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SOCIAL DYNAMICS AND COOPERATION: THE CASE OF NONHUMAN PRIMATES AND ITS IMPLICATIONS FOR HUMAN BEHAVIOR

KATHERINE A. CRONIN

Comparative Cognitive Anthropology Group,
Max Planck Institute for Psycholinguistics,
Wundtlaan 1, 6525 XD Nijmegen, The Netherlands
katherine.cronin@mpi.nl

ANGEL SÁNCHEZ

Grupo Interdisciplinar de Sistemas Complejos (GISC),
Departamento de Matemáticas,
Universidad Carlos III de Madrid, 28911 Leganés,
Spain and Instituto de Biocomputación y,
Física de Sistemas Complejos (BIFI),
Universidad de Zaragoza,
50018 Zaragoza, Spain
anxo@math.uc3m.es

The social factors that influence cooperation have remained largely uninvestigated but have the potential to explain much of the variation in cooperative behavior observed in the natural world. We show here that certain dimensions of the social environment, namely the size of the social group, the degree of social tolerance expressed, the structure of the dominance hierarchy, and the patterns of dispersal, may influence the emergence and stability of cooperation in predictable ways. Furthermore, the social environment experienced by a species over evolutionary time will have shaped their cognition to provide certain strengths and strategies that are beneficial in their species' social world. These cognitive adaptations will in turn impact the likelihood of cooperating in a given social environment. Experiments with one primate species, the cottontop tamarin, illustrate how social dynamics may influence emergence and stability of cooperative behavior in this species. We then take a more general viewpoint and argue that the hypotheses presented here require further experimental work and the addition of quantitative modeling to obtain a better understanding of how social dynamics influence the emergence and stability of cooperative behavior in complex systems. We conclude by pointing out subsequent specific directions for models and experiments that will allow relevant advances in the understanding of the emergence of cooperation.

Keywords: Social behavior; nonhuman primates; cooperation; cottontop tamarins; Saguinus oedipus; complex systems.

1. Introduction

Examples of cooperation are scattered throughout the Animal Kingdom. Bottlenose dolphins (*Tursiops sp*) form alliances of two to three males to capture and maintain access to females for periods lasting from hours to weeks, and alliance membership can be stable for up to 20 years [14]. In the Red Sea, groupers (*Plectropomus pessuliferus*) and giant moray eels (*Gymnothorax javanicus*) combine specialized hunting skills to create an interspecific team that can capture prey better together than either could alone [9]. Chimpanzees (*Pan troglodytes*) in some wild populations cooperatively hunt monkeys and work in stealthily coordinated teams to patrol the boundaries of their territory and investigate neighboring communities [5, 42]. Complex systems, such as insect or human societies, have arisen and continue evolving because of cooperative behavior; in fact, from hunter-gatherer societies to nation-states, cooperation is the decisive organizing principleof human society [44]. Cooperation in all its forms has generated a great deal of observational, experimental and theoretical work, but the pattern of its occurrence remains far from understood in the natural world.

Cooperation is defined here as two or more individuals working together to achieve a common goal [21]. From an evolutionary perspective, cooperation of this sort does not pose a dilemma when individuals obtain more benefits by teaming up with others than they would obtain by working alone, as long as there is some mechanism in place to resist invasion by individuals who reap the benefits of others' cooperative efforts ("cheaters") [4, 48]. Several such mechanisms have been identified in the literature, ranging from kin selection through reciprocity to assortativity or network reciprocity [45]. Benefits of cooperation may come in the immediate form of calories from prey, decreased predation risk, or increased access to potential mates, for example, but are assumed to translate into an increase in individual fitness, defined by the number of offspring that survive to reproductive age, measured relative to others [48].

In the above context, this paper adds to the current literature on cooperation and particularly on its emergence and sustainability in complex systems because it touches upon an issue which has been overlooked both in experiments and models. Indeed, understanding *why* individuals cooperate from an evolutionary perspective, to increase fitness, does not inform us of *how* individuals manage to achieve cooperation in their social environments. Amidst a great deal of research on cooperative interactions, there has been little attempt to explain when cooperation emerges in social groups and when its expression is constrained. Cooperation necessarily involves multiple individuals and is thus social in nature, yet somewhat ironically we understand very little about the social conditions that influence the emergence and stability of cooperative behavior. Therefore, an understanding of the social circumstances that promote cooperation is needed. Although there are impressive examples of cooperation throughout the animal world, the taxonomic order Primates shows a great deal of variation in social dynamics [38] and the cooperation

of many primate species has been extensively studied [reviewed in 57]. By initially focusing on this well-studied taxa, an examination of how the social environment facilitates or constrains cooperative expression is possible. We will thus learn several lessons that should inform subsequent experimental or theoretical work on cooperation in complex systems.

