Chimpanzees are vengeful but not spiteful

Keith Jensen*, Josep Call, and Michael Tomasello

Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, D-04103 Leipzig, Germany

Communicated by Raghavendra Gadagkar, Indian Institute of Science, Bangalore, India, June 15, 2007 (received for review January 3, 2007)

People are willing to punish others at a personal cost, and this apparently antisocial tendency can stabilize cooperation. What motivates humans to punish noncooperators is likely a combination of aversion to both unfair outcomes and unfair intentions. Here we report a pair of studies in which captive chimpanzees (*Pan troglodytes*) did not inflict costs on conspecifics by knocking food away if the outcome alone was personally disadvantageous but did retaliate against conspecifics who actually stole the food from them. Like humans, chimpanzees retaliate against personally harmful actions, but unlike humans, they are indifferent to simply personally disadvantageous outcomes and are therefore not spiteful.

cooperation | fairness | other-regard | punishment | reciprocity

People will willingly suffer a cost to punish others. Although this does not sound like a formula for cooperation, something that humans are exceedingly good at, theoretical models and experimental evidence show that in the absence of punishment, cooperation does not survive the degrading influence of free-riders (1). Punishment, in the biological sense, is a strategy that decreases the occurrence of a behavior, and it is typically selfish in that it provides a future benefit for the individual such as the reduction of harmful behavior received from others (2)[†]. Punishment can make an act of spite, incurring a cost to impose a cost on another individual, beneficial in the long run and is therefore a means to an end. Spite, on the other hand, is the decreasing of the welfare of another individual as an end in itself, just as proximate-level altruism has increasing the welfare of another as the ultimate end (3). Negative reciprocity makes spite selfish just as positive reciprocity does for altruism (4). We use the term "spiteful" for proximate-level spite to distinguish it from ultimate-level spite[‡].

A special form of punishment has been revealed in economic experiments such as the ultimatum and public goods games. This "altruistic punishment" (7) provides benefits in the form of increased cooperation to others, whereas the punisher alone bears the costs. It could be argued that on a short time-scale, such unselfish punishment is spitefully motivated, and altruistic outcomes are an unintended byproduct; to our knowledge, the underlying motivations behind altruistic punishment remain to be shown. What might motivate punitive and possibly spiteful behaviors is that, instead of acting solely selfishly and counting only one's own gains and losses, people appear to compare their outcomes with those of others and appraise the motives behind the actions of others. The punishment of others based on unfair outcomes (8, 9) or intentions (10–13) has been argued to be a central and possibly unique feature of human cooperation.

There is currently controversy about whether nonhuman primates also have a sense of fairness (in the sense of personally disadvantageous outcomes). Capuchin monkeys (*Cebus apella*) and chimpanzees (*Pan troglodytes*) reject food offered by experimenters when conspecifics receive better food, perhaps because they perceive the situation as unfair (14, 15). However, other studies suggest alternative explanations other than a sense of unfairness (16–19). For instance, great apes beg more for food when there is an expectation that an experimenter will give them better food when she gives it to a partner (19). These studies call into question whether non-human primates are averse to personally disadvantageous outcomes. Two further studies have even challenged whether chimpanzees are other-regarding when they can control the outcomes themselves. When chimpanzees had the opportunity to deliver cost-free benefits to conspecifics, they failed to show other-regarding preferences (20, 21). One of these studies also gave the chimpanzees the opportunity to control personally disadvantageous outcomes by acting spitefully, and their disinclination to do so led to the conclusion that our closest living relatives are not other-regarding (21). Nonhuman animals do retaliate against others, and this can serve, among other things, to maintain cooperative behavior (2, 22–24). However, it is not known whether animals other than humans react to harmful actions directed toward them by retaliating against the perpetrator, and whether they react to disproportionate outcomes by behaving spitefully toward the fortunes of others.

Results and Discussion

Here we report two studies in which chimpanzees had the opportunity to respond to different personally disadvantageous situations by inflicting costs on conspecifics. In a first study, chimpanzees were given the opportunity to prevent a conspecific from eating at no benefit to themselves, that is, spitefully. This is similar in spirit to a "money-burning" game in which human adults could pay to reduce the amount of money held by another individual either out of envy or a sense of fairness (25). Two separate groups of chimpanzees (A group, $n = 9$; B group, $n = 4$) were tested in dyads within their groups. There were four conditions, with order counterbalanced across subjects. In the partner-feeding test condition, an actor and a partner were in adjacent cages and faced each other across an inaccessible space in which a food table stood. The partner could reach the food through a mesh panel; the actor could not reach the food, but she could pull a rope, causing the table to collapse and the food to fall beyond the reach of both of them. We compared this condition to three others. In the baseline condition (two versions), there were pieces of plastic and inedible bamboo stems on the table and no partner, to measure the general tendency of chimpanzees to pull the table over. In the self-feeding control condition, the actor could eat the food on the table, to measure the ability to inhibit pulling when it was not sensible to do so. In the nobody-feeding control condition, food was on the table, but there was no partner present, to measure general frustration at being unable to access out-of-reach food.

