Cooperation from an Evolutionary Perspective

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Abstract My interest in cooperation was present before I started investigating it in humans. The research on a cooperative breeder species, the common marmoset, made it clear to me that cooperation was not a straightforward phenomenon. Cooperators also competed with each other, and strived to gain advantage even in a group that depends on cooperation for its own survival. How should that happen in humans? Evolutionary theory offered, from my point of view, the best perspective to understand these apparently opposing behaviors. For many years, I looked at cooperation in children, using game theory as an instrument to gain some insights. An invitation to participate in a symposium on religious behavior inspired me to look at a behavior that often comes together with both cooperation and competition—group coalition. So, I used religion, or its absence, as the factor promoting cooperation. After almost 30 years studying cooperation, more than ten of them in humans, I believe I have unveiled some of the motives that lead both humans as well as marmosets to collaborate and to compete. I have also contributed to bring a biological perspective into Brazilian Psychology, which I consider as my greatest achievement.

My interest in cooperation was present before I started investigating it in humans. During my graduate studies starting in 1980 at Universidade Federal de São Paulo (UNIFESP), my supervisor, Dr. Orlando Bueno, suggested that I should investigate the behavior of a primate native to the Northeast of Brazil where I lived and worked, which was scarcely studied back then. This suggestion from my supervisor and his willingness to supervise a project that was unrelated to what he worked with at the time was a generous offer that represented a breakthrough in my career. The common marmoset (*Callithrix jacchus*) was interesting to me for many reasons, including the fact that its behavior was very different from that of other well- studied African and Asian primates, and also because they had a social system marked by cooperation and by female dominance.

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For more than 20 years, I investigated the behavior of marmosets and became increasingly fascinated by these unique primates. My Ph.D. dissertation, in 1990, was on the cooperative care of infants. By then, marmosets had taught me that cooperation is not a straightforward phenomenon. Cooperators also compete with one another and strive to gain an advantage, even in groups that depend on cooperation for their own survival. Both male and female marmosets compete for breeding positions, and breeding females fiercely prevent subordinates from breeding, and even kill their infants when subordinates escape breeding suppression. Nevertheless, infants are carried and fed by non-breeding individuals (Yamamoto et al. 2010). The balance between cooperation and competition is fascinating and, in my opinion, evolutionary theory offers the best perspective to understand these apparently contradictory behaviors.

The balance between cooperation and competition is also true for humans, considered to be one of the most cooperative and prosocial species. Just like marmosets, human beings need the help of others to survive when they are born and for the rest of their lives. Babies need care, feeding and affection, and the interactions that happen at the beginning of life will build the foundations for future social bonds. To me, as a psychologist, human behavior was a source of wonder and curiosity, and the new area of Evolutionary Psychology soon captured my attention.

With an evolutionary approach in mind, Evolutionary Psychology proposes a solution to tackle the question that has long been debated: the dichotomy between nature and nurture, biology and culture. The answer to this apparent contradiction between human diversity and universality arises with models that use complementary levels of explanation and consider cultural complexity to be a reflection of biological complexity. In the words of Bussab and Ribeiro (1998), man is *biologically cultural*. However, back in the early 2000s, while Evolutionary Psychology was a well-known and acknowledged branch of Psychology in North America and Europe, it was virtually unknown in Brazil. A few researchers that investigated topics such as animal behavior, ethology, and ecology showed interest and started exploring this new discipline. Among them were the scientists that formed the Working Group in Evolutionary Psychology at the *Associação Nacional de Pesquisa e Pós-Graduação em Psicologia*—ANPEPP (National Association of Research and Graduate Studies in Psychology) in 2004. Under the joint coordination of Professor Emma Otta, from Universidade de São Paulo (USP), and myself, we assembled a group of 12 researchers formed by psychologists, biologists, a sociologist, an anthropologist, and a physician, in order to discuss Evolutionary Psychology and put forward some collaborative research. Two consequences that marked my career as an evolutionary psychologist soon followed.

The first consequence was my first Ph.D. supervision of an Evolutionary Psychology project, dealing with cooperation in children, from 2004 to 2008. The student was Anuska Alencar, who developed a protocol to test cooperation in children that we have been using to this day. Cooperation was a source of interest for us because it has been a controversial topic among evolutionary minded scientists, including Darwin himself. At first sight, cooperation, altruism, and prosocial behavior look like anomalies in the animal kingdom, humans included. This happens because of the idea that evolution is all about competition, and therefore every indi-

vidual should struggle to override others and not cooperate with them. Popular science books, such as *The Selfish Gene* (Dawkins 1976), have contributed to spreading this idea, particularly among those that did not read them[1].