To this end, the paper is organized as follows: in Sec. 2, we present the main features characterizing social dynamics of primates in order to allow us to discuss in depth their relevance as to how cooperation may be established and stabilized. This discussion is carried out at a theoretical and abstract level in Sec. 3, whereas subsequently Sec. 4 presents the available evidence of the effect of social factors on cooperative behavior for the case study of one primate species in which cooperative behavior has been extensively studied, the cottontop tamarin (*Saguinus oedipus*). Finally, Sec. 5 puts together the ideas of Sec. 3 with the results of Sec. 4 and discusses how this emerging body of knowledge of social behavior should inform further modeling and experimentation of cooperative interactions, particularly of human behavior in complex environments. The paper is closed with a brief, summarizing conclusion section.

2. Primate Social Dynamics

Hinde [33] proposed a conceptual, descriptive framework for examining social structure involving three principal levels: level one consists of isolated interactions between individuals, level two is created by the relationships between individuals and described by the content, quality and temporal patterns of their interactions, and level three generates the social structure described by the content, quality and patterning of the level two relationships. The social grouping patterns of the living primates are diverse and can be coarsely categorized as asocial (solitary), family groups, harems consisting of one-male multi-female groups (sometimes co-occurring with groups of "bachelor" males whose social group lacks a female), and multi-male, multi-female groups [56, 64].

The socioecological model has provided the most influential explanation for why primate species vary in their social structures, proposing that variation in social structures results from variation in ecological pressures. Simply put, the distribution and abundance of food influences the number of females in a group as well as the competitive or cooperative nature of female relationships, and the quantity and spatial distribution of females will in turn influence the number of males [63, 74]. The socioecological model remains influential and explains much of the observed diversity in the Primate Order [but see Ref. 65].

The resultant social structure can be described on multiple dimensions that vary across species. Many of these dimensions provide information about the characteristics of the social interactions of individuals in that society that we argue can be used to predict when cooperation should be likely. These dimensions are not independent of one another and include group size, the amount of social

tolerance expressed, the structure of the dominance hierarchy, and the patterns of dispersal.

- *Group size* is the number of individuals that associate with each other more than they associate with individuals who belong to another group. Primate group sizes range between 1 and 115 individuals [37].
- *Social tolerance* is a concept that captures the probability that individuals will be in proximity to conspecifics around valuable resources with little or no aggression [55, 71]. A species with small inter-individual distances when foraging and low rates of aggression would be characterized as high in social tolerance; a species with low social tolerance would typically show large inter-individual distances when foraging and an increase in the frequency of aggressive interactions when constrained to forage in close proximity to others.
- The *structure of the dominance hierarchy* is characterized in two complementary ways, by its linearity and steepness. The linearity of a dominance hierarchy provides information about the degree of transitivity between individuals of different ranks whereas the steepness indicates the degree to which individuals differ from each other in winning aggressive encounters or access to resources [68].
- The *dispersal pattern* of a species indicates which sex typically emigrates at puberty. This is a characteristic that is rather stable within a species, and functions to minimize inbreeding risk. In some species the males disperse, in other species the females disperse, and in a few species neither sex typically disperses.

3. How Can the Social Environment Influence Cooperation?

Collectively, the dimensions above characterize a large part of the primate social environment. The expression of cooperative behavior likely depends on an interaction between the immediate social environment as well as the evolved psychological predispositions of individuals. Contrary to what is usually done in the literature, namely focusing on the latter and trying to understand how evolution can explain why individuals cooperate, we are going to examine what might be the possible influences of social factors on cooperation. Although cooperation can occur between dyads as well as trios and larger parties, the discussion below will refer to dyads for the sake of simplicity. All arguments apply equally well to cooperative units larger than the dyad.

3.1. *The immediate social environment*

The immediate, or current, social environment should affect the opportunity for and stability of cooperative behavior in directions that may be predicted by the dimensions above, beginning with group size. The group size of a species will determine the maximum number of potential cooperative partners that are available, all other social factors withstanding. In larger groups there will be more partner choice, which can positively influence the emergence and stability of cooperation [45]. Thus,

primates living in larger social groups may be more likely to exhibit cooperative behavior than those in smaller groups. However, the number of potential partners will then be reduced by the limitations imposed by the social dynamics of the group.

The degree of social tolerance should constrain the number of cooperative partnerships that can be realized out of all possible partnerships given the group size. In cases where individuals have the opportunity to cooperate to obtain valuable resources such as food or mates, the degree of social tolerance expressed by the social group will influence the ability of individuals to maintain the necessary proximity to one another in the presence of this resource [67]. If a group is highly tolerant and most individuals are able to be in close proximity to most other individuals around resources, then the number of potential partnerships should not be much reduced from all possible combinations given the group size. However, if the group has low social tolerance and only select individuals can gather together without risk of aggression around valuable resources, the potential for the emergence of cooperative behavior should be minimized.

