

Give unto others: genetically unrelated cotton-top tamarin monkeys preferentially give food to those who altruistically give food back

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Altruistic food giving among genetically unrelated individuals is rare in nature. The few examples that exist suggest that when animals give food to unrelated others, they may do so on the basis of mutualistic or reciprocally altruistic relationships. We present the results of four experiments designed to tease apart the factors mediating food giving among genetically unrelated cotton-top tamarins (*Saguinus oedipus*), a cooperatively breeding New World primate. In experiment 1 we show that individuals give significantly more food to a trained conspecific who unilaterally gives food than to a conspecific who unilaterally never gives food. The apparent contingency of the tamarins' food-giving behaviour motivated the design of experiments 2–4. Results from all three experiments show that altruistic food giving is mediated by prior acts of altruistic food giving by a conspecific. Specifically, tamarins do not give food to unrelated others when the food received in the past represents the by-product of another's selfish actions (experiments 2 and 3) or when a human experimenter gives them food (experiment 4) as did the unilateral altruist in experiment 1. By contrast, if one tamarin gives another food without obtaining any immediate benefit, then the recipient is more likely to give food in return. Overall, results show that tamarins altruistically give food to genetically unrelated conspecifics, discriminate between altruistic and selfish actions, and give more food to those who give food back. Tamarins therefore have the psychological capacity for reciprocally mediated altruism.

Keywords: reciprocal altruism; intentionality; contingency; evolution; primates; cooperation

1. INTRODUCTION

Trivers (1971) proposed that genetically unrelated individuals can maintain a stable system of cooperation so long as they engage in reciprocal altruism. Field and laboratory studies of vampire bats, baboons, vervet monkeys, chimpanzees and guppies (Packer 1977; Seyfarth & Cheney 1984; Wilkinson 1984, 1987; Millinski 1987; de Waal 1989) appeared to provide early support for Trivers' intuition. More recent studies and analyses have raised questions about the empirical work (Pusey & Packer 1997; Noë *et al.* 2001). Specifically, although work on jays (Stephens *et al.* 2002) and capuchins (de Waal 2000) provides some evidence for cooperation among genetically unrelated individuals, other studies have either failed to replicate the earlier findings (Bercovitch 1988; Noë 1990; Hemelrijk & Ek 1991) or have demonstrated that the pattern of altruistic behaviour can be better accounted for by by-product mutualism or some other form of indirect reciprocation (Connor 1995, 1996; Stephens *et al.* 1997); but other work has explicitly shown that reciprocal altruism is unstable and rare (Reboreda & Kacelnik 1993; Clements & Stephens 1995; Heinsohn & Packer 1995). If reciprocal altruism is a weak mechanism in animal societies, then its presence in humans suggests a unique and critically important evolutionary innovation, one that may have emerged as a result of differences in the requisite

psychological mechanisms as well as the socioecological pressures on human social organization (Hill 2002).

The primary goal of the present work is not reciprocal altruism *per se*, but rather some of the necessary psychological mechanisms. We argue that a critical first step in understanding reciprocation is to show that animals distinguish between altruistic and selfish actions. We therefore focus on the mechanisms underlying food giving among genetically unrelated cotton-top tamarins to clarify some of the necessary psychological prerequisites for the evolution of reciprocal altruism. Our experiments provide three main contributions to the growing literature on cooperation. First, we present a clear example of altruistic food giving among unrelated individuals. This is important given the relative rarity in the animal kingdom of food giving among non-kin (Stevens & Gilby 2003), and the significance of food sharing in human evolution (Isaac 1978; Blurton-Jones 1984, 1987; Hawkes *et al.* 1991; Hill & Kaplan 1993; Wrangham *et al.* 1999; Hames 2000; Hill 2002). Second, we provide evidence that tamarins are more likely to give food to a conspecific who unilaterally gives food back as opposed to a conspecific who unilaterally refrains from giving food; this suggests that food giving may be based on contingent behaviour. Third, we show that tamarins distinguish between altruistic food giving as opposed to by-products of selfishness or simple reinforcement contingencies; individuals are more likely to give food to an individual who has altruistically given food in the past than to individuals who give food as a result of selfish attempts to procure their own food.

