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Joint Ventures Require Joint Payoffs: Fairness among Primates

WALL STREET IS SOMETIMES COMPARED TO A DARWINIAN JUNGLE. Nice guys finish last, it is said, and only the strong survive. This is an adequate enough description, but not entirely true, neither for the stock market nor for life in the jungle. When Richard Grasso, head of the New York Stock Exchange, revealed a pay package for himself of close to $200 million, there was public outcry. As it happened, on the very same day that Grasso was forced to resign, my team published a study on monkey fairness. Commentators could not resist contrasting Grasso with capuchin monkeys, suggesting he could have learned a thing or two from them (Surowiecki, 2003).

Obviously, in a social system built on individual strength, the strong have an advantage. But as soon as the system introduces additional factors relevant for survival, the picture changes. The present topic of fairness deals with the influence of cooperation: obviously there would be no need to worry about fairness if everyone acted independently. Cooperation is widespread in the animal kingdom. Even the simple act of living together represents cooperation. In the absence of predators or enemies, animals do not need to stick together, and they would in fact be better off living alone. The first reason for group life is security.

On top of this, many animals actively pursue common goals. By working together they attain benefits they could not attain alone. This

means that each individual needs to monitor the division of spoils. Why would one lioness help another bring down a wildebeest if the other always claims the carcass for herself and her cubs? One cannot have joint efforts without joint payoffs. With cooperation comes sensitivity to who gets what for how much effort. When we became cooperative animals, we abandoned the right-of-the-strongest principle and moved on to a right-of-the-contributor principle. The latter is no less Darwinian than the former.

Not all economists recognize our cooperative side, though. People are seen as profit maximizers driven by pure selfishness. In Thomas Hobbes's words, "Every man is presumed to seek what is good for himselfe naturally, and what is just, only for Peaces sake, and accidentally" (Hobbes, 1651, part iii). In this view, sociality is but an afterthought, a "social contract" that our ancestors entered into because of its benefits, not because they were attracted to each other. For the biologist, this imaginary history is as wide off the mark as can be. We descend from a long line of group-living primates, meaning that we are naturally equipped with a strong desire to fit in and find partners to live and work with. This evolutionary framework is gaining ground within economics under the influence of a new school, known as behavioral economics, which focuses on actual human behavior rather than marketplace abstractions. Behavioral economists are the children of Adam Smith, but not the one who wrote about the pursuit of self-interest in *The Wealth of Nations*. They rather follow the one who wrote *A Theory of Moral Sentiments.* This is, of course, the same Adam Smith, but in this other major work, rarely read in business schools, Smith emphasized sympathy and the way kindness begets kindness (Smith, 1759).

Animal behavioral economics is a fledgling field that lends support to the new theories by showing that basic human economic tendencies and preoccupations—such as reciprocity, the division of rewards, and incentives for cooperation—are not limited to our species. They probably evolved in other animals for the same reasons as in us. This is why Rawls (1972), who is so popular in the social sciences and

philosophy, actually asked the wrong question. Rawls explored assumptions underlying a fair society without showing much interest in the actual evolutionary trajectory that has led our species to its concern about fairness and justice. This concern was taken for granted. But the real question is not to what degree we care about fairness, but how we came to care about it at all.

This is not to dismiss the heuristic value of Rawls's "original position" as a way of getting us to reflect on what kind of society we would wish to live in. The original position refers to a "purely hypothetical situation characterized so as to lead to certain conceptions of justice" (Rawls, 1972: 12). But even if we do not take Rawls' original position literally, adopting it only for the sake of argument, it still distracts from the more pertinent argument that we should be pursuing, which is how we became what we are today. What parts of human nature led to a preoccupation with fairness, and what was the role of natural selection in shaping this preoccupation? In other words, what good did a sense of fairness do to our ancestors? We stem from a long line of social primates, and whatever abstract rationale for fairness philosophers may come up with, there must have been very concrete advantages associated with it in the past.