Should members of the group maintain sufficient proximity for the cooperation (which may vary depending on the cooperative challenge), social tolerance may impact an individual's ability to cooperate with others who are present in an additional way. In a group with high social tolerance, individuals should experience a social atmosphere with less risk of aggression around resources that would presumably allow individuals to better attend to and perform the cooperative task. In this scenario of reduced social stress, presumably an individual has greater cognitive resources to allocate to the cooperative challenge, which could lead to more instances of successful cooperative problem solving [similar arguments have been made in regards to social tolerance and social learning, see Refs. 15 and 57].

The linearity of the dominance hierarchy provides an indication of the amount of transitivity between individuals of different dominance ranks. In a society with a nonlinear dominance hierarchy, the group is more egalitarian and it will be less predictable ahead of time which individuals will obtain benefits. Amongst individuals in a nonlinear dominance hierarchy there would exist a greater number of potential cooperative partners with whom the opportunity to obtain (or retain) the benefits of cooperation is nearly equal, compared to more linear hierarchies. Given that individuals should be more likely to engage in cooperation if they obtain enough benefits from cooperating to outweigh the costs invested, one might expect more potential cooperative dyads in groups with nonlinear dominance hierarchies. However, it may also be possible that lack of linearity in a dominance hierarchy produces uncertainty amongst potential cooperators about the allocation of rewards that may lead to social stress in a low tolerance society and, as described above, minimize cooperative performance. Thus the influence of dominance linearity may interact with social tolerance such that nonlinearity only increases cooperative opportunities in a group if the group is high in social tolerance.

The steepness of the dominance hierarchy by definition reflects the magnitude of the differences obtained between individuals of different ranks. Therefore a steep

hierarchy would correspond with a society in which a larger proportion of the possible cooperative dyads would produce benefits than would be distributed unequally between individuals. Even if the benefits obtained by an individual outweigh the costs that individual invested in the cooperative act, some would argue that witnessing another individual obtain more rewards than oneself for the same amount of effort is frustrating [52] or aversive [e.g. 73] and may therefore lead to a decrease in future cooperation. Thus, a society in which the dominance hierarchy is steep may consist of fewer dyads likely to repeatedly engage in cooperation, and the stability of cooperation would be compromised.

These posited influences of dominance steepness and linearity rest on the assumption that primates do not share the spoils of their labor based on the amount of effort invested. To date, evidence of sharing based on investment in naturally occurring nonhuman primate cooperation comes from one population of wild chimpanzees located in Taï National Park, Côte d'Ivoire [4]. If effort-based resource distribution occurs in other primate populations, these groups may be released from the constraining effects of dominance structure proposed here. However, to date the evidence for sharing spoils based on labor is limited and there are other factors that explain resource distribution after successful chimpanzee hunts [43].

Finally, the dispersal patterns may influence patterns of cooperation within the group because the nondispersing sex has more opportunity to form long-term relationships with others of the same sex in their group. When individuals are engaged in long-term relationships, the probability of repeated interactions is high, and the opportunity to reciprocate or make up for losses incurred in previous interactions is greater than between individuals in engaged in short-term relationships [66]. Avoiding a net loss in repeated interactions with a long-term partner need not be cognitively demanding nor involve any calculated score keeping, as symmetrical, long-term relationships may result in a balance of benefits over a series of repeated interactions [e.g. 19, 71].

Therefore, the immediate social environment should influence the opportunity for cooperative interactions in predictable directions, as well as the distribution of benefits that results from the cooperative effort. This distribution of benefits may then feedback into an individual's likelihood of engaging in cooperation again at the proximate level, e.g. by reinforcing cooperative behavior of individuals, and therefore influence the stability of cooperation, should it emerge. Although the discussion has thus far focused on the emergence and stability of cooperation within one's lifetime, the distribution of benefits may influence the evolution of cooperative systems as well if the benefits gained by cooperative individuals are indeed translating into increased reproductive success [48].

3.2. *The psychology of potential cooperators*

The immediate social environment will influence the opportunities for cooperative interactions and the distribution of benefits that result from cooperation, but the

psychology of the species will influence how these opportunities are interpreted and acted upon. The psychological predispositions that characterize each species are subject to natural selection just as physical traits are, given that there is variation in the population and differential reproduction associated with this variation. The fitness of primates depends upon navigating a complex social world of potential enemies, allies and mates, a milieu that varies from one species to the next; therefore species are likely to be equipped with psychological strengths and strategies that have proven advantageous in the social domain of their evolutionary past [2, 10]. Depending on the exact constellation of the social dimensions described above, the specific psychological predispositions that would have provided a fitness advantage and have been selected would vary across species, which may in turn differentially impact the propensity of the species to exploit opportunities to cooperate with conspecifics.