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2. GENERAL METHODS

(a) Subjects

Cotton-top tamarins are cooperative breeders, native to the rainforests of Colombia (McGrew & Feistner 1992). Each group member helps rear the young, which involves food sharing, carrying, and defence against predation. Test subjects were all born in captivity and live in social groups consisting of a breeding pair and in some cases, one or two sets of offspring. All experiments involved five to seven genetically unrelated adults; during tests, we paired individuals from different cages.

All subjects had participated in earlier experiments on vocal communication, speech perception, object perception, number and tool use. Of most direct relevance to the current experiments, and in particular the set-up described below, are the string of studies on tool use that involve pulling an object to obtain a distant piece of food (Hauser 1997; Hauser *et al.* 1999, 2002).

(b) Apparatus and set-up

The apparatus consisted of a tray with an inverted L-shaped tool (figure 1a). When food was on the actor's side, pulling the tool's stem brought the food within reach. The central measure in these experiments is, therefore, the actor's pulling behaviour, both the number of pulls and their temporal patterning in relation to their partner's behaviour.

For each trial, an experimenter presented the tray in view, but out of reach, thereby enabling each player to see the set-up. Subsequently, the tray was placed in position and left in this position for up to 3 s. If the actor pulled within 3 s, the experimenter removed the tray; if the actor failed to pull within the 3 s period, the tray was removed. We filmed all trials.

For each session (see § 2c), we used a random number generator to determine the order of conditions within session, which individuals would be paired up, which player would have access to the tool first, and for experiment 3, the player-specific pay-offs; in paired tests, a player with access to the tool on the first trial of session 1 started session 2 as the recipient (i.e. the second player started with the tool on session 2).

(c) Solo sessions

Before experiment 1, and in between all paired sessions of each of the subsequent experiments, we tested all focal subjects alone on sessions of 24 trials each (figure 1b). There were two treatment factors: barrier and reward. On sessions when the barrier was present (A), subjects were presented with an approximately equal number of trials in which they could obtain a food reward (A1, A2) as trials in which they could not (A3, A4). Similarly, when the barrier was absent (B), subjects received trials in which they could obtain food (B1–B3) and trials in which they could not (B4). For our experimental cooperation games, the main interest is condition A3, which we consider the altruistic food-giving condition.

All five subjects alternated solo barrier and no-barrier sessions on consecutive days, continuing to run until they reached criterion. A criterion was defined as always pulling on conditions A1, A2, B1, B2 and B3, but never on A3, A4 and B4. Some animals reached criterion in as little as three weeks, whereas others required 8–12 weeks. Once subjects reached criterion they were run on one final solo barrier session, in which an unrelated animal was placed next to the test chamber but not in the adjacent compartment. This condition was run to assess whether the presence of another individual would cause subjects to pull

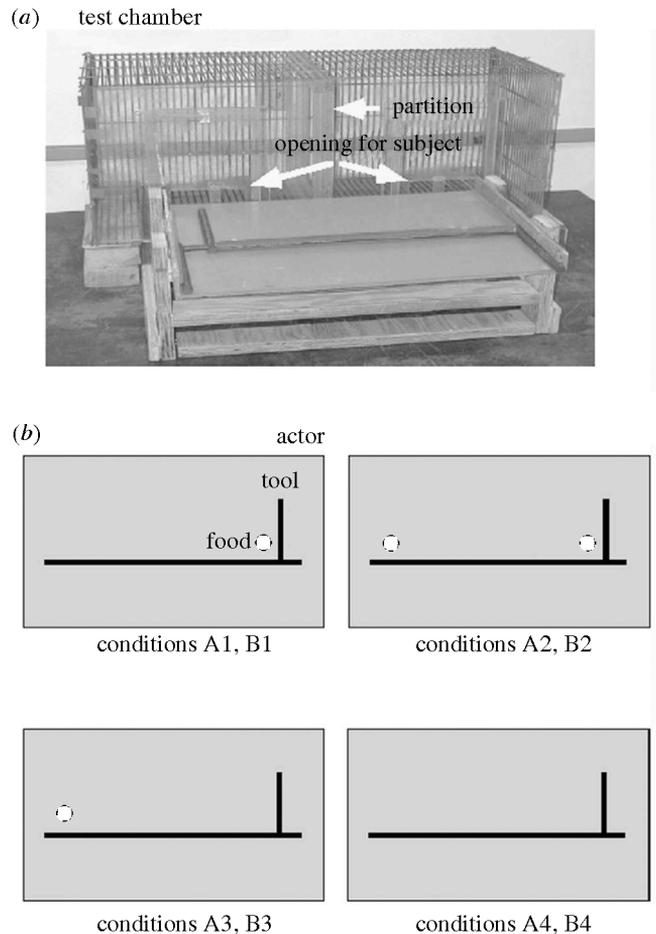


Figure 1. (a) Apparatus for solo and cooperation set-ups. (b) Conditions for solo and cooperation experiments (A, with barrier; B, no barrier).