RECIPROCITY AND GRATITUDE

Ever since Kropotkin (1902), the proposed solution to the evolution of cooperation among nonrelatives has been that helping costs should be offset by return benefits, either immediately or after a time interval. Formalized in modern evolutionary terms by Trivers (1971), this principle became known as *reciprocal altruism.*

Reciprocal altruism presupposes that: a) the exchanged acts are costly to the donor and beneficial to the recipient; b) the roles of donor and recipient regularly reverse over time; c) the average cost to the donor is less than the average benefit to the recipient, and d) except for the first act, donation is contingent upon receipt. Although the initial work on cooperation (especially from the prisoner's dilemma perspective) focused primarily on the payoff matrix to

distinguish between reciprocity and mutualism, more recent efforts have included a significant time delay between given and received services as an additional requirement for reciprocal altruism (e.g., Taylor and McGuire, 1988).

The above outlines the steps of an evolutionary argument about how reciprocal cooperation may have come into existence. As such, it applies to organisms from fish to humans. This should not be taken to mean, though, that reciprocal help in human society is essentially the same as in guppies. This would be a fundamental error: the above theoretical framework only deals with the *ultimate* reasons for the existence of reciprocal exchange—that is, it provides an explanation for why animals engage in such behavior, and how it enhances fitness. It does not tell us how cooperation is achieved, and what kind of psychology underlies it, which is commonly referred to as the *proximate* explanation (Brosnan and de Waal, 2002).

Chimpanzees exchange multiple currencies, such as grooming, sex, support in fights, food, babysitting, and so on. This marketplace of services, as I dubbed it in *Chimpanzee Politics* (de Waal, 1982 [1998]), means that each individual needs to be on good terms with higher ups, foster grooming partnerships, and—if ambitious—strike deals with like-minded others. Chimpanzee males form coalitions to challenge the reigning ruler, a process fraught with risk. After an overthrow, the new ruler needs to keep his supporters contented: an alpha male who tries to monopolize the privileges of power, such as access to females, is unlikely to keep his position for long. It is advice that goes back to Niccolò Machiavelli.

One of the commodities in the chimpanzee marketplace is food. Food sharing lends itself uniquely to experimental research, because the quantity and type of food available, the initial possessor, and even the amount of food shared can be manipulated. Active food sharing, a rare behavior, consists of one individual handing or giving food to another individual, while passive food sharing—by far the more common type—consists of one individual obtaining food from another without the possessor's active help (see figure 1).

Figure 1 A cluster of food-sharing chimpanzees at the Yerkes Field Station. The female in the top-right corner is the possessor. The female in the lower-left corner is tentatively reaching out for the first time. Whether or not she can feed will depend on the possessor's reaction. Photograph by Frans de Waal.

We exploited the tendency of chimpanzees to share by handing one of them a watermelon or some branches with leaves. The owner would be at the center of a sharing cluster, soon to be followed by secondary clusters around individuals who had managed to get a major share, until all food had trickled down to everyone. Claiming another's food by force is almost unheard of among chimpanzees—a phenomenon known as "respect of possession." Beggars hold out their hand, palm upward, much like human beggars in the street. They whimper and whine, but aggressive confrontations are rare. If these do occur, they are almost always initiated by the possessor to make someone leave the circle. She whacks them over the head with a sizable branch, or barks at them in a shrill voice until they leave her alone. Whatever their rank, possessors control the food flow (de Waal, 1989).

We analyzed nearly 7,000 approaches, comparing the possessor's tolerance of specific beggars with previously received services. We had detailed records of grooming on the mornings of days with planned food tests. If the top male, Socko, had groomed May, for example, his chances of obtaining a few branches from her in the afternoon were much improved. This relation between past and present behavior proved general. Ours was the first animal study to demonstrate a contingency between favors given and received. Moreover, these food-for-grooming deals were partner specific: May's tolerance benefited Socko, the one who had groomed her, but no one else (de Waal, 1997a).

It was further found that grooming between individuals who rarely did so had a greater effect on subsequent food sharing than grooming between partners who commonly groomed. There are several interpretations. It could be that grooming from a partner who rarely grooms is more noticeable, leading to increased sharing by the food possessor. Chimpanzees may recognize unusual effort and reward accordingly. Second, individuals who groom frequently tend to be close associates, and favors may be less carefully tracked in these relationships. Reciprocity in close friendships may not have the high degree of conditionality found in more distant relationships. These explanations are not mutually exclusive: both will lead to a reduced level of conditionality the more common exchanges are in a relationship.