For example, in some species the ability to monitor the behavior of others and coordinate one's own behavior accordingly is central to the survival of their own offspring and their close relatives. This is the case in cooperative breeders whose behavior is described in more detail below. Therefore, one hypothesis is that cooperative breeders have undergone natural selection to be psychologically predisposed to monitor the behavior of others and coordinate their behavior flexibly with them [e.g. 16]. Cooperative breeders presented with the opportunity to cooperate outside the offspring-rearing context may be poised to reach a cooperative solution because they have a psychological bias to attend to the partners' behavior and are skilled at coordinating with others. Experiments aimed at testing the cooperative behavior of a cooperatively breeding species outside of the offspring-rearing context are discussed in more detail below.

Determining how exactly the psychology of a species has been shaped over time by their past social environment is empirically challenging, perhaps even impossible, but it is certain that the psychology of a species will have been subject to natural selection in ways that differ across species [10]. What is proposed here is that evolved psychological differences will influence the emergence of cooperation across species in concert with the characteristics of the immediate, current social environment.

4. Case Study: Cooperative Breeders and Cooperative Problem Solving

To investigate the role of social environment and evolved psychology on the emergence and stability of cooperative behavior, a we turn to a selection of experiments conducted with a captive colony of cottontop tamarins (*Saguinus oedipus*), cooperatively breeding monkeys endemic to Colombia. The social behavior and cognition of cottontop tamarins has been studied in detail for nearly 30 years [reviewed in 59, 62]. Below is an overview of the social environment of cottontop tamarins and a description of some experiments that begin to elucidate the role that social environment and evolved psychology play in the emergence of cooperative behavior in

nonhuman primates. The lesson we will learn from those experiments will be used to pose specific questions about humans in the closing section.

4.1. *Social environment of cooperative breeding primates*

In cooperatively breeding systems, offspring care is provided not only by the biological parents, but also by "helpers" or "alloparents" who delay or forgo their own reproduction entirely while rearing the offspring of the breeding pair. This breeding system has evolved independently in multiple taxa, and is seen in about 120 mammalian species and 150 avian species [50]. In primates, only one taxonomic Family, the *Callithrichidae*, which consists of more than 30 species of marmosets and tamarins, exhibits cooperative breeding. In callithrichids, a social group is typically comprised of one socially monogamous breeding pair and their adult and juvenile offspring who gain inclusive fitness benefits by helping rear younger siblings [26, 59]. In cottontop tamarins specifically, the interbirth interval for the breeding pair is six months, and dams give birth to twins that can weigh up to 20% of the mothers' body weight collectively. The twins require continuous carrying for the first month of life and continue to be carried for up to 12 weeks [75]. Furthermore, the biological mother is often pregnant with the next litter and nursing the previous litter simultaneously. Thus, the energetic burden of offspring is extremely high, and in fact the number of helpers present is predictive of infant survival [58, 62].

Callithrichid life involves constant monitoring and coordination with group mates in order to coordinate the cooperative rearing of young. Group sizes in the wild are typically between six to nine individuals [62]. Although some unrelated individuals might join groups as helpers [53], the average relatedness among group mates is presumably high and neither sex regularly disperses. Mature offspring, mothers and fathers coordinate behavior for infant care, travel, food sharing and predator detection [11, 62]. Because the twin offspring must be constantly carried by one or two group members, transfers between carriers require monitoring of the behavior of the infant and the other helpers, and flexible spatial and temporal coordination between helpers. Like other callithrichids, cottontop tamarins are strongly dependent on group mates for survival and reproductive success. Their relationships have been described as valuable and secure, with frequent affiliation and infrequent aggression [1, 54].

4.2. *Cooperation experiments*

In order to investigate the cooperative behavior of tamarins outside the offspring-rearing context, tamarins were presented with a cooperative task that required high social tolerance and behavioral coordination between partners. The apparatus (Fig. 1) was designed such that tamarins needed to simultaneously pull two handlesin order to release food rewards, but the handles were located too far apart for one tamarin to reach both. The requirement of simultaneous pulling was enforced by elastic bands attached to each handle; only when tension was applied to both
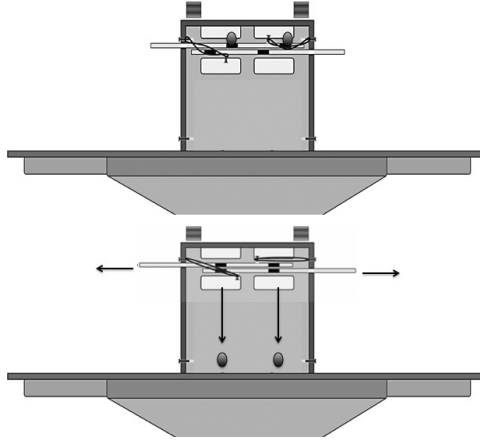
Fig. 1.   The cooperation apparatus. The top panel depicts the apparatus when it is unsolved. Grey ovals represent food rewards. When the trays (white horizontal bars) are simultaneously extended from either side as shown by the horizontal arrows in the bottom panel, the holes in the trays (black spaces) align and the food rewards fall through. Small openings near the bottom of the apparatus (not shown) allow the tamarins to reach through and retrieve the food reward. Elastic bands cause the trays to retract once tension is released and therefore ensure that two tamarins must work together to solve the task.