on condition A3. Subjects never pulled on this condition. The fact that individual tamarins do not pull the tool when they are unable to obtain food for themselves suggests that there is some cost to pulling.

In between paired sessions of each experiment, each player ran a solo barrier session. If subjects failed to reach criterion on solo runs, they were re-run; in over 95% of solo runs, actors performed as predicted.

3. EXPERIMENT 1

Experiment 1 was designed to assess whether tamarins will give food to a familiar, but unrelated conspecific, and discriminate between individuals who give food and those that do not. Although prior work reveals that tamarins recognize individuals by voice (Weiss *et al.* 2001), the following experiment was designed to assess not only that they recognize individuals, but that they identify and recall individuals in terms of their cooperativeness or tendencies to give food, and give more food to those that have given food to them in the past. Evidence of identification, recall and contingent actions represent critical ingredients of reciprocally altruistic relationships.

(a) Methods

We tested five cotton-top tamarins, three adult females (UB, EN and EM) and two adult males (SP and ID). Each of these

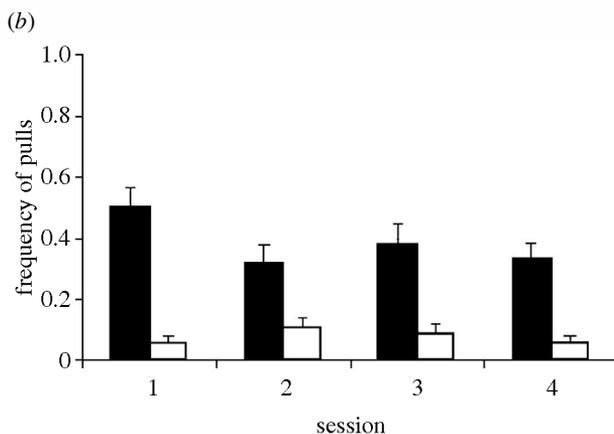


Figure 2. (a) Illustration of an actor pulling the tool to give food to a recipient. (b) Mean (s.e.m.) frequency of pulls by non-stooge subjects ($n = 5$) for the altruist stooge (black bars) and defector stooge (white bars) across the four sessions of play.

subjects played against one of two tamarin stooges: a unilateral 'altruist' trained to pull on every trial and a unilateral 'defector' trained to refrain from pulling on every trial. Both stooges were adult females living in different cage groups, and unrelated to all test animals.

Each subject played alternating 24-trial sessions with the altruist and defector for a total of four sessions with each; we randomly assigned three subjects to start with the altruist and two with the defector. Of these initial assignments, the stooge started with access to the tool on the first trial for half of the sessions. Although it would have been desirable to use multiple stooges of each type, this proved impossible as these were the only subjects in the colony to consistently act in the same way each session, independent of opponent.

(b) Results and discussion

Across all four sessions, subjects pulled (figure 2a) significantly more often for the altruist ($X = 38\%$) than for the defector ($X = 7\%$; $z = 8.17$, $p < 0.00005$, $n = 480$; figure 2b). All five subjects showed this effect independently of whether they started with the altruist or defector. This pattern holds even when we analyse only the first trial of sessions 2, 3 and 4, when the subject had not yet played with the stooge that day (83% for the altruist, 30% for the defector; $z = 2.53$, $p = 0.01$, $n = 22$). This suggests that subjects discriminate between stooges, even in the absence of immediate prior experience. For sessions with the altru-