Of all existing examples of reciprocal altruism in nonhuman animals, the exchange of food for grooming in chimpanzees comes closest to demonstrating memory-based, partner-specific exchange. In our study, there existed a significant time delay (that is, a few hours) between favors given and received; hence, the favor was acted upon well after the previous positive interaction. Apart from memory of past events, for this to work we need to postulate that the memory of a received service, such as grooming, induces a positive attitude toward the same individual. In humans, this psychological mechanism is known as "gratitude," and there is no good reason to call it anything else in chimpanzees (Bonnie and de Waal, 2004).

CAPUCHIN COOPERATION

Even though laboratory work on primate cooperation goes back to Crawford (1937), few experimental studies have been conducted since. What is especially lacking is the experimental manipulation of "economic" variables, such as the relation between effort, reward allocation, and reciprocity. Recently, this situation has changed thanks to experiments on capuchin monkeys.

These monkeys show high levels of social tolerance around food and other attractive items, sharing them with a wide range of group members both in captivity and the field. This level of tolerance is unusual in nonhuman primates, and its evolution may well relate to cooperative hunting. Perry and Rose (1994) confirmed earlier reports that wild capuchins capture coati pups and share the meat. Since coati mothers defend their offspring, coordination among nest raiders may increase capture success. Rose (1997) proposed convergent evolution of food sharing in capuchins and chimpanzees, since both show group hunting (as do humans, for that matter). The precise level of cooperation is irrelevant for such evolution to occur: all that matters is that hunting success increases with the number of hunters. Under such circumstances, every hunter has an interest in the participation of others, something that can be promoted through subsequent sharing.

We mimicked this situation in the laboratory by having two capuchin monkeys work together to pull in a counterweighted tray at which point one or both of them would be rewarded (figure 2). This is similar to group hunts in which many individuals surround prey, which only one among them will capture. Our monkeys were placed in a test chamber separated from each other by a mesh partition. One monkey (the winner) of a pulling pair received a cup with apple pieces. Its partner (the laborer) had no food in front of it, hence was pulling for the other's benefit. Food was placed in transparent bowls so that each monkey could see which one was about to receive the food.

From previous tests we knew that food possessors may bring food to the partition, where they permit their neighbor to reach for it through the mesh. On rare occasions, they push pieces to the other. We

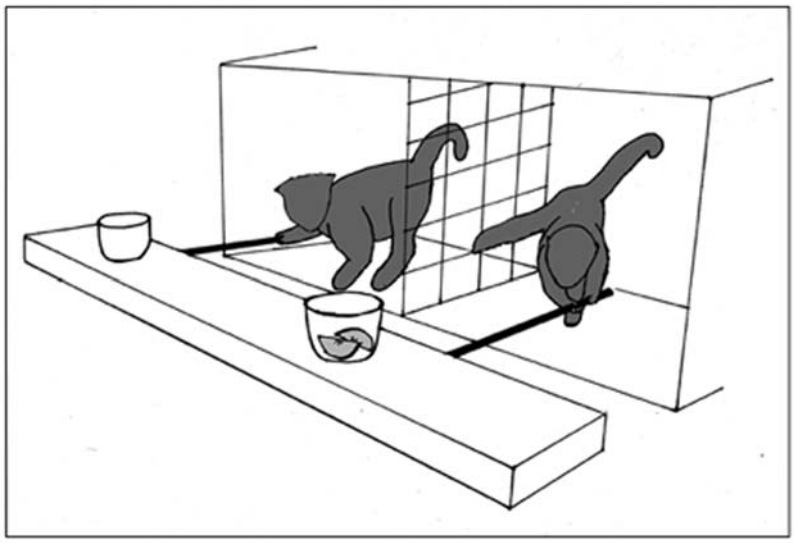

Figure 2 The test chamber used for the cooperative pulling task in capuchin monkeys inspired by Crawford's (1937) classical study. Two monkeys are situated in adjacent sections of the test chamber, separated by a mesh partition. The apparatus consists of a counter-weighted tray with two pull bars, with each monkey having access to one bar. The bars can be removed. In the solo effort test, two monkeys were in the test chamber, but only one monkey had a pull bar and only this individual's food cup was baited. In the mutualism test, both monkeys were required to pull their respective pull bars, and both food cups were baited. In the cooperation test depicted here, both monkeys were required to pull, but only one individual's food cup was baited. Drawing by Sarah Brosnan.