handles simultaneously could the trays inside the apparatus align in such a way that the food could fall through to the actors. Prior to testing, subjects were trained on an apparatus that was lacking one tension band, so it was possible for a single subject to solve the task by pulling one side first, and then the other. All subjects reliably solved the task in this configuration, and their behavior indicated that they correctly predicted the rewards to fall directly below their placement on the tray. Tamarins were never trained to coordinate their actions; simultaneous pulling was not required for success until the testing began [for details of training see 16]. The apparatus was transparent and the rewards (small pieces of food) were visible from the outset. In order to be successful the cooperators needed to be in close proximity around this desirable resource, monitor the behavior of their partner, and coordinate behavior accordingly.

In a series of controlled experiments, Cronin and colleagues utilized this apparatus to investigate cooperative problem solving in a captive colony of cottontop tamarins maintained at the University of Wisconsin–Madison. All experiments were conducted with monogamous pairs of tamarins who did not currently have offspring present. All subjects were unrelated to their partners, and had lived together with their mate for at least five years. Behavioral data indicated that they shared a long-term, stable bond with their unrelated partner [61].

In the first experiment [16], we investigated whether cottontop tamarins could demonstrate basic behavioral cooperation, that is, we measured whether tamarins could coordinate action in time and space to meet a common goal [5, 21]. Although partners had to come into proximity around the valuable food rewards, the social

tolerance required was relatively low because the rewards were visibly pre-divided in space; prior to solving the task it was evident that a single reward on each side of the apparatus was poised to fall into the reach of each actor (Fig. 1). We found that all tamarin pairs tested were able to solve this task. Furthermore, behavioral data suggests that they understood the role of the partner in the task and were not just successful by chance cooccurrence of individual behaviors [67]. Tamarins pulled less often during control conditions when their partner was not available to help, and developed a technique of sustained pulling in which one tamarin would extend the handle and wait for their partner to pull before releasing [16].

Comparing the performance of tamarins directly to other species should be done with caution considering the use of different apparatuses and methods across studies, however the performance measures available (latency to solve the task, efficiency) [16] suggested that tamarins attained this cooperative solution as well or better than all nonhuman primate species that have been studied in similar cooperative paradigms [e.g. 7, 8, 12, 13, 28, 40, 41].

The cooperative success of the tamarins in the first experiment may have been due in part to the clear and equal division of rewards. We questioned how the cooperative performance of the dyads would change if individuals were not equally rewarded for their actions, and presented the same dyads with a scenario in which only one individual could benefit on each trial (Fig. 2) [19]. During the first experiment, each pair of tamarins had developed a strategy in which one individual regularly occupied the left side of the apparatus and one regularly occupied the right. Therefore, in the second experiment, we simply baited the left side of the apparatus on all trials on one day, and then on the next day we baited the right side on all trials. We continued to alternate the baited side in this manner for ten days. To release the single reward, both individuals again needed to work simultaneously, however, only one individual would be rewarded on each trial and it was apparent prior to solving the task which individual would obtain the reward.

Tamarins continued to solve the majority of trials presented under this new reward scenario, although the percentage of trials solved in this unequal reward experiment was less than in the equal reward experiment [19]. Therefore, when
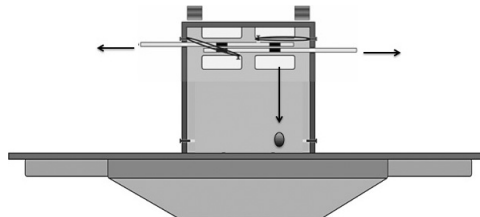

Fig. 2. The reward trajectory for the alternated reward scenario (experiment 2). The side of the apparatus that was baited was alternated across days; here the right side of the apparatus was baited and the figure depicts the trajectory of the reward after both handles have been simultaneously extended. Only the tamarin on the right would be able to access this reward.

transitioning from a cooperative situation in which both partners were rewarded equally to a situation in which only one was rewarded, the tamarins did respond to the decrease in their individual gain and solve fewer trials. Although this decrease was significant, cooperation still occurred on more than 75% of trials. (A trial was considered unsuccessful if the task was not solved within three minutes of baiting. In the case of failure, the 10-trial session was ended and the tamarins were scored as failing the remainder of the trials in that session; thus percent success was conservatively calculated). Therefore, tamarins predominantly maintained their cooperative behavior even when they did not receive any tangible benefits for their efforts that day. They were willing to maintain a high level of cooperation when only their pairbonded mate was rewarded [for detailed data on pair performance across sessions, see Ref. 19], for limitations of provisioning behavior of tamarins, see Refs. 17 and 18].