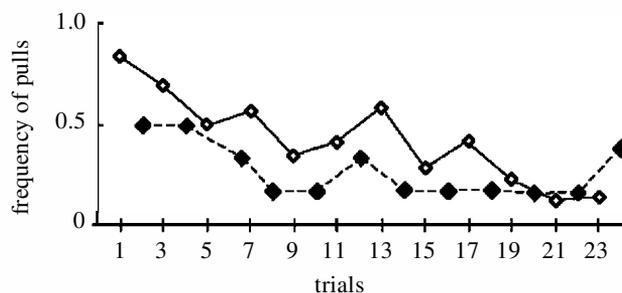


Figure 3. Mean frequency of pulls by non-stooge subjects with the altruist, comparing sessions where the non-stooge pulled first (all odd trials, open diamond and solid line) with sessions where the altruist pulled first (even trials, filled diamond and dashed line).

ist, there is a significant decrease in pulling across trials within session ($F = 25.23$, $p < 0.00005$, d.f. = 1), but no significant change across sessions ($F = 2.06$, $p = 0.11$, d.f. = 3); excluding the first session, the non-significant decrease across sessions disappears completely ($F = 0.26$, $p = 0.77$, d.f. = 2). The drop within session—common in almost all repeated games of human cooperation—combined with between-session stability, suggests that subjects may estimate the end of the game, dropping the level of food giving towards the end when there is perhaps less cost, and then increasing again for each new session. The lack of a drop across sessions is somewhat unexpected given that the stooge is a unilateral cooperator. Subjects may require additional sessions to recognize the stooge's consistency, or may simply display a baseline propensity to reward generous behaviour in addition to reciprocal tendencies; we return to this first possibility in the subsequent experiments. Subjects showed no trends within or across sessions for the defector.

One explanation for the differential food giving is that subjects simply acquire a rule: pull for the altruist and not for the defector. If this is the case, our experiments provide little evidence for contingent food giving. As a first step in addressing this possibility, we looked at sessions with the altruist, contrasting cases where the non-stooge subject had an opportunity to pull first or second. Figure 3 reveals that non-stooge subjects give more food in sessions where they pull first and the altruist responds (43%) than when the altruist pulls first (26%, $z = 2.49$, $p = 0.001$, $n = 240$). It appears that when the altruist pulls second, the subject reacts to this pull as a contingent exchange, and this elevates the overall level of food giving. Additional support for this interpretation comes from looking at only those sessions in which the non-stooge subject pulled first, followed by the altruist stooge in trial two, then again by the subject in trial three. If the altruist's trial two pull followed a trial one pull by the subject, subjects overwhelmingly pulled in trial three (83%). By contrast, no subject pulled in response to an altruist pull when the subject had not pulled in trial one (0%, $z = 2.42$, $p = 0.02$, $n = 14$). Although it is not possible to completely control for individual session-specific heterogeneity in pulling, these analyses support the hypothesis that subjects respond differently to an altruist's actions when it was contingent.

Results provide evidence that tamarins give food to genetically unrelated conspecifics without obtaining an

immediate benefit. We describe this act as altruistic because there is an energetic cost involved in pulling the tool, no immediate benefit to self, but a direct benefit to the recipient. Further, when subjects are alone, they do not pull the tool if the food is inaccessible, and they rarely pull for the defector; work in progress aims to quantify the costs and benefits of this action by placing weights on the tool (increasing costs) and manipulating the pay-offs to the recipients. The fact that subjects rapidly discriminated between the altruist and defector, raises the possibility that cooperation may depend on the reputation or image scores of other players, as it does in human games of cooperation (Nowak *et al.* 2000; Milinski *et al.* 2002). Minimally, it shows that tamarins discriminate among individuals based in part on information about their reinforcement or food-giving history.

4. EXPERIMENT 2

Experiment 1 suggests that tamarins give more food to an unrelated individual if that individual gives food back. This raises the hypothesis that food giving in tamarins depends upon the perceived motivations of other individuals, and especially, that food is given at some cost to the giver. An alternative hypothesis is that food giving in tamarins is simply influenced by a history of reinforcement. Said simply, a tamarin is more likely to pull the tool and give food to another if it has received food in the past, independently of how it obtained such food. If this hypothesis is correct, then tamarins would be as likely to pull the tool in the A3 condition when they received food from a machine, a human or a tamarin who delivered food as a mere by-product of otherwise selfish actions. Experiments 2–4 are designed to evaluate these alternative explanations. In experiment 2, we explicitly ask whether the level of altruistic food giving between untrained tamarins is elevated by a period of food exchange that results from mutualistic actions.