In fact, cooperation makes a lot of sense from an evolutionary perspective, particularly among social animals.[2] Cooperation increases the chances of survival and reproduction of individuals in a group. These chances may increase even more through taking advantage of the cooperative efforts from others. So, the question: Why do individuals cooperate instead of preying upon others? Probably because some conditions favor the occurrence of cooperation, such as kinship (nepotism) and reciprocity. I have been investigating the latter, looking at cooperation among unrelated individuals, triggered by reciprocity and reputation.[3] I mentioned before that humans are considered one of the most cooperative species. However, it has been suggested that humans are cooperative because they are taught to be so and because such behavior is compelled by social norms. So, are we naturally cooperative or are we cooperative because culture teaches us to cooperate? Although many authors since the early studies by Piaget (1999) suggest that young children are selfish, many evolutionary oriented studies suggest that cooperative behavior may be observed as early as at 14 months (Warneken and Tomasello 2007). House et al. (2013), in a study of six different societies, including traditional ones that presented a wide variation in culture and subsistence strategies, including groups of foragers, herders, horticulturalists, and urban dwellers, suggested that prosocial behavior is influenced by both biology and culture. Very young children showed similar prosocial behavior throughout all six societies, but in their early teens they displayed levels of prosociality that reflected the behavior of adults in their respective societies.

From this and other studies age was shown to have an important effect on the children's decisions to share or not to share. Hamlin and Wynn (2011) showed that 6- to 8-month-old infants were able to distinguish prosocial and antisocial behaviors,

[1] It is important to emphasize that altruism, from an evolutionary point of view, has quite a different meaning to altruism from a moral point of view. This latter meaning refers to those behaviors that confers benefits to someone else. From an evolutionary perspective, a behavior is altruistic only when it benefits another individual at a cost for the actor's fitness, in other words, for his/her survival and/or reproduction. Thus, an altruistic moral behavior may or may not be altruistic from an evolutionary perspective. House (2016) defines cooperation as the behavior that is costly to an actor, while benefiting other individuals. That definition may be entangled at times with that of pro-social behavior, which the same authors define as a behavior that brings benefits to others, as the cost to the actor may not always be clear.

[2] We usually think about humans and other vertebrates when discussing cooperation. Curiously enough, Griffin et al. in a paper from 2004, report cooperation among bacteria, which is enhanced when they belong to the same lineage, i.e., are related. Moreover, one of the better studied societies are those of eusocial insects, like ants and bees. Cooperation in these insects includes forsaking reproduction in favor of a queen and even dying for its community, which represented Darwin's special difficulty. The occurrence of cooperation in bacteria and insects suggests that this trait may be much older, evolutionarily, than we could suppose.

[3] Direct reciprocity describes the willingness to cooperate in response to another's cooperation. Indirect reciprocity, on the other hand, occurs when individuals help those that help others, in other words, those that have a good reputation.

and to show preference for helpful individuals. 18-month-old children spontaneously cooperate with adults (Warneken and Tomasello 2006) and a little later, at 24 months, coordinate their behavior with a peer to get a reward (Brownell et al. 2006). Vaish et al. (2011) report that 3year old are able to identify norms and norms violations and show empathy. Children as young as 5-years old are aware of their reputation and act more generously when observed (Leimgruber et al. 2012), and are more concerned to keep their reputation to their own group compared to another group (Engelman et al. 2013).

With a dual hypothesis in mind, the influence of biology and of environment/culture, we chose to work with economic games to standardize the experimental condition. The games we chose were the public goods game (PGG) and the tragedy of the commons (TC). For many reasons, the first one proved to be the most fruitful. It basically involved giving the children three small wafers[4] over a number of sessions and asking them to either donate all, none, or part of it to a common fund. The total donations, increased threefold by the experimenter, were equally shared among all participants. In the original study and further ones (Alencar et al. 2008; Dutra et al. 2018; Silva et al. 2016) using the same protocol, we investigated the effects of adult influence on the cooperation in an iterated PGG. The types of influence involved were: positive and negative verbal feedback and vigilance by an adult observer, in addition to a control condition. Feedback was open to the group, but the identity of the donor was kept anonymous. General anonymity was, therefore, granted in the two feedback conditions, and in the vigilance condition, the donor was only anonymous to their peers.