contrasted collective pulls with solo pulls. Under the latter condition, the partner lacked a pull bar, and the winner handled a lighter tray on its own. We counted more acts of food sharing after collective than solo pulls: winners were in effect compensating their partners for received assistance (figure 3; de Waal and Berger, 2000).

Furthermore, the partner pulled more frequently after successful trials. Since 90 percent of successful trials included food transfers to the helper, capuchins are assisting more frequently after having received food in a previous trial. The simplest interpretation of this result is that motivational persistence results in continued pulling after successful trials. But

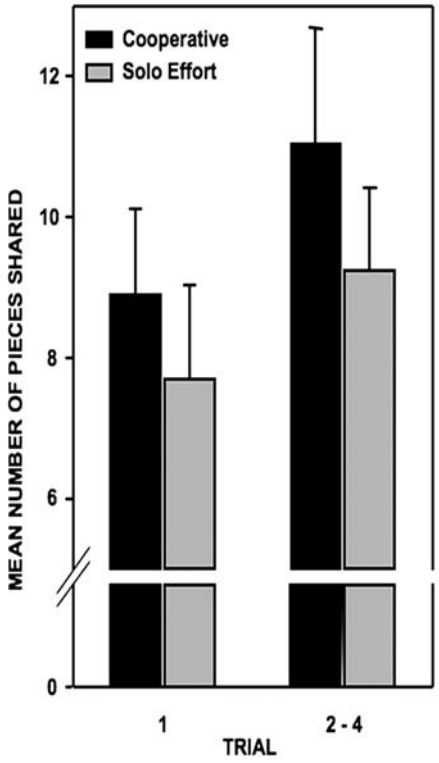

Figure 3 The amount of food sharing in successful cooperation tests (see figure 2) versus solitary controls. The mean number of times the partner collected food items through the mesh was significantly higher after cooperation than when food was obtained without help of the partner. From de Waal and Berger (2000).

a causal connection is also possible—that is, that pulling after successful trials is a response to the obtained reward and the expectation of more.

EXPECTATIONS ABOUT REWARD DIVISION

During the evolution of cooperation it may have become critical for parties to compare their own efforts and payoffs with those of others. Negative reactions may ensue in case of violated expectations. A recent theory proposes that aversion to inequity can explain human cooperation within the bounds of the rational choice model (Fehr and Schmidt, 1999). Similarly, cooperative animals seem guided by a set of expectations about the outcome of cooperation and access to resources. De Waal (1996: 95) proposed a *sense of social regularity,* defined as: "A set of expectations about the way in which oneself (or others) should be treated and

how resources should be divided. Whenever reality deviates from these expectations to one's (or the other's) disadvantage, a negative reaction ensues, most commonly protest by subordinate individuals and punishment by dominant individuals."

The sense of how others should or should not behave is essentially egocentric, although the interests of individuals close to the actor, especially kin, may be taken into account (hence the parenthetical inclusion of others). Note that the expectations have not been specified: they are species typical. Some primates are so hierarchical that the subordinate cannot expect anything from the dominant, whereas in other primates the dominants are prepared to share and, correspondingly, the subordinates have evolved all sorts of strategies (begging, whining) to extract food (de Waal, 1996). These animals negotiate about resources, such as in the following anecdote involving two female capuchin monkeys in the pulling task.

Cooperative pulling was done with two females, Bias and Sammy. In this case, both cups were baited. Sitting in separate sections of the test chamber, they successfully brought the food within reach. Sammy, however, was in such a hurry to collect her rewards that she released the tray before Bias had a chance to get hers. The tray bounced back, out of reach of Bias. While Sammy munched on her food, Bias threw a tantrum. She screamed her lungs out for half a minute until Sammy approached her pull bar again. She then helped Bias bring in the tray a second time. Sammy did not do so for her own benefit, since by now her own cup was empty. Sammy's corrective response seemed the result of Bias's protest against the loss of an anticipated reward. This example shows cooperation, communication, and the fulfillment of an expectation, perhaps even an obligation.