The design of experiment 2 was based on pilot data suggesting that altruistic food giving among untrained (non-stooges) and unrelated tamarins tends to decrease across sessions when the same pair plays (E. Chuang, unpublished data). Our goal, therefore, was to quantitatively test for decreases in food giving over repeated plays of the same game within a pair, and to determine whether increasing the pay-offs associated with food giving would reverse the downward trend leading to higher levels of food giving.

(a) Methods

We tested the same five cotton-top tamarins as in experiment 1. The interval of time elapsed between this experiment and the previous one was approximately one month.

Each of the five actors played a game consisting of five sessions; each actor played a total of three games, one against each of the genetically unrelated, non-cage mates. Sessions 1, 2, 3 and 5 consisted of 24 trials of the altruistic food-giving condition (figure 1*b*, condition A3). In session 4, we altered the pay-off structure such that pulling the tool brought one piece of food for the recipient and one for the actor (figure 1*b*, condition A2); we call this the by-product food-giving condition. For all five sessions the tool alternated between players on every trial so that each player had 12 opportunities to pull within a session.

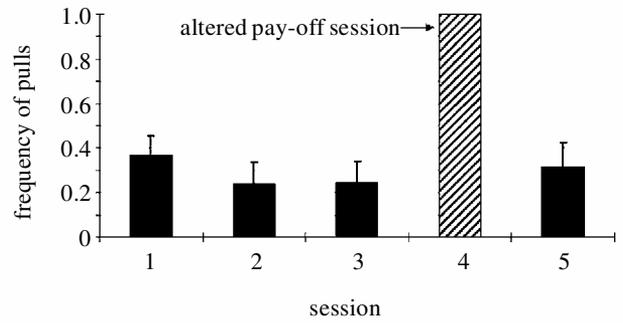


Figure 4. Results from experiment 2 in which subjects played three sessions of condition A3 (actor pulls and gives food to recipient but obtains none, solid black bars), a fourth session of condition A2 (pulling brings food to the actor and opponent, hatched bar) and a final session of condition A3. Data plotted are mean (\pm s.e.) frequency of pulls.

We expected cooperation to decline from session 1 to 3. In session 4, we expected both players to pull on every trial because they would gain a piece of food, and also give one to their opponent. Assuming 100% pulling in session 4 due to mutualism, we can then ask how each player perceives this round. If subjects perceive such actions as altruistic, then we would expect a significant increase in the frequency of pulls in session 5 over the level of pulling in session 3. By contrast, if subjects perceive the pattern of pulls in session 4 as by-products of selfish behaviour, then the frequency of pulls in session 5 should either decrease or stay the same relative to session 3.

For the purposes of modelling, sessions 1 to 3 are played as finite repeated games in which player 1 (and then 2) may pay cost c to give player 2 (player 1) pay-off m , presumably with $m > c$. This stage game is repeated 12 times each session, with subjects switching roles between sessions. To study the effect of the fourth session we ran a Probit regression on sessions 1 to 3 and 5. We cluster on subject so that our estimates are robust to assumptions about intra-subject correlation. Estimating the equation:

$$\Pr(\text{pull} \neq 0) = \Phi(\beta_1 \times \text{trial} + \beta_2 \times \text{session 1} + \beta_3 \times \text{session 2} + \beta_4 \times \text{session 5} + c),$$

we report coefficients transformed at the mean. Our session variables are all dummies, and again we cluster by subject.

(b) Results and discussion

Analyses (figure 4) reveal coefficients on trial, session 1, session 2, and session 5: -0.0096 ($p = 0.012$), 0.125 ($p < 0.0005$), -0.003 ($p = 0.97$) and 0.0735 ($p = 0.29$, $n = 792$), respectively. These values indicate a significant drop in pulling from sessions 1 to 3 whereas the coefficient on 'session 5' (i.e. the change from session 3 to 5) is not significant: in other words, the fourth session did not cause a significant increase in subject's fifth session pulling. This provides support for the hypothesis that freely behaving tamarins distinguish between altruistic acts of food giving and by-products of selfish behaviour. Specifically, tamarins do not increase the level of altruistic food giving simply because they have received food in the past. Rather, to impact upon the level of altruistic food giving, it appears that prior actions must also be altruistic.

