalf of other third parties. In addition, our species seems to exhibit these prosocial tendencies in third party cases from early in life (Hamlin, Wynn, Bloom, and Mahajan, 2011), across all human cultures tested to date (Heinrich et al., 2006), and fairly automatically (Rand, Greene, and Nowak, 2012).

Despite the widespread observation of third party punishment and reward in the human species (Fehr and Fischbacher, 2004), there has been to date no experimental evidence that other

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primates care about what happens to other individuals in third party situations. Riedl, Jensen, Call, and Tomasello (2012) developed an elegant experimental situation in which chimpanzees could punish those who stole food from others. In their set-up, subject chimpanzees had the opportunity to pull a heavy rope to open a trapdoor that dropped food that another conspecific was eating into an inaccessible location. The researchers then varied how that conspecific "thief" had obtained the food. In one case, the conspecific obtained the food by stealing it from the subject himself; in this case, Riedl et al. found that chimpanzees opened the trapdoor at high rates, ostensibly taking a small cost to punish an individual who had stolen food from them (see Jensen, Call, and Tomasello (2007) for a similar result). In contrast, when the thief had stolen the food from a third unrelated chimpanzee, subject chimpanzees tended not to release the trapdoor. Indeed, chimpanzees' rates of releasing the trapdoor in this case of third party case were as low as a case in which there was no thief chimpanzee and no victim involved. As part of our positive neuroscience project, we have observed similar results in our own lab on a capuchin monkey test of third party punishment. Leimgruber, Sanchez, Widness, and Santos (in preparation) allowed subject capuchins to watch how a second conspecific stooge monkey behaved toward an unrelated individual in a donation set-up. In some conditions, this stooge monkey behaved prosocially toward the third monkey, whereas in others he behaved selfishly, giving the smallest possible payoff. After witnessing the stooge monkey's behavior toward the third party, subjects then had a chance to donate food to the stooge. The question of interest was whether subjects would reward generous behavior and punish selfish behavior. Like chimpanzees, capuchins showed no evidence of third party punishment— subjects did not donate differently to the stooge monkey based on his behavior toward a third party. Taken together, this work suggests that primates lack an important aspect of human prosocial preferences— in contrast to what's

observed regularly in humans, primates' prosocial tendencies may not extend to third party cases[1]; primates don't selectively punish or reward another conspecific except in cases in which they themselves were directly affected by that individual's behaviors.

4.2 Uniquely human advantageous inequity aversion. The second domain in which human prosocial preferences seem to obviously differ from those of other primates stems from situations of inequity. Much research has demonstrated that humans have a set of social preferences for avoiding cases in which rewards are distributed unevenly or unfairly across individuals. Overall, humans tend to be averse to inequity and will often take costs to ensure fair outcomes (Camerer and Thaler, 1995; Fehr and Schmidt, 1999). This aversion is perhaps unsurprising in cases of *disadvantageous inequity*, situations in which the individual in question receives less than is fair. However, people also show aversion to cases of *advantageous inequity*, situations in which they themselves benefit from having more than is fair. A number of experimental economic games have shown that people readily take costs to avoid having more than their fair share (Fehr and Schmidt, 1999). In this way, people tend to be almost as concerned that others' payoffs are fair as they are that their own payoffs are fair.

In the past few years, primate researchers have investigated whether other primates also share human-like preferences for avoiding inequity. In a famous study, Brosnan and de Waal (2003) argued that capuchins react negatively to cases of disadvantageous inequity. Brosnan and de Waal found that capuchins would stop performing a task if the reward they received (e.g., a low-valued cucumber) that was less valuable the reward given to a conspecific for performing a similar task (e.g., a high-valued grape). Although some researchers have failed to observe similar levels of inequity aversion in both capuchins (Dubreuil, Gentile, and Visalberghi, 2006; Silberberg, Crescimbene, Addessi, Anderson, and Visalberghi, 2009; Sheskin, Ashayeri, Skerry,

and Santos, under review) and other primates (Bräuer, Call, and Tomasello, 2006; but see

Brosnan, Schiff, and de Waal, 2005), many have argued that primates do share human-like

responses to cases of disadvantageous inequity (e.g., Brosnan, 2006). However, no research to

date has shown that primates react negatively to cases of advantageous inequity, cases in which

the subject gets unfairly more rewards than another individual. Indeed, Brosnan (2006)

anecdotally noted that the stooge monkeys who received the high valued rewards in her original

Brosnan and de Waal (2003) rarely rejected the higher valued reward when the subject monkeys

received less. In fact, they sometimes preferred this advantageously inequitable situation:

> "in several situations in which the subject rejected the cucumber slice, the partner would
> finish their grape and then reach through the mesh to take the subject's cucumber and eat
> it as well! Apparently to monkeys, cucumbers taste better if you have already had a
> grape." (Brosnan, 2006, p. 176)

To more directly test whether monkeys possess an aversion to advantageous inequity, we

developed a test in which capuchin monkeys could choose between experimenters who had

previously behaved either fairly or advantageously unfairly. Sheskin and colleagues (under

review) first introduced capuchins to experimenters who provided either a fair payoff (one that

was equal in value to that of a conspecific partner) or an advantageously unfair payoff (one that

was better than the partner's). After being introduced to the behavior of these fair and unfair

experimenters, subjects had the chance to obtain a high-valued reward from either the

experimenter who had previously behaved fairly or the one who had previously behaved

unfairly. Sheskin et al. found that monkeys performed at chance, failing to express a preference

for the experimenter who behaved fairly over one who behaved advantageously unfairly[2];

monkeys basically ignored how the experimenter treated another conspecific so long as they

themselves received a high-valued reward. In this way, monkeys' behavior seems to differ

robustly from that of humans; humans are actively willing to take costs to avoid situations of

advantageous inequity (e.g., Fehr and Schmidt, 1999), whereas monkeys seem indifferent to advantageous inequity situations even at no cost (Sheskin et al., under review).