All chimpanzees collapsed the table and therefore had experience with the consequences of pulling the rope. Furthermore, in the self-feeding control condition, chimpanzees collapsed the table they were eating from in only 3% of trials, showing they

Author contributions: K.J., J.C., and M.T. designed research; K.J. performed research; K.J. analyzed data; and K.J., J.C., and M.T. wrote the paper.

The authors declare no conflict of interest.

*To whom correspondence should be addressed. E-mail: jensen@eva.mpg.de.

[†]We use synonyms for punishment, such as retribution, retaliation, and vengeance, to avoid confusion with the various uses of punishment in evolutionary biology, social psychology, and experimental psychology.

[‡]True spite, in which there are no direct future fitness benefits to the actor, can theoretically evolve but only in very limited circumstances (5, 6).

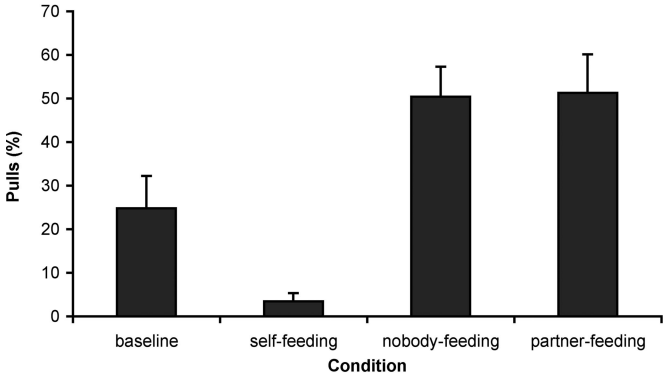

Fig. 1. Mean percentage of trials (±SEM) in which chimpanzees collapsed an inaccessible food table (Study 1). In the baseline, plastic pieces were on the table; in the self-feeding condition, food was accessible to the actor; in the nobody-feeding condition, food was inaccessible, and no partner was present; and in the partner-feeding condition, food was accessible to the partner but not to the actor.

could inhibit pulling. Across the four conditions, chimpanzees behaved differently (Friedman's $\chi^2_3 = 23.54$, $P < 0.001$; Fig. 1), and this was the same for each of the two groups. In the two conditions in which food was out of reach, presumably evoking frustration, they were more likely to collapse the table than in the baseline in which no food was involved (nobody-feeding, Wilcoxon $T^+ = 88.00$, $n = 13$, $P = 0.001$; partner-feeding, $T^+ = 88.00$, $n = 13$, $P = 0.001$). They were also more likely to collapse the table in these two conditions when food was out of reach than in the self-feeding condition when they themselves were eating (nobody-feeding, $T^+ = 90.00$, $n = 13$, $P < 0.001$; partner-feeding, $T^+ = 76.50$, $n = 13$, $P = 0.001$). Importantly, chimpanzees were equally likely to collapse the table in the nobody- and partner-feeding conditions ($T^+ = 28.50$, $n = 13$, $P = 1.0$), suggesting they were indeed motivated by general frustration at not being able to eat out-of-reach food and not especially by a personally disadvantageous situation.

In this first study, chimpanzees in the key partner-feeding condition were simply faced with the situation of another chimpanzee eating desirable food. Because primates may be inhibited from taking food from others by a respect for possession (26), we reasoned that chimpanzees would be more responsive to the resulting disparity if the food they were in the process of eating was actually taken from them. In a second study, therefore, actors were first given an opportunity to eat from a sliding food platform before the experimenter or another chimpanzee took the food away (Fig. 2). As before, actors could respond by pulling a rope and collapsing the food table so that no one, including themselves, could get the food. Eleven chimpanzees from one group were tested. Each chimpanzee played the roles of actor and partner once with each other chimpanzee. There were four conditions. In the outcome disparity condition, the experimenter pulled the food away from the actor and gave it to the partner to eat. In the theft condition, the partner pulled the food away from the actor and then ate it. In a control condition for general frustration, the experimenter took the food away from the actor, but there was no partner present (loss condition), and there was also a baseline condition with inaccessible pieces of plastic on the table to measure spontaneous rate of pulling.