5. EXPERIMENT 3

Experiment 1 suggests that tamarins pulled at a high rate (38%) for a trained unilateral altruist who always pulled, but rarely pulled (7%) for a trained unilateral defector who never pulled. Results from experiment 2 suggest that the mere procurement of food from another conspecific is insufficient to increase the level of food giving. Together, these results raise a further question: does the kind of contingent behaviour observed depend on the perceived motivation for pulling? More specifically, does the level of contingent pulling depend on the rewarding experience of receiving food from a partner independently of whether the partner pulls while incurring a cost (altruistic) or a benefit (by-product mutualism)? To test between these alternative explanations, we set up a game in which one player's pulls are mutually rewarding, while the other player's pulls are singularly altruistic.

(a) Methods

Two of the adult females (UB and EN) and one of the adult males (SP) from experiment 2 participated in experiment 3. We added on a second mated pair, adult male PB and adult female RB, and gave these subjects training on solo sessions until they reached criterion.

In experiment 3, only two aspects of our method changed from experiment 1: only non-stooge tamarins played, and we altered the pay-offs for each player. When player 1 (P1) pulled, he/she obtained a piece of food and gave three pieces to player 2 (P2). By contrast, when P2 pulled, he/she obtained no food but gave two pieces to P1. Consequently, if both players pulled on their respective turns, each received a total of three pieces after one round. When P1 pulled, however, he/she obtained food for this action. By contrast, when P2 pulled he/she obtained no food. Given that P1 was expected to pull on every trial for selfish reasons alone, the crucial question underlying the design of this experiment is: does P2 perceive P1's pulling as selfish or altruistic? More to the point, does the contingent pulling observed against the unilateral altruist in experiment 1 depend on the perceived cause of the altruist's behaviour? If giving food to another depends on having received food in the past, independently of the perceived motivation and costs associated with prior giving, then P2 should pull at high rates. By contrast, if giving food depends on having received food from an individual who altruistically incurred the costs of pulling but received no immediate benefits, then P2 should rarely if ever pull for P1.

Each subject played a total of four sessions in either the P1 or P2 position before switching to a new partner and the alternative position. Each session consisted of 24 trials, with the tool alternating between players on every trial so that each player had 12 opportunities to pull within a session. Across the four sessions within each block, the players' roles as P1 and P2 remained constant. For the first session of each block, the players' respective positions on the right and left sides of the barrier were randomly determined, along with who would be given access to the tool on the first trial. These variables alternated after every session. After completing a block of four sessions, the players switched to new partners and alternate roles. Thus, over the course of the experiment, each subject played P1 and P2 at least once, and was paired against partners of both the same and opposite sexes, but always genetically unrelated individuals from a different cage. A total of eight blocks (32 sessions) were completed, plus two control blocks (eight sessions) that were identical to the other eight except that the pay-off on every trial consisted of

one piece of food for the actor and three for the recipient; the assumption underlying these control trials is that because food is available for both players on each trial, subjects will always pull when they have access to the tool.

(b) Results and discussion

Results suggest that subjects are indeed sensitive to the costs borne by their partners when deciding whether to pull. P1 subjects almost always pulled the tool, providing P2 with food in 97% of 384 trials. In this regard they behaved similarly to the trained altruists in our previous experiment, except that they pull in the presence of an immediate reward. Despite this, subjects playing P2 pulled only 3% of the time, compared with an average of 38% for the unilateral altruist in experiment 1. Both collectively and separately for each actor, this difference is statistically significant using a two-sample *z*-test for different means ($p < 0.0005$). Indeed, P2 subjects' overall pulling levels were significantly less than even the pulling they had earlier demonstrated when partnered with the trained defector in experiment 1. These results suggest that subjects discriminate between altruistic acts of pulling and by-product mutualism or pulling motivated by personal reward.

6. EXPERIMENT 4

All three experiments presented thus far suggest that tamarins are more likely to give food to another if their partner has altruistically given food to them in the past. There is, however, an alternative explanation that cannot yet be ruled out, and that plagues several other studies of cooperation in animals (de Waal 2000; Stephens *et al.* 2002; de Waal & Davis 2003). Specifically, it is possible that tamarins, and perhaps other animals as well, would show the same levels of altruism if they played against a human or machine that contingently rewarded such actions. For example, in work on jays, it is not yet clear whether the patterns of cooperation demonstrated between conspecifics would be replicated by a jay playing against a machine offering comparable levels of reward. The same argument applies to tamarins playing the unilateral altruist in experiment 1. Specifically, does it matter to the recipient that the food obtained comes from a tamarin or can simple contingent reinforcement trigger altruistic food giving independently of the source of such reinforcement? Here, we test this hypothesis by allowing a human experimenter to substitute in for the unilateral tamarin altruist, thereby replicating the pattern of reinforcement but not its source.

