

Underlying mechanisms and evolutionary roots of prosocial behaviors in non-human animals

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Abstract

Prosocial behaviors are defined as any acts that benefit others, and are classified into three subtypes: sharing, helping, and comforting. These behaviors are particularly present in humans and are often considered as the hallmark of our societies. However, the underlying mechanisms and evolutionary roots of prosocial behaviors are still not fully understood.

Comparative cognitive scientists address these questions by assessing whether and under what circumstances other animal species express prosocial behaviors. Over the years, a wide range of species, representing different cognitive capacities and social organizations, have been tested, enabling identification of prosocial behaviors in a wide variety of taxa. However, the diversity of the experimental paradigms used has given rise to considerable disparity in the results, challenging the validity of some paradigms for revealing properly a species' prosociality.

Current major theories place inequity aversion and an emotionally based bookkeeping system as two potential proximate mechanisms sustaining prosocial behaviors, principally with respect to evaluation and choice of a recipient. Importantly, inequity aversion is suggested to have coevolved along with a species' cooperative capacities. Further, recent findings suggesting the presence of a basic form of second-order emotions in prosocial and cooperative non-human species appear in line with the hypothesis of a mediational role of emotions in prosociality, suggested by the emotionally based bookkeeping system.

However, most studies have focused on our closest living relatives, the non-human primates, in which the most-studied species are known to be cooperative. Furthermore, contradictory results characterize the literature on both primates and non-primate species. Thus, before drawing any firm conclusions about the underlying mechanisms and evolutionary roots of prosociality, additional studies are needed that include the use of new experimental paradigms and extend the field of enquiry to less

cooperative species as well as non-primate ones. The current thesis aims at addressing these limitations by conducting a series of experiments on three different and relevant species, using original procedures.

Chapter 2 asks whether the use of alternative paradigms could reveal in New World capuchin monkeys the presence of altruism, the ultimate form of prosocial behavior previously reported to be absent in this cooperative species. The study described in Chapter 2 uses an adaptation of two paradigms that previously revealed altruism in great apes, a taxonomic group (including ancestral humans) that diverged from ancestral monkeys about 40 million years ago. Pairs of capuchins were tested first in a costly and operant food sharing paradigm (Experiment 1-1), where the operator could unlock a door to invite a recipient into his room and share his food. The second experiment (Experiment 1-2) was a less costly targeted-helping paradigm, where the operator's food was secured but he could unlock a container to deliver food to a recipient. While our small sample size precludes definitive conclusions, the results suggest that capuchins were unwilling to share their food, but were sometimes capable of helping selected recipients. Similar to chimpanzees, we observed in capuchins that requesting behaviors may be a key element for deciding which recipient to benefit. These findings highlight the importance of the experimental paradigm in the study of prosociality; however, because we cannot be entirely sure that operators sufficiently understood the experimental situations, the ecological validity of our paradigms remains to be confirmed.

In line with Chapter 2, Chapter 3 asks whether another original paradigm could enhance our understanding of prosociality (and its mechanisms) in a relatively understudied and non-cooperative New World primate species, squirrel monkeys. The fact that squirrel monkeys do not routinely cooperate in the wild has been proposed to explain why no compelling evidence of prosocial tendencies has been reported so far, and why they failed to show inequity aversion in a token exchange paradigm. The study described in Chapter 3 (Experiment 2) tested squirrel monkeys in an original version of the tray-pulling paradigm, where an operator monkey was able to pull a tray baited with food to within reach of itself and a conspecific recipient. Testing monkeys with different types of social relationships, frequencies of pulls by operators were examined in three different food distributions: equal, qualitative inequity (higher value reward for the recipient) and quantitative inequity (no reward for the operator). Results indicate that whereas male operators did not adjust their pull frequencies according to recipient presence or

identity, female operators pulled the tray less often in the quantitative inequity distribution when paired with an out-group female recipient than when tested alone. Despite squirrel monkeys' lack of cooperation, these findings suggest a potential form of inequity aversion restricted to females; as yet no clear evidence of prosociality has been observed in this species. However, caution is required concerning our interpretation, as another hypothesis could explain our data with females' reactions resulting from social arousal caused by the presence of out-group female recipients rather than from inequity aversion *per se*.

To broaden the range of species studied in the context of prosocial behaviors, Chapter 4 focuses on another relatively non-cooperative but non-primate species, pet cats. Motivational and behavioral issues make it difficult to investigate prosociality in cats using conventional operant paradigms. We tackled this limitation by investigating instead the presence of a secondary emotion, given the presumably important role of emotions in prosocial behaviors, and recent findings suggesting a primary form of jealousy in pet dogs. Thus, the study described in Chapter 4 (Experiment 3) adapted for cats an experimental paradigm used with dogs, to assess whether cats showed any form of jealousy with regard to their owner. Cats witnessed their owner and an unfamiliar experimenter petting a "social" object (i.e. potential rival: a realistic-looking soft-toy cat) and a non-social object (furry cushion). Results indicate that although cats reacted more intensely toward the soft-toy cat previously petted by their owner, unlike dogs, they did not express any further behaviors strongly indicative of jealousy. We acknowledge that more ecologically valid procedures could lead to a better understanding on this issue. Whilst these results did not reveal any compelling evidence of jealousy in cats; they do promote new consideration of the existence of some prerequisite cognitive bases for jealousy to emerge in cats. Thus, the study described in Chapter 4 could open new avenues for the study of prosociality in multiple species, especially when the use of operant tasks appears challenging.

All our studies revealed potentially important issues regarding ecological validity of our newly developed experimental paradigms. In addition, the study described in Chapter 3, along with other recent findings, raised questions about the validity of the extensively used exchange paradigm for revealing inequity aversion in non-human animals, on which most of the major theories are based. It therefore seems crucial for future studies to assure that study animals have a good understanding of the task, or to

develop more intuitive tasks to allow proper identification of prosocial behaviors as well as fairer comparisons between species. Moreover, studies in Chapters 3 and 4 suggest the potential presence of some hypothesized mechanisms underlying prosociality (inequity aversion, mediational role of emotions) in two non-cooperative species (respectively, squirrel monkeys and domestic cats). These findings might challenge the idea of a straightforward link between these mechanisms underlying prosociality and cooperation, although no evidence of prosociality has yet been reported in squirrel monkeys or cats. However, it is also possible that these species' cooperation capabilities have been underestimated, especially given the rarity of these species in the comparative social cognition literature. Therefore, it might be worthwhile to pursue investigation of these two species' prosocial capabilities, as well as other potential mechanisms involved in prosocial behaviors.

Altogether, the studies that comprise this thesis provide new empirical evidence on the presence of prosocial behaviors as well as some of the hypothesized underlying mechanisms in three relevant non-human species. Thus, this thesis contributes to the literature on non-human prosocial behaviors. Additional work will be needed to achieve a more holistic understanding of the underlying mechanisms and evolutionary roots of these behaviors.