Conclusions

Although other primates do behave prosocially in experimental tasks some of the time, overall primate prosociality seems to differ from that of humans in a few respects. First, primate prosocial preferences in experimental tasks seem relatively fragile and subject to far more contextual factors than those of humans. Second, other primates appear to critically lack two of the prosocial preferences observed widely in the human species— primates show no aversion to cases to advantageous inequity and are unwilling to take costs to punish others in third party situations.

Taken together, the primate studies we've conducted and reviewed here suggest both important similarities and differences between human and non-human social preferences, ones that have valuable implications for neuroscientists interested in the neural basis of social preferences. On the one hand, these studies hint that primate reward systems may, like those of humans, be wired to respond to events that help others— at least under some circumstances. Future work using macaque neurophysiological techniques could potentially test these claims directly by employing the sorts of donation tasks reviewed above (for an example, see Chang, Gariepy, and Platt, 2013). On the other hand, the findings reviewed here suggest that reward processing in primate brains is likely to differ from humans in two critical respects. First, in contrast to humans (de Quervain et al., 2004), primates are unlikely to recruit neural areas associated with rewards when paying costs to punish others. Second, we predict that primates' reward regions will fail to respond less when primates receive unfairly high payoffs (e.g.,

Tabibnia et al., 2008; Zaki and Mitchell, 2011). In these two cases, we expect to find divergence in primate and human response patterns, with primate reward regions more tuned to selfish rather than prosocial rewards. Through experiments like these, neuroscientists could explore how differences in brain activity across species could potentially explain variation in the prosocial preferences observed across species.

Endnotes

[1] Note that some primatologists have argued that naturalistic cases of third party policing (situations in which a dominant individual will intervene in a fight involving two unrelated individuals) may reflect cases of third party punishment. However, many researchers have argued that these cases of naturalistic policing do not qualify as true examples of third party punishment (see discussion in Riedl et al., 2012).

[2] Monkeys in the Sheskin et al. (under review) study also failed to show a preference for a fair experimenter over one who behaved disadvantageously unfairly, again suggesting that primates' preference for equity may be fragile even in cases of disadvantageous inequity (see also Silk and House, 2012).

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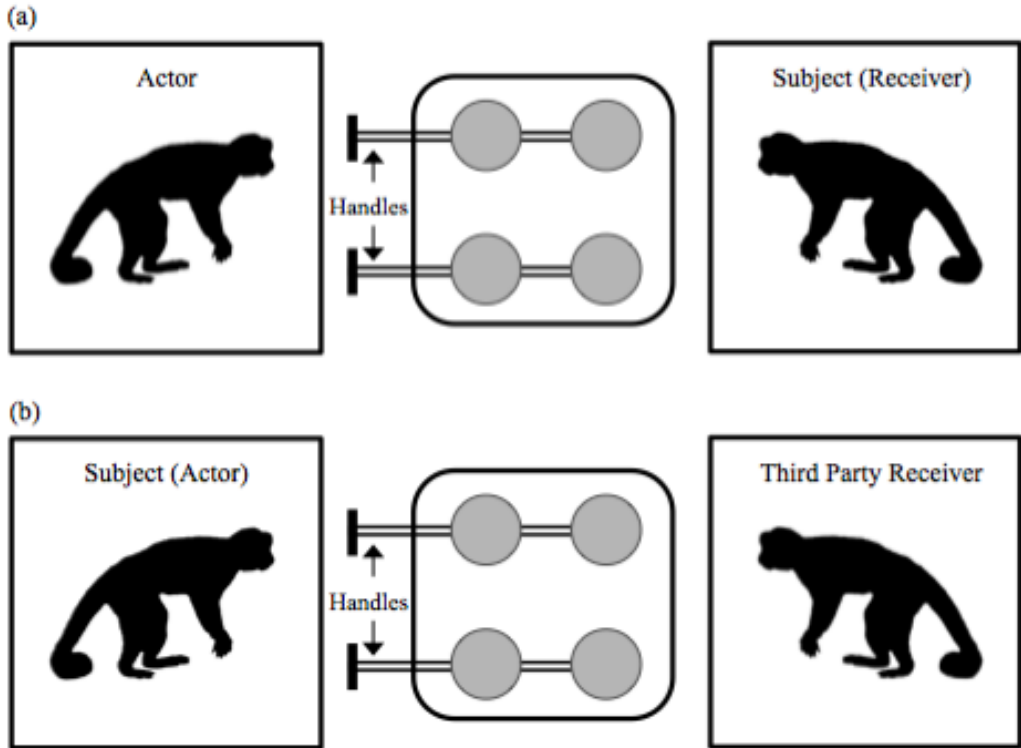
Figure 1. Schematic of testing setup used in Leimgruber et al. (under review): (a) an actor monkey was given the opportunity to pull one of two handles. Pulling either handle delivered the same reward to the actor, but one of these handles delivered a good (prosocial) payoff to the subject and the other handle delivered a bad payoff; (b) the subject was then given the opportunity to choose whether to deliver a good or bad payoff to a third monkey.