Cronin and colleagues hypothesized that the tamarins' cooperative performance under this alternated reward scenario was in part enabled by the long-term relationship between cooperators. Their tolerance of the temporarily inequitable reward distribution may have been influenced by the fact that their partner was someone with whom they shared a long-term, stable bond. As has been proposed by de Waal & Luttrell [71] and discussed above, when individuals are engaged in long-term, egalitarian relationships, temporary imbalances in costs and benefits between actors are not so disruptive to behavior. Effects of varying relationships on cooperative success and inequity tolerance have been evaluated in other species providing preliminary support for this interpretation [3, 7, 40, 72]; however to test this hypothesis the performance of newly established tamarin pairs would have to be compared with the performance of the long-term partners in this study. Nonetheless, it seems that the simplest explanation of the tamarins' continued cooperation under this alternated reward scenario is that they do not "keep score" with each other, and cooperative behavior is able to persist in this social environment characterized by long-term, egalitarian relationships.

The previous experiment demonstrated that cooperatively breeding tamarins maintain cooperation when only one individual benefits, but what was removed from the cooperative equation was the uncertainty about which actor would obtain the benefits. As de Waal [69] pointed out, in addition to dominance, social tolerance is another determinant of resource acquisition, but the resources from this cooperative opportunity were pre-assigned to actors. Therefore, in a third variant of the cooperation task, we modified the apparatus such that a single reward was delivered equidistant from both subjects upon completion of the cooperative act, and the identity of the rewarded animal could not be known before the tamarins engaged in cooperation (Fig. 3). This design has resulted in the breakdown of cooperation by some other primate species [e.g. 27, 70] and by dyads characterized by low (but not high) social tolerance [40].

The results of the centered reward experiment indicated that the introduction of this uncertainty did not influence the tamarins' cooperative performance relative
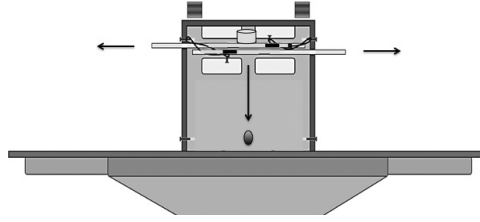
Fig. 3. The reward trajectory for the centered reward scenario (experiment 3). The trays were different than the previous experiments; each tray had a single hole and the reward was initially positioned equidistant from both subjects atop the trays in the clear cylinder. The figure depicts the trajectory of the reward after both handles have been simultaneously extended. Both tamarins were able to reach this reward.

to when the single reward was pre-assigned; tamarins solved nearly the same percentage of trials as the previous experiment (76% versus 78%). Although we did not build into the design of the experiment a mechanism by which actors would be equally rewarded, a near equal reward distribution resulted between partners [19].

How this reward distribution resulted is important for understanding how the social environment of this species enables stable cooperation. Upon solving the task, the single reward was released between the two cooperators. On nearly every trial, both tamarins would reach quickly for the reward, and one would emerge with it. When both reached for the reward, which they nearly always did, we observed an equal chance that either would obtain it. In other words, there were not individuals who were more or less skilled at retrieving the reward. Once a tamarin successfully retrieved a reward, the individual in possession of the reward never actively transferred food to their partner. Therefore, the equality observed did not result from some purposeful enactment of fairness by the tamarins, but the high social tolerance that enabled both individuals to reach for the reward without risk. In species with lower tolerance or a steeper hierarchy, two individuals would not be equally able to attempt to obtain the reward due to the risk of aggression associated with snatching food in this manner.

Aggression following reward retrieval by one cooperator was virtually absent. In this experiment, following 234 trials on which a reward was released (or 351 min of observation) there were only five instances of behaviors that could be interpreted as indicative of aggression, equating to a rate of only one potentially aggressive incident every 39 trials. This was not higher than the rate of aggression observed in the previous experiment where the rewarded individual was known prior to cooperation. Given that there was no apparent aversion to temporary inequity (tamarins did not stop engaging in the task following a trial in which their partner obtained the reward) and that there was no risk to trying to obtain the reward, cooperation remained stable among tamarin dyads.

The cooperation experiments conducted with cottontop tamarins begin to elucidate the role that social factors may play in the emergence and stability of cooperative behavior, and suggest that in a highly tolerant society in which aggression

is rare and access to food is not regulated by a steep or linear hierarchy, cooperation readily emerges between individuals engaged in long-term relationships and their cooperation is stable to fluctuations in payoff. Furthermore, the tamarins' performance on the cooperative task may have been facilitated by psychological adaptations to cooperative breeding, such as attention to the social behavior of group-mates and ability to coordinate behaviors with others. However, without more examination of variation across potential dyads and careful comparisons across species with different evolutionary histories and current social dynamics, the contribution of each factor to the cooperative behavior of tamarins cannot be teased apart.