Accordingly, all children in our studies, aged 5–12, were less generous in the control condition, which was the least informative to their peers. But our results also suggested that this effect becomes stronger with age, probably as a reflex of an increase in moral awareness and also in the development of theory of mind. An interesting trend, also reported in other studies, was a shift in the children's behavior between 8 and 9 years of age, when they become more aware of their reputation, and show an increase in generous behavior in the vigilance condition in comparison to younger children. A recent paper summarizes our results and reflects the studies of Ph.D., M.Sc., and undergraduate students (Dutra et al. 2018).

Despite the long-term effects of vigilance and negative feedback, the children decreased their donations over time in all conditions. However, in a recent paper we proposed that the kind of incentive used may prevent such a decrease in cooperative behavior (Silva et al. 2016). Using stickers instead of wafers, children created an informal barter market, using stickers as the trading currency. This kept their interest in donating to the public fund, in order to create variety and increase trade. It also suggested to us that there are ways to promote prosociality in children, and to teach them that cooperation may be advantageous for everyone.

From an educational point of view, we also wanted to promote cooperation in children without the use of tokens, but also because it makes us feel good and/or because it is the right thing to do. A study conducted by another M.Sc. student,

[4] Brazilian ethical committees do not allow the use of money as a reward in scientific studies.

Mayara Medeiros, sought to emulate this kind of behavior using cartoons as a priming (Medeiros 2015). Children with and without symptoms of conduct disorder watched prosocial or antisocial cartoons or no cartoons at all. After that, they were offered the option to share some trinkets they had just won with their best friend. Children that did not present symptoms of conduct disorder behaved as expected, increasing sharing after the prosocial video and decreasing it after the antisocial one in comparison with the control condition. Children that presented symptoms, however, shared more of their trinkets after the antisocial priming, showing what is called a reverse priming. These results are potentially useful for promoting prosociality in children who present this kind of behavior.

Cooperation proved to be a fruitful theme of investigation, and other projects are currently in development, involving both children and adults. Of particular relevance are the projects on group coalition that I will discuss later.

The second consequence of the ANPEPP working group was the proposal and approval of a collaborative grant by CNPq (National Council in Scientific and Technological Development) and MCT (Ministry of Science and Technology) in 2005, the Millennium Institute of Evolutionary Psychology, the only one in Psychology among the 34 approved in the whole country. These grants were directed to outstanding research groups in Brazil and the approval of our project was a recognition of both Psychology and Evolutionary Psychology. Under my coordination and Maria Lúcia Seidl de Moura's vice-coordination (Universidade do Estado do Rio de Janeiro, UERJ), it involved a network of 17 scientists from nine different Brazilian universities, besides a team of postdoctoral researchers and graduate and undergraduate students. Five years later, at the end of the project, we were a vibrant research network, having become the group of reference for Evolutionary Psychology in Brazil and also recognized internationally as such. We closed the project in 2009, celebrating the 150 years of Darwin's *The Origin of the Species*, with the *I Symposium on Evolutionary Psychology: Plasticity and Adaptation*, organized in Natal, the home of the project. Five years later, as another sign of our international standing, we organized, again in Natal, the *26th Conference of the Human Behavior and Evolution Society* with a wide international attendance. We also organized the *I Brazilian Meeting of the Human Behavior and Evolution Society* in 2015, in Gramado, and hosted in Natal, in 2018, the *II Brazilian Meeting of the Human Behavior and Evolution Society*, organized by Fívia Lopes (Universidade Federal do Rio Grande do Norte, UFRN).

Ever since the Millennium Project, most of my efforts have been directed at the investigation of human subjects, although I have never lost my interest in marmosets, and have been collaborating with my colleagues, Maria de Fátima Arruda and Arrilton Araújo, from UFRN, trying to better understand their social and reproductive behavior. However, from the start of the Millennium Project, all my students have investigated cooperation and related themes in humans. An invitation in 2008 by Jay Feierman (University of New Mexico) to participate in a symposium on religious behavior at the *XIX Biennial Conference of the International Society for Human Ethology* inspired me to look at a behavior that often includes both cooperation and competition—group coalition. This was already a topic of interest of mine,

as I had been collaborating with Dr. Leda Cosmides from University of California, Santa Barbara, and the Millennium group in research on race and group coalition. But in this case, I used religion, or its absence, as the factor promoting cooperation. Religious individuals identify themselves as a group and we were curious to know if non-religious individuals, atheists, and agnostics would also perceive themselves as a group.