(a) Methods

This experiment was designed so that the conditions of the test session would exactly match the 'altruist' test sessions of experiment 1, except that a passive partner (PP) who incurred no costs replaced the altruist as the test subject's (TS) partner. The critical condition involved flipping the tool handle over towards the experimenter and out of PP's reach. One piece of food was placed on the side opposite the tool handle, thus mimicking the A3 condition. Whenever this condition was presented, the human experimenter pushed the bar so that TS could reach the food. If pulling in the A3 condition is driven primarily by the procurement of food, then TS should pull at a rate compara-

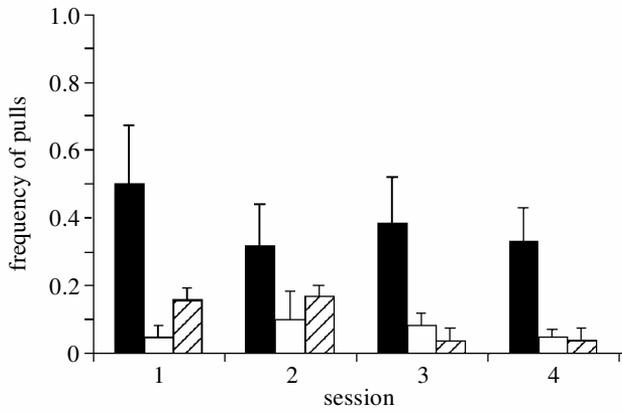


Figure 5. Combined results from experiments (black bars, pulls for altruist; and white bars, pulls for defector) and 4 (hatched bars, pulls for human). Presented are mean (s.e.m.) frequency of pulls.

ble to that observed by subjects playing the unilateral altruist in experiment 1. By contrast, if pulling in the A3 condition depends on playing with a partner who pulls altruistically, then TS should pull infrequently, at a rate that approximates subjects' pulling with the unilateral defector in experiment 1.

The test subjects used were three males (SP, PB and ID) and three females (EN, RB and EM). The passive partners were two males (RW and DD) and one female (SH). PP training sessions consisted of 12 trials in which the experimenter pushed the bar towards the apparatus.

In test sessions, the tool handle again alternated sides after every trial so that each actor had 12 trials with the tool handle on his side. TS received all A3 condition trials; PP received all modified versions of the A3 condition with the tool flipped. During tool flipped condition trials, the experimenter waited until TS's attention was focused on the tray and the experimenter before pushing the bar towards the apparatus.

(b) Results and discussion

In contrast to experiment 1, where TS pulled 38% of the time for the unilateral altruist, in this experiment TS pulled only 10% of the time (48 out of 480 trials); this pattern was consistent across all individuals. This rate of pulling is significantly different from the altruist sessions in experiment 1 ($z = -12.63$, $p < 0.0005$, $n = 480$). Further, the pulling rates in experiment 4 are only slightly, though significantly, higher from the 7% rate for which they pulled for the defector in experiment 1 ($z = 2.18$, $p = 0.03$, $n = 480$). Subjects' patterns of pulling were, therefore, more similar to those observed against the defector in experiment 1 than the altruist.

Similar to experiment 1, subjects displayed a significant drop of 12.5% in pulling between the first two sessions and the last two ($z = 4.56$, $p < 0.0005$, $n = 480$), but no drop between sessions 3 and 4 ($z = 0.03$, $p = 0.976$, $n = 240$; figure 5). Within the last two sessions there was also no significant decrease in pulling across trials ($F = 3.23$, $p < 0.07$, d.f. = 1). These results are consistent with our findings in experiment 1. The initial drop between sessions is consistent with subjects requiring some experience before recognizing the non-contingent nature of their rewards; eventual between and within session stability suggests that subjects have learned that they are rewarded regardless of their behaviour, and that sub-

jects do not attribute these rewards to their partners. Indeed, in the final two sessions subjects pulled only 3.75% of the time, even less than they pulled for the defector in experiment 1 ($z = 1.97$, $p = 0.02$, $n = 240$). This suggests that at least some of the pulling for the defector in experiment 1 may have been selfishly motivated by an attempt to get her to pull, as opposed to an altruistic food giving.

