

## The Tangled Roots of Prosocial Preferences

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There is a growing body of evidence that humans have pronounced preferences for outcomes that benefit others, equitable distributions of resources, and punishment of transgressors of social norms (Fehr & Fischbacher 2003). Food sharing and division of labor play central roles in almost all human foraging societies. Like other primates, humans show nepotistic preferences, but they also extend altruism to unrelated members of their communities and can orchestrate cooperation in large groups. Researchers in the human sciences are now pondering fundamental questions about the evolutionary forces that gave rise to human social preferences, and have produced a growing body of research on the ontogeny and phylogeny of social preferences within the primate order.

I want to focus on a body of experimental work that was designed to probe the origin of preferences for outcomes that favor others (prosocial preferences). In these experiments, subjects are presented with choices that have different material payoffs for themselves and others; the choices that subjects make allow us to draw inferences about their preferences. Although these kinds of laboratory studies are clearly artificial, they are useful for two reasons. First, they provide systematic information about individuals' preferences for one outcome over another. Second, the procedures are simple enough that we can make meaningful comparisons between different age classes, societies, and even species.

In the Prosocial Game, a subject is presented with two options. One option provides a reward to the subject and another individual; the other option provides a reward only to the

subject. For convenience, I will refer to these as the 1/1 and 1/0 options, respectively (the actor's payoff is given on the left, the recipient's payoff is given on the right). In each trial, the actors can choose the 1/0 option, the 1/1 option, or do nothing. It is possible that actors might prefer the 1/1 option because they have a prepotent bias for larger numbers of rewards (even if not all rewards are available to them), so a non-social control condition is included for comparison to the test trials.

The Prosocial Game has been played with children ranging from 1.5 to 10 years of age. In a study of toddlers, Brownell et al. found that eighteen-month-old infants did not choose 1/1 more often when a familiar adult recipient was present than when there was no recipient present (Brownell et al. 2009). At 25 months of age, children chose 1/1 more often when a recipient was present than when they were alone, but only when the recipient verbally expressed desire for the food reward. Neither 18- nor 25-month-olds demonstrated spontaneous prosocial behavior. However, as children mature, they are more likely to make prosocial choices. Children from 3 to 7 years old prefer outcomes that confer benefits on their partners, and this preference becomes more pronounced as they get older (Thompson et al. 1997; Fehr et al. 2008; Moore 2009; House et al. in prep).

The change in children's prosocial behavior as they mature tells us that *something* happens over the course of time to alter children's behavior in the prosocial game. Children might become more *aware* of the desires of others; children might become more *sensitive* to the desires of others; or children might be socialized to behave more prosocially. The first two explanations would be categorized as developmental explanations, while the last explanation would be a social or cultural explanation.

One way to distinguish between the developmental and cultural explanations is to find out whether the ontogenetic trajectory of preferences is conserved among children in diverse societies. We are collaborating with a group of social scientists to conduct the prosocial game with children in a number of societies. We have not completed these analyses yet, but do see some cross-cultural uniformities in the Prosocial Game.

Another approach is to examine prosocial preferences in other primates, particularly other great apes. Similarities between children and chimpanzees would support developmental explanations over cultural ones. There have now been several studies of chimpanzees' behavior in the prosocial game (Silk et al. 2005; Jensen et al. 2006; Vonk et al. 2008, Yamamoto & Tanaka 2010). The same pattern of findings emerged from all of these studies: chimpanzees were as likely to choose the 1/1 option when another chimpanzee was present as when they were alone. Not even mothers consistently provided rewards to their own offspring (Jensen et al. 2006; Yamamoto & Tanaka 2010).

Thus, children and chimpanzees behave differently in very similar experimental settings. Children take advantage of opportunities to deliver food rewards to others, even when sharing is costly, while chimpanzees do not. If these findings are robust, they suggest that the psychology that underlies prosocial behavior in humans, particularly food sharing, evolved after humans and chimpanzees diverged from their most recent common ancestor. This would be a very important finding, so it is very important that we consider it critically.

The chimp results were surprising to many people because they seemed very hard to reconcile with other things that we know about chimpanzees. Chimpanzees have highly developed social cognition and can master collaborative tasks in the lab. In the wild they

cooperate in a diverse range of situations and share food. According to some researchers, notably Frans de Waal, chimpanzees also display empathy and possess rudimentary moral sentiments. If this is correct, then our results are anomalous.

Perhaps chimps have prosocial preferences about the distribution of food, but didn't understand that they could use the devices in the Prosocial Game to deliver rewards to others. However, marmosets (with much smaller brains and less sophisticated social cognition) seem to be able to figure this out and behave in a prosocial way (Burkhart et al. 2008). In addition, Jensen et al. (2006) explicitly tested the chimpanzees' understanding of the experimental apparatus and confirmed that the chimpanzees knew how to use the device to deliver rewards to the other enclosure.