5. Application to Experiments and Modeling

We have proposed that the social dynamics of nonhuman primates impact the emergence and the stability or resilience of cooperative behavior. The cooperative behaviors we have discussed involve two or more individuals working together to acquire some resource. We have argued that the opportunity to cooperate and the distribution of the resource obtained will be impacted by social factors such as the size of the group, the amount of tolerance expressed in the group, the structure of the dominance hierarchy, and the presence of long-term relationships. The preceding section has shown examples of these influences in the case of cottontop tamarins. We are thus in a position to ask: Do these considerations apply to humans? What experiments could address this issue? What are the mechanisms arising that should be incorporated in models of human social behavior?

It is important to realize that the questions we are raising here have an impact at two different levels. First, the relation between sociality and cooperation must be a key to understanding how early human societies developed from small groups of hunter-gatherers. Second, given the highly socialized environments in which human interaction takes place today, the effect of the factors we are discussing here must permeate most of the endeavors carried out by groups, corporations, or, in fact, any hierarchical organization.

5.1. *Experiments*

Empirical work has demonstrated that components of human cooperation assessed through economic games such as the Dictator Game, Ultimatum Game, Third Party Punishment Game, Prisoner's Dilemma and Public Goods Games differ in predictable ways across cultures [30–32] and within cultures [39]. Some of this variation is predicted by community size [e.g. 32, 39] and kinship patterns of dispersal [39]; factors hypothesized to be influential in nonhuman primate cooperative expression as well. These recent works are certainly an indication of the relevance of social factors in human cooperation and point to the need for specifically designed experiments test the ideas proposed above.

Indeed, the relationship between social dynamics and cooperation posited above for nonhuman primates makes *predictions* specifically in the context of coordination games that generate rewards whose distribution among the participants is not preassigned. One direct way to investigate whether human societies differ in similar contexts would be through experiments such as a Stag Hunt Game, in which the subjects should try to coordinate in the payoff-dominant equilibrium, followed by an Ultimatum Game, in which they have to decide how to share the total outcome. Such a setup is comparable to the experiments described in Sec. 4 and would allow us to find out whether human behaviors differ in ways that can be predicted by the influences suggested to be important to nonhuman primates. This type of assessment would help to determine whether our species is constrained by similar dynamics as other primates, and also shed some light on potential universal constraints to cooperation in a scenario that commonly occurs in the real world. Of the important aspects of social dynamics discussed above, the linearity and steepness of the dominance hierarchy and the degree of social tolerance have not been operationalized (often) for human societies. One could imagine these traits to be assessed more readily in corporations than cultures, an environment that could provide an informative testbed for the hypothesis that performance on a coordination game without predivided benefits would be predicted by these social dynamics important to nonhuman primates.

In the case of nonhuman primates, the division of rewards may be predicted by the actors to some degree by the dominance hierarchy and group-typical social tolerance. Unlike many economic games, the payoff structure to each actor is not known ahead of time [but see 20, 36], but the total pot to be obtained by the successful cooperative team may be. Experiments with humans that integrate uncertainty the distribution and quantity of benefits would provide much-needed information about whether reward uncertainty interacts with social dynamics in humans in the same way that it appears to in nonhuman primates, namely with reward uncertainty making cooperation unstable in societies with steep, linear hierarchies and low social tolerance.

In this discussion, a key point is that exploring sociality means relaxing the anonymity condition proper to most economic experiments. In fact, much of the influence of social dynamics on cooperative behavior in nonhuman primates relies on an awareness of the identity of one's cooperative partner(s). Clearly there are valuable reasons for maintaining anonymous relations amongst participants in experimental assessments of cooperative decision making, but it would be of interest to learn how revealing partner identities (specifically knowledge of a higher or lower ranking partner) would influence strategy choice in the coordination for nondivided rewards scenario described above. Perhaps this could be accomplished unidirectionally, by allowing one subject an option to learn of their partner's identity in secret but not vice-versa, minimizing the potential influences of reputation and reciprocity. In this respect, an interesting alternative to experiments within corporations is to stick to volunteer subjects, and assign them a ranking either by

solving some test, by competing in some game, or even at random, and then proceed with the specific economic experiment (which could be as above a combination of a coordination game and a bargaining game, or other social dilemmas).

5.2. *Modeling issues*

The assessment of the role of social dynamics on primate (human and nonhuman) cooperation allows the suggestion of features that should be considered in models or simulations order to better reflect information that may be important to understanding the emergence and resilience of cooperation. Before entering into the specific issues, it is clear from this discussion that in a social context individuals do not interact randomly, nor do they interact with every other one. Therefore, modeling approaches based on well-mixed populations or mean-field approaches will not be able to capture the social influences addressed here. Yet it is clear that any reasonable model will need to include an interaction network, and possibly and imitation network that is not necessarily the same [22, 47]. A word of caution is in order here, as very recent results predict [24] that networks do not affect the outcome of a Prisoner's Dilemma game played by humans, but they can still have an influence on the behavior found in other games, as several theories predict [51]. On the other hand, links between nodes (individuals) are far from homogenous in primate societies (humans included). Primates are embedded in a social network that represents the probability of interaction with another node. It is becoming increasingly common to utilize association matrices to define social networks, but one lesson to be learned from this discussion of nonhuman primate behavior is that the data utilized to create the network should be relevant to the cooperative context. An association matrix defined by proximity in a context where valuable resources are absent may be very different from one when they are present, yet the latter situation is the context that presents cooperative opportunities.