These results provide further evidence that tamarins distinguish altruistic actions from other actions that result in food disbursement. They further show that high levels of reinforcement are not sufficient to engage high levels of food giving. Not only does the action of food giving appear to require a cost, or at least no immediate benefit, but such cost-benefit consequences have to be borne by a conspecific. Future work will assess whether tamarins would act in the same way towards a more closely related heterospecific (e.g. other New World monkeys) as well as to a conspecific that is out of view.

7. GENERAL DISCUSSION

Results from four experiments show that tamarins give food to genetically unrelated conspecifics from different groups, even though they obtain no immediate benefit from doing so. Also, tamarins distinguish between altruistic and selfish actions. In experiment 1, we showed that tamarins were more likely to give food to a unilateral altruist than to a unilateral defector. These results cannot be accounted for by a simple reinforcement hypothesis as evidenced by the results from experiments 2–4. Specifically, in experiment 2 we showed that if subjects play a game in which giving food to another is also self-rewarding, such actions fail to raise the level of altruistic food giving. In other words, tamarins appear to recognize this game as an instance of by-product mutualism as opposed to altruism in which giving food to another yields no direct benefit. In experiment 3 we showed that although one player (P1) consistently rewarded the other (P2) by pulling the tool, the food given was a by-product of otherwise selfish actions to obtain food. As a result, the second player, P2, did not give food to P1. In experiment 4 we showed that if the test subject was always rewarded with food by a human experimenter on the trial following its turn with the tool, thereby mimicking the set-up in experiment 1 with the unilateral tamarin altruist, that low levels of altruistic pulling ensued; the levels of pulling were comparable to those involving the unilateral defector in experiment 1. This result shows that reinforcement with food is not sufficient to engage altruistic food giving in tamarins; what is apparently needed to engage this system is a tamarin that pulls food for another in the absence of receiving a direct, immediate benefit.

These results add to the growing literature on altruistic actions in animals in several significant ways. First, there are few clear cases of altruistic food giving among unrelated animals, especially when contrasted with cases of tolerated food taking or sharing (de Waal 1989, 2000; de Waal & Berger 2000; de Waal & Davis 2003). The few cases that do exist have been explained by appealing to the theory of reciprocal altruism (Wilkinson 1984, 1987). Minimally, the experiments presented here show that tam-

arins will give food to unrelated conspecifics without receiving an immediate benefit.

Our results also enabled us to show that tamarins discriminate between altruistic and selfish actions, attending to the specific details of conspecific behaviour as opposed to more general patterns of reinforcement. This is important, and stands in contrast to some of the recent work on cooperation in jays and capuchins in which it is not yet clear whether comparable patterns of behaviour would be observed with a reinforcement machine. We raise this point not to undermine the significance of the findings on these other species, but rather to highlight the fact that in the case of tamarins, a distinction is made between general reinforcement and reinforcement provided by a conspecific. Similar effects should be explored in other animals.

Finally, results on tamarins provide an ideal situation in which to explore reciprocal altruism as many of the key psychological ingredients are already in place. In particular, there is evidence of individual recognition, including the possibility that tamarins attribute reputations or image scores to others. In experiment 1, tamarins readily discriminated between a stooge who always gave food and a stooge who never gave food. Given this discrimination, it is now possible to explore whether tamarins recall such attributes, and use them in future interactions, as appears to be the case in capuchins (de Waal 2000). Results from all four experiments suggest that the pattern of pulling is contingent on what other tamarins do. Contingency is central to reciprocation. Tamarins also show sensitivity to altruistic as opposed to selfish actions. Said differently, they discriminate between intentional acts of food giving and by-products or accidents of otherwise selfish behaviour. In humans, at least, this capacity is central to all sorts of morally relevant behaviour. Last, given the general structure of the method employed, it is now possible to explore how different pay-offs, costs and game structures influence the dynamics of food giving, enabling the use of game theoretic models to assess the kinds of underlying strategies available and employed to achieve stable levels of cooperation. Together with recent findings in jays and capuchins, our results suggest that human cooperation may have evolved from psychologically ancient mechanisms, present in both closely and distantly related animals (see Millinski 1987; Dugatkin 1997; Hrdy 1999; Hauser 2000; de Waal & Davis 2003).

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