In collaboration with Dr. Fivia Lopes from UFRN, and two graduate students, Monique Leitão and Rochele Castelo-Branco, we developed an online game that allowed us to measure in-group bias among religious and non-religious groups. Our results showed what we were expecting: both believers and non-believers perceived themselves as a group, but among the believers, this applied to only Evangelists and devout Catholics (Yamamoto et al. 2009). Moreover, cooperation was stronger between atheist, Evangelist, and devout Catholic in-groupers.

However, in-group bias is socially relevant not only because it favors cooperation but also because it can be related to negative behaviors, such as out-group derogation. Evers (2015) combines both sides of this in-group bias by proposing that humans are "empathetic xenophobes." This motivation is so strong that Tajfel et al. (1971) demonstrated that people would show those tendencies even when included in arbitrary groups, without any previous social meaning, called minimal groups. In collaboration with Wallisen Hattori, a former post-doc and now at Universidade Federal de Uberlândia (UFU), and two graduate students, Tiago Bortolini and Eduardo Oliveira, we compared in-group effects in meaningful and non-meaningful social groups (Bortolini 2012; Oliveira 2015). We used a PGG protocol very similar to the one used with children but compared two conditions: one where donations resulted in direct benefits, and another where they had no direct benefits, as the content of the common goods were to be delivered to unknown, absent group members. Our minimal groups were represented by letters and the meaningful ones, again, by religion. This comparison allowed us to investigate the possible effects of the affective component of group identification, present in meaningful groups, in contrast to the cognitive component, present in minimal groups.

Our results confirmed those from the previous study, providing further evidence of prosocial behavior by devout religious and atheist participants. Moreover, both minimal and meaningful groups displayed preferential cooperative behavior towards their in-group members. However, group markers proved to be more powerful in the non-benefit condition for the highly identified groups (i.e., the socially meaningful ones), when compared to minimal groups. This is an example of a benefit provided by group association, contingent altruism. On the other hand, it also brings costs, in the form of donations to absent and unknown group members, through depersonalized trust (Brewer 1999), which carry no guarantee of reciprocity.

I have invested more than 30 years of my professional life studying cooperation, more than a decade of which has been dedicated to studying it in humans. I believe that, during the course of my studies, I have unveiled some of the motives that lead both humans and marmosets to collaborate and to compete. In marmosets, cooperation is necessary given the reproductive system that includes twin births, heavy newborns (as much as 23% of the mother's weight), a postpartum estrus with the

possibility of a new pregnancy a few weeks after giving birth, and later, providing food for infants. The heavy burden calls for the assistance of helpers to ensure infant survival. The evolutionary solution was a communal breeding system, in which most group members collaborate in infant care. However, breeding spots are limited, particularly for females, as even with broad cooperation, the raising of infants brings costs to caregivers and restrictions to the number of infants a group is able to support. Therefore, females engage in fierce competition for breeding spots and males provide support for the communal rearing of infants. A highly successful breeding system depends upon the balance between these two aspects, competition and cooperation (Yamamoto et al. 2010).

The bewilderment expressed by Darwin (1859/1996) when referring to cooperation is also present in the mind of an evolutionist studying this theme in humans. Not for the same reason presented by Darwin, however, who believed that the expression of cooperation, particularly by eusocial insects, could present a fatal blow to his theory. What may disconcert an evolutionist is the extension of prosocial behavior, and especially in humans, its apparent disconnection to fitness.[5] Humans direct prosocial behavior towards people they know they will never meet again in their whole lifetime, and sometimes show extreme behavior, that may endanger their lives when protecting a complete stranger.

An important part of the desire to help and to cooperate is present at the very beginning of life, as we have seen before. However, this disposition is shaped by culture as we develop. This makes a lot of sense for a highly social species that depends on conspecifics to survive. A loner would probably not be able to survive and reproduce during our evolutionary past. However, cooperating would not be enough, as there are social norms regarding proper behavior that may differ widely among cultures. The combination of biology and culture results in elaborate forms of cooperation and prosociality that are unique in their form, but that also expresses the biological predisposition to help and act prosocially towards our conspecifics.