It is possible that chimpanzees might be motivated to help others but have a poor understanding of what they want. Could actors have been uncertain about recipients' desires in our experiments? We don't think this is very likely, because we analyzed videotapes of experimental trials in which potential recipients used begging gestures before the actors made their choices. Recipients consistently directed their begging gestures toward the baited tray, but actors did not consistently respond to these gestures by delivering food (Vonk et al. 2008; Silk et al., unpublished data). It is possible, however, that the chimpanzees did not interpret begging gestures directed toward the baited tray in the same way as begging gestures directed toward themselves (Jensen, pers. comm.).

Another piece of evidence that bears on this question indirectly comes from a different set of experiments conducted with chimpanzees in Leipzig. Hare and colleagues (2000,2001) created an experimental protocol in which a subordinate chimpanzee was paired with a more

dominant group member. Food rewards were hidden behind barriers in a central enclosure, so that both were visible to the subordinate, but only one was visible to the dominant chimp. The subordinate saw the food being placed in the enclosure, but the dominant did not. After the foods were hidden, the chimps were given access to the central enclosure. The dominants headed directly for the visible food reward, while the subordinate chimpanzees headed directly for the reward that was hidden from the dominant. A series of control experiments suggests that the chimpanzees knew what the dominant had seen, anticipated what he would do, and used this knowledge strategically. Similar findings come from an even more demanding experiment conducted by Kaminski et al. (2008).

If chimpanzees “understand the goal-directed actions and perceptions, and even knowledge (in the sense of what another has seen in the immediate past), of others” (Kaminski et al. 2008: 233), then it seems likely that they would also have some understanding of others’ desires. If chimpanzees have some understanding of other’s desires and they are concerned about the welfare of others, the results of the prosocial experiments are doubly surprising.

An alternative is that chimps are concerned about the welfare of others, but their preferences are muted or reversed when food is at stake. Chimps might think of food as a zero-sum resource, so giving food to others automatically reduces the amount available for themselves. But if the chimps in our experiments considered food a zero-sum resource, they would systematically choose the 1/0 option over the 1/1 option, and they did not do that.

Chimps might not actively deny others foods, but still not be inclined to provide them to others. At first, this seems to be inconsistent with the fact that chimps are one of the few primates that regularly share food: mothers allow their offspring to cadge food from them, and hunters often allow others to consume some portion of their kills. However, the processes and motives that underlie food sharing are not entirely clear. Some have argued that males use meat as a bargaining chip in political negotiations with potential allies and rivals (Boesch & Boesch 2000). Others contend that meat is a commodity that is exchanged among reciprocating partners (Mitani 2006, Gomes & Boesch 2009).

However, it has also been suggested that food transfers are a form of tolerated theft-- that food is transferred under pressure from conspecifics (Gilby 2006; Stevens 2004). Stevens (2004) found that food transfers in chimpanzees declined when individuals that possessed food were separated from potential recipients by a partition. Mothers may allow their offspring to take scraps to prevent them from launching noisy tantrums, and males may give up pieces of carcasses to prevent rivals from trying to take more by force. If sharing is coercive, then begging gestures might be implicit demands (which could escalate), not simply signals of desire.

This perspective is consistent with the behavior of some individuals in social preference experiments. Jensen et al. (2006) conducted an experiment in which actors could *prevent* recipients from obtaining food by manipulating the apparatus; if they did nothing, the recipient would receive food. Overall, actors were equally likely to do nothing in the test and control conditions, suggesting that they were indifferent about the consequences for recipients. Two of the 6 chimpanzees that they tested chose to do nothing more often in the test conditions than in the control condition when they were paired with particular partners, a seemingly

altruistic response. However, because the actors then “begged from or harassed these recipients immediately afterwards, the motivations were probably misguidedly selfish” (Jensen et al. 2006: 1019).

In our experiments, we could only analyze begging at one of the two sites because of the quality of the video recordings. At this site, the chimpanzees were separated by a distance of about 2.5 m. Although the chimps could see and hear their partners’ begging gestures, they could not touch them or interact directly and recipients could not profit from escalating from begging to aggression. This may have protected actors, and reduced their inclination to respond to recipients’ gestures.

At this point, I think we need to have an open mind about what these experiments tell us about prosocial preferences in chimpanzees. Chimps’ behavior in these experiments is different from the behavior of human children, and different from their responses in other experimental settings (Warneken et al. 2007). But it is not clear how to tie all of this up together into a single neat package.