A cross-species perspective on the 'selfishness axiom'

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Henrich et. al. describes an innovative research program investigating crosscultural differences in the selfishness axiom (in economic games) in humans, yet humans are not the only species to show such variation. Chimpanzees and capuchin monkeys deviate from the standard self-interest paradigm in refusing absolute gains that are relatively less than those of a conspecific. However, it is less clear whether these species also show the other-regarding preferences seen in humans.

It is assumed, both explicitly and implicitly, that animals (including humans) attempt to maximize their own self interest. After all, this is fundamental to natural selection and many behaviors are demonstrably motivated by self-interest. In some areas of economics, this has been translated into an assumption that a truly self-regarding person would accept any offer that was positive, as, for instance, in the Ultimatum Game discussed above. However, as Henrich et al. note, people from a variety of cultures appear more interested in relative than absolute benefits, indicating that interest in fairness is a universal human characteristic. Recent research has shown that two species of nonhuman primates, capuchin monkeys (Cebus apella) and chimpanzees (Pan *troglodytes*), may behave similarly. These primates will refuse previously acceptable rewards if their rewards differ from those of a companion (Brosnan & de Waal, 2003; Brosnan, Schiff, & de Waal, 2005), indicating that they are more interested in their *relative* benefit in comparison with a conspecific partner than in absolute benefits. This is similar to the logic explaining people's reactions to the Ultimatum Game and provides a beginning for the exploration of a 'sense of fairness' in nonhuman species (Brosnan, in press).

Moreover, as with people from different cultures, chimpanzees show great variation in the level of response dependent upon the social group from which they originated. (Bear in mind that this variation may or may not be based on the same sorts of cultural or socioecological factors as it is in humans.) These differences are not based on the sex or the rank of the individual (nor relatedness, as all were adults paired with nonkin), but chimpanzees from a social group in which virtually all of the individuals grew up together showed virtually no reaction to inequity, while those in a more newly formed social group responded relatively strongly. Psychology research has shown that people respond very differently to inequity when in close or positive relationships than when in distant or negative ones (Clark & Grote, 2003; Loewenstein, Thompson, & Bazerman, 1989), and perhaps nonhumans react similarly. Chimpanzees that grew up together may have intimate, kin-like relationships and hence respond to relative inequity quite differently than chimpanzees introduced to each other as adults.

While nonhumans apparently react to inequity, and this reaction may be impacted by the social environment of the individual, these results do not perfectly mirror those of humans. This is in part because of experimental constraints (the primates did not have anonymous interactions, nor were they allowed to choose the reward distribution themselves) and in part because it is unclear how to compare these chimpanzee groups to human sociopolitical groups. Regarding the former, in a follow-up experiment with capuchin monkeys, individuals were paired with a group mate to solve a mutualistic cooperation task for two rewards. Rewards were sometimes the same and sometimes different (one better than the other). Pairs that were more equitable in the division of rewards in the unequal condition were far more successful in all situations than those in which one individual dominated the better rewards (Brosnan, Freeman, & de Waal, submitted). While this is not a perfect match for the Ultimatum Game, it indicates that monkeys do pay attention to their partner's actions in determining reward division. They may 'reject' a partner who is not generous, perhaps by simply failing to cooperate and 'reward' a generous partner with continued cooperation (see also de Waal & Davis, 2003). Regarding the latter constraint (comparing human and chimpanzee groups), male chimpanzees in particular may need to cooperate frequently for territory defense and hunting, indicating that, as with some human societies, these individuals should have an interest in fairness and, perhaps, display other-regarding preferences.

We know that some nonhuman primates react to being relatively underbenefitted compared to a conspecific, which is irrational according to a strict self-interest paradigm. However, due to the fact that the primates were unable to determine the distribution of resources (excepting in the follow-up study mentioned above), this research cannot compare partner response directly to any of the games discussed in Henrich et al's paper, nor can we effectively comment on the potential for other-regarding preferences in chimpanzees or capuchin monkeys. However, one bit of evidence indicates that these primates may be less other-regarding than humans are. In the experimental setup, the primates were able to share food with each other. However, there was virtually no sharing between the privileged individual and their less well-endowed partner (no instances in capuchin monkeys and less that 1% of interaction in the chimpanzees). Both of these species are known to be good food sharers and, indeed, we saw some sharing in the other direction (the privileged individual consuming the less valuable food). Previous research has indicated far greater levels of food sharing. It is interesting, therefore, that the relatively benefited individuals did not exert more effort to equalize rewards.

Studying such behaviors in nonhuman species may be an excellent way to further our knowledge of the selfish axiom and other-regarding behavior. Not only do nonhuman primates provide a possible glimpse of the evolutionary trajectory of these behaviors, but investigation of their behavior may give us a greater insight into our own behavior. Other socially complex food-sharing species, such as the social carnivores, may display similar tendencies and provide further insight (e.g. Bekoff, 2004).

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