An additional aspect that models must take into account is that even within a specific choice of context for the social network, a static picture may often be inaccurate. In fact, some interactions between nodes could eliminate links depending on the outcome of that interaction. Analogously, individuals may change the strategy underlying their behavior as a function of the development of the interactions. Further complications arise from the fact that all these dynamics can take place at different time scales. On the first issue, some modeling has been done in terms of co-evolving networks [25], but to study the social factors discussed here requires a different approach that takes into account the mechanisms in some detail. In particular, an issue that has not been very much studied is that of models with heterogeneous agents, both in terms of (possibly weighted) links and on their own characteristics. As with the experiment, social features require distinguishable agents, and this is rarely taken into account in models of cooperation [see Ref. 35]. This would be most interesting in connection with the question about

hunter-gatherer groups prior to the Neolithic transition, where introducing social considerations in a model such as that of Boyd *et al.* [6] may lead to new and deeper insights.

As far as the learning or strategy dynamics are concerned, given what is known about the near-universal influence of reinforcement learning in nearly every species studied (actions that result in benefits are repeated, those that result in loss are not), inclusion of a reinforcement learning mechanism [34] that determines not only whether actions will be repeated but also with which nodes may bring simulations closer to representing cooperative behavior as it is expressed in the natural world. Current knowledge about learning in humans and other animals indicates that learning should occur over a strategy set, not simply over immediately preceding actions.

A word is in order here regarding the availability of data on social networks. Nowadays, very large scale studies are being carried out by resorting to the use of the so-called "big data", such as communication among users of mobile phones, relationship maps built from twitter feeds, and so on. While such large-scale studies are certainly interesting and provide very valuable information about human behavior, for the purpose we are considering here more detailed data (on possibly smaller sets) might be needed in order to properly account for the factors relevant in a social context. This immediately raises questions of privacy and other ethically important points, which may require quite some preliminary work on how these data should be made available and handled. In fact, it may be useful to resort to more sociological studies, carried out in small communities with much detail about their social context, such as [23, 49]. In this context, it is important to note that all these issues relate to data obtained in an "observational" manner, i.e. by monitoring the activity of people who are unaware of being followed. This is a very useful procedure which would be tantamount to observing primate groups in their own natural environment. However, it is often the case that this type of data does not allow one to address specific questions of interest, nor does it provide good statistics of particular points that do not occur often in a natural context. Therefore, it will be necessary to complement those "observational" data by "interventional" results, in which the natural environment is modified to focus on the point or points that the researchers want to elucidate. This will probably require the development of some kind of large-scale experimental facility suitable to handle groups with numerous individuals, which is a very difficult task indeed (see Ref. 29 for a related discussion).

A final remark concerns the way models themselves are built. Increased communication between those who model the social behavior of humans and those who observe the social behavior of other animals should generate beneficial ideas on both sides; in addition to suggesting factors for modelers to consider in their attempts to understand and predict cooperative behavior of agents, those who study the behavior of animals will be introduced to quantitative tools that can aide in testing hypotheses. At this time the proposed influence of these social factors remains open

to testing and we are far from predicting how these social dimensions interact with one another to promote or inhibit cooperative expression. This quest would benefit from modeling techniques that could make predictions that could be tested against observations in the natural world.

6. Conclusion

Although the topic of cooperation has fascinated biologists and psychologists for decades, the proximate, social factors that influence the expression and stability of cooperation in the animal kingdom have remained largely uninvestigated. It is argued here that certain features of the social world, including the size of the social group to which an individual belongs, the social tolerance expressed in that group, the structure of the dominance hierarchy, and the patterns of dispersal, will influence the probability of cooperative expression and the stability of cooperative behavior. In addition, the social environment experienced by a species over evolutionary time will have shaped their cognition to provide certain strengths and strategies that are beneficial in their species' social world. These cognitive adaptations will also impact the likelihood of cooperating in a given social environment.

One productive route toward an understanding of whether these social dimensions influence the expression of cooperative behavior across primates specifically, and animals more generally, may be through a quantitative modeling approach. The specific case of human cooperative behavior is of the utmost importance and in that respect the proposals we have made in the previous section guide the way to human experiments to test the ideas we have presented. Hints as to how this quest would benefit from modeling techniques that could make predictions that could be tested against observations in the natural world have also been provided. Work along these directions would be an invaluable contribution to understanding the social roots of human cooperation.

Acknowledgments

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