In our studies, we have addressed the effect of biology, through age and sex, and the environment, as we varied public vs private conditions, the influence of praise and disapproval, and group allegiance. Age is highly significant but sex does not seem to interfere with the willingness to cooperate, at least in our studies. This result goes against scientific evidence that suggests that women are more empathic, and therefore should display more prosocial behavior. The literature is highly controversial, and we are working on new protocols that we expect will contribute to further understand this particular variable. The effect of an audience is highly effective in promoting cooperation and prosocial behavior, particularly in adults and children over 8 years of age, suggesting that reputation is an important factor in promoting cooperation. However, in children, we have only tested the effect of an adult witness, and it would be interesting to test the influence of peers. Praise and disapproval, when directed at a group and not at an individual, showed mixed effects depending on age, with disapproval being more effective than praise for older

[5] Fitness, in evolutionary theory, is defined as the ability of an individual to survive, reproduce, and propagate its genes to the next generations.

children (8 and more), while the inverse was true for younger ones. One important contribution regarding the studies with children is that we provided evidence from a population that is scarcely studied in Psychology, which are lower SES children from a South American country that, together with Central America, represents approximately 0.7% of published results in top developmental Psychology journals.[6] Of relevance is the fact that we found the same shift in cooperative behavior at around 8-9 years of age that are reported for middle class, English-speaking, and European children, suggesting a widespread similarity in behavior and a strong developmental trend.

Our publications, both on marmosets and humans have been received with interest and are frequently cited. Our studies are mostly in agreement with findings from other scientists from different countries; however, we have added new information to the international literature in the kind of populations that we study: in marmosets, free-ranging natural groups, and in children, low-income urban individuals, outside of mainstream countries.

Wild marmosets have to deal with foraging, protection from predators, exposure to the climate, and competition for resources with conspecifics in a much more complex social and physical environment than that of captivity. Accordingly, differences in behavior should be expected between wild and captive individuals. Behavioral patterns that are analogous in the field and in captivity indicate hardwired behaviors that are resistant even to huge changes in the environment. A comparison of wild and captive samples, therefore, helps us to understand the limits and the flexibility of marmosets' behavior.

In humans, cultural differences may result in diverse behavioral patterns while similar cultures should result in similar behavior. Yet, as discussed before, most investigations have been carried out in the so-called Western countries, which are assumed to share very similar cultural patterns. However, the great majority of the so-called Western countries are represented by English-speaking and European countries, and the majority of samples come from the middle classes. Therefore, studies like ours, that use low SES samples from less represented countries, may expand the scope of evidence when results are corroborated and add new questions when they are not.

For all these reasons, our publications have attracted international attention and collaboration, and contributed to the understanding of the issues we have addressed. These publications have favored the discussion, sometimes heated, of aspects of humans and marmosets' behavior, as well as their potential implications and interpretations. This, I believe, is how science advances.

One of the objectives of the Millennium Project, as described before, was to disseminate Evolutionary Psychology in Brazil. We accomplished this by publishing papers in Portuguese in Brazilian journals, by organizing symposia and roundtable discussions in Brazilian events, and also by editing a manual on Evolutionary

[6] Nielsen et al. (2017) report that only 0.7% of published papers in top developmental Psychology journals described results from South and Central America populations, while English language-speaking countries and Europe represent 90%.

Psychology in Portuguese (Otta and Yamamoto 2009) to be used by graduate and undergraduate students. That was a very successful enterprise, as the book was widely used all over the country. Presently we have a new expanded and revised edition (Yamamoto and Valentova 2018). I consider that the effort was well applied, mainly by its contribution to the dissemination of a biological perspective of Psychology in Brazil, more even than Evolutionary Psychology per se.

The biological perspective has been looked upon with suspicion by a part of the psychological community in Brazil, as it has been considered deterministic. Of course, all of us admit that behavior is determined. There is disagreement as to how much of it is determined and its origin. The critics of the biological perspective advocate that it does not allow for the influence of environmental and subjective variables in the determination of behavior. However, the idea of multiple determination, which is central to the biological perspective, considers that any behavior is influenced by physiological, genetic, environmental, cultural, developmental, and evolutionary factors. This idea, consolidated by Tinbergen (1963) while considering the determination of behavior, discards determinism. This more comprehensive approach to the role of biology in the determination of behavior helps to approximate the biological perspective to the more social ones. The dissemination of Evolutionary Psychology in Brazil played an important role in that approximation. I consider my contribution in the process of bringing a biological perspective into Brazilian Psychology as my greatest achievement.

How do I see the future of our research on cooperation? I believe that we have established a sound research group, and the next steps are already outlined. The protocols we have developed can be used to answer questions posed by our studies and to unravel variables that are not well clarified by former studies. Two new paths are on our horizon: the introduction of physiological measures and the investigation of new populations scarcely studied, such as children raised in quilombola communities[7] and collective farms in Brazil, characterized by cooperative systems, which may give rise to more prosocial children.

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