Working with the same capuchin colony, Sarah Brosnan explored reactions to reward division. She would offer a monkey a small pebble, then hold up a slice of cucumber as enticement for returning the pebble. The monkeys quickly grasped the principle of exchange. Placed side by side, two monkeys would gladly alternate exchanges for cucumber. If one of them would get grapes, however, whereas the other

stayed on cucumber, things took an unexpected turn. Grapes are much preferred. Monkeys who had been perfectly willing to work for cucumber, suddenly went on strike.

Each session consisted of 25 exchanges by each individual, and the subject always saw the partner's exchange immediately before their own (figure 4). Among the conditions tested on all subjects were: a) an Equity Test, in which subject and partner did the same work for the same lower-value food; b) an Inequity Test, in which the partner received a superior reward (grape) for the same amount of effort; c) an Effort Control Test, designed to elucidate the role of effort, in which the partner receiving the higher-value grape without any task-performance; and d) a Food Control Test, designed to elucidate the effect of the presence of the reward on subject behavior, in which grapes were visible but not given to another capuchin.

Figure 5 shows that individuals who received lower-value rewards showed both passive refusals (for example, no exchange of the token, ignoring the reward) and active negative reactions (throwing out the token or the reward). Compared to tests in which both received identical rewards, the capuchins were far less willing to complete the exchange or accept the reward if their partner received a better deal (Brosnan and de Waal, 2003). Capuchins refused to participate even more frequently if their partner did not have to work (exchange) to get the better reward, but was handed it for "free." Of course, there is always the possibility that subjects were just reacting to the presence of the higher-value food, and that what the partner received (free or not) did not affect their reaction. However, in the Food Control Test, in which the higher-value reward was visible, but not given to another capuchin, the reaction to the presence of the high-valued food decreased significantly over the course of testing, which is the opposite change from that seen when the high-value reward went to an actual partner. In the latter case, the frequency of refusals to participate rose over the course of testing (Brosnan and de Waal, 2004).

To reject unequal pay—as people do as well—goes against the assumptions of traditional economics. If fitness maximization were all

Figure 4 A monkey in a test chamber returns a token to the experimenter with her right hand while steadying the human hand with her left hand. Her partner looks on. The capuchin does not see the reward she is to receive prior to successful exchange. Drawing by Gwen Bragg and Frans de Waal after a video still.

that mattered, one should take what one can get, and never let resentment or envy interfere. Behavioral economists, on the other hand, assume it is the evolution of emotions that preserves the spirit of cooperation. In the short run, caring about what others get may seem irrational, but in the long run it keeps one from being taken advantage of. It is in everyone's interest to discourage exploitation, free riding, and cheating.

Reciprocity is a vulnerable strategy, hence some sort of enforcement is required. It is a lot of trouble, though, to keep a watchful eye on cheaters and the flow of favors. This is why our own species most of the time relies on simple forms of reciprocity. We form buddy rela-

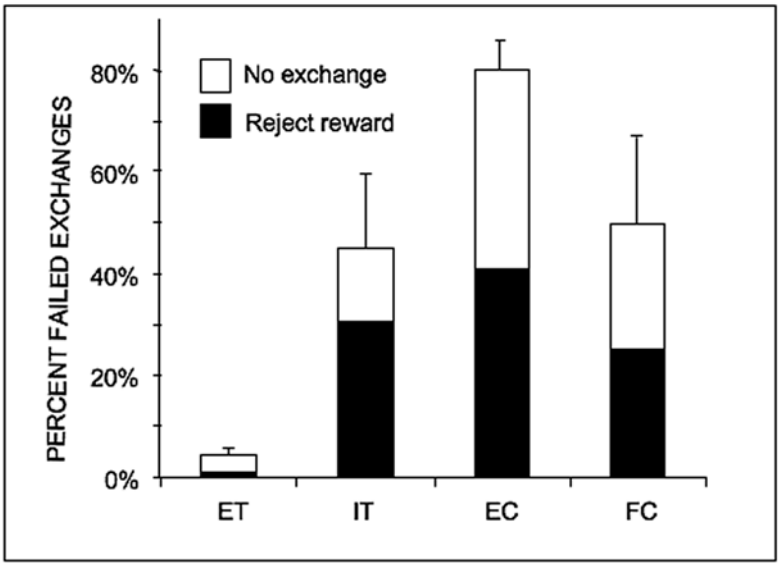

Figure 5 Mean percentage + SEM of failures to exchange for females across the four test types. Black bars (RR) represent the proportion of nonexchanges due to refusals to accept the reward, white bars (NT) represent those due to refusals to return the token. SEM is for combined nonexchanges. ET = Equity Test, IT = Inequity Test, EC = Effort Control, FC = Food Control. The Y-axis shows the percentage of nonexchanges. From Brosnan and de Waal (2003).

tions with partners who have withstood the test of time. With spouses and good friends we relax the rules, and in fact consider keeping track of favors a bad sign reflecting lack of trust. Inequity matters less in these relations. When it comes to distant relations, such as those with colleagues and strangers, on the other hand, we do keep mental records and react strongly to imbalances, calling them "unfair."

Moderately conditional mutual aid is also common in primates, not only among kin but also among close friends and associates. Contingency between given and received benefits decreases with closeness of the relationship. Conversely, the impact of a single act on future exchanges will be greatest in more distant relationships, as we found in our chimpanzees (de Waal, 1997a). Similar issues have been addressed in close versus distant human relationships by Clark and Grote (2003) and Smaniotto (2004).

When we repeated the inequity experiments on chimpanzees, we found indeed the strongest reactions to the exchange task with grapes and cucumber between chimpanzees who were least familiar with each other, whereas the members of a colony that had lived together for over three decades barely reacted at all (Brosnan, Schiff, and de Waal, 2005). Possibly, the greater the familiarity, the longer the time frame over which chimpanzees evaluate their relationships. As a result, they are less affected by day-to-day fluctuations in close relations.

CONCLUSION

The egocentric sense of fairness demonstrated in our primate relatives is merely a fancy description of envy. It is the pain felt at the sight of those better off than we are. This is a far cry from the larger sense of fairness, the one that makes us also worry about those worse off than ourselves. But consider the following anecdote by de Waal (1997b) on bonobos, close relatives of the chimpanzee, used in studies of language:

Sue Savage-Rumbaugh took care of a female, Panbanisha, while the rest of her bonobo colony was being tended by other staff. Panbanisha was receiving different food, such as raisins and extra milk. As Sue brought these goodies to her, the other bonobos saw what was happening and called. They obviously wanted the same stuff. Noticing this, Panbanisha seemed troubled, even though the situation was in her favor. She asked for juice, but when it arrived, instead of accepting it, she gestured to the others, waving an arm in her friends' direction and vocalizing at them. They responded with their own calls and then sat down next to Panbanisha's cage, waiting to get juice, too. Sue said she had the distinct impression that Panbanisha wanted her to bring the others what she herself was getting.

This is not enough to conclude that a sense of fairness exists in other animals, but what fascinates me is the connection with resentment. All one needs for the larger sense of fairness to develop is *anticipation* of the resentment of *others*. There are excellent reasons to avoid arousing bad feelings in those around us. Someone failing to share will be excluded from future feeding clusters. At worst, the one being envied

risks being beaten up. Was this why Panbanisha avoided conspicuous consumption in front of her fellows? If so, we are getting much closer to the source of the fairness principle: conflict avoidance.

From humble beginnings noble principles can arise. I see the evolution of the fairness principle starting with resentment if you get less, then moving to concern about how others will react if you get more, and ending with declaring inequity a bad thing in general. It is through such step-by-step progressions that evolution works. If the goal is to maintain cooperative relationships by ensuring payoffs for everybody, hence a widespread motivation to participate in joint efforts, the evolution of the fairness principle is really not that hard to explain. The parallels between human and animal responses to inequity seem to tell this story. A truly evolutionary discipline of economics recognizes this shared psychology, and considers the possibility that we embrace the golden rule not accidentally, as Hobbes thought, but as part of our background as cooperative primates.

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