As in Study 1, all actors had experience collapsing the table, and in only 0.5% of trials did they collapse the table while they could continue eating. Chimpanzees collapsed the table with different frequencies in the four conditions ($\chi^2_3 = 19.32$, $P < 0.001$; Fig. 3). They were most likely to collapse the table in the theft condition [as compared with the outcome disparity condition ($T^+ = 51.00$, $n = 11$, $P = 0.014$), the loss condition ($T^+ = 52.00$, $n = 11$, $P = 0.008$, and the baseline condition ($T^+ = 55.00$, $n = 11$, $P = 0.004$)]. However, importantly, they were no more likely to collapse the table in the outcome disparity condition than in the loss condition ($T^+ = 38.00$, $n = 11$, $P = 0.307$) [although they did so more than in the baseline ($T^+ = 45.00$, $n = 11$, $P = 0.004$; $T^+ = 28.00$, $n = 11$, $P = 0.016$) for both conditions respectively]. It is possible that the mere sight of another individual pulling a rope caused the actors to do the same. However, this is unlikely, because chimpanzees are not particularly proficient imitators (27), and stimulus enhancement is not possible, because there were two different ropes involved. Simultaneous rope-pulling does not always occur spontaneously even in cooperative situations (28, 29). Furthermore, because actors never once pulled the rope to get the food more quickly while the experimenter was putting food on the table, it seems unlikely they pulled the rope to get food back in the theft condition. We conclude that the chimpanzees thus reacted vengefully against an individual who stole from them, but they

Fig. 2. Experimental setup for Study 2. A sliding platform sits on a collapsible table in an inaccessible booth. The actor is in the actor's cage; in test conditions, the door to the partner's cage (on the right) would be closed. The actor can pull a rope causing the platform to collapse and the food to fall to the floor and out of reach.

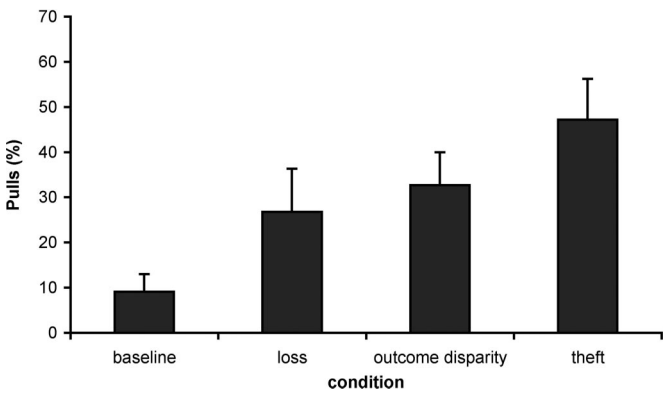

Fig. 3. Mean percentage of trials (±SEM) in which chimpanzees collapsed a food table in response to losing the food (loss), losing the food to a conspecific (outcome disparity), and having the food taken by a conspecific (theft) (Study 2). In the baseline condition, plastic pieces were on the table, which was out of reach of the actor.

Table 1. Change in behavior across 10 sessions

Condition	Standardized β	Standard error	t ratio	P value	95% bounds Upper	95% bounds Lower
Response, baseline	0	0.868	0	1.0	2.001	−2.001
Response, loss	−0.656	1.099	−2.459	0.039	−0.168	−5.236
Response, outcome disparity	−0.234	1.218	−0.679	0.516	1.981	−3.635
Response, theft	−0.656	1.378	−2.460	0.039	−0.212	−6.568
Theft	0.556	1.136	1.893	0.095	4.771	−0.469

Results are based on a linear regression after first testing for significance with a Fisher's omnibus test ($\chi^2_{10} = 19.01$, $P = 0.04$).

did not react to personally disadvantageous outcomes when that same individual was given the food by a human experimenter.

We examined four variables that might have affected the results: kinship, dominance, reciprocity, and time. First, pairs of individuals who were closely related to one another behaved no differently toward one another than unrelated individuals. Second, there was no correlation between dominance rank (based on a test of cofeeding intolerance) and being robbed in the theft condition (Mantel's matrix correlation $r_M = -0.094, n = 11, P = 0.551$), but across all trials, subjects were less likely to collapse the table when food was stolen by a more dominant individual ($r_M = 0.409$, $n = 11$, $P = 0.006$). Third, whether a chimpanzee stole from another in the theft condition was in no way related to whether he or she had previously been robbed by that individual ($r_M = -0.077, n = 11, P = 0.508$), and across all trials, there was no reciprocity in the sense that individuals did not collapse the table more against individuals who had previously collapsed the table against them. Finally, responses to loss and theft declined across the 10 sessions, whereas there was no change in responses to the baseline and outcome disparity conditions (Table 1); furthermore, there was a trend toward an increase in theft, suggesting that retribution did not have an effect on noncooperative behavior.

If chimpanzees were motivated toward vengeance against others out of anger [moral outrage (30)], as humans are with second-party punishment in the ultimatum game (31), we predicted that theft would arouse them [measured as intensity of displays and tantrums (32, 33)] more than would outcome disparity and loss. Chimpanzees were indeed aroused differently in the four conditions ($\chi^2_3 = 13.67$, $P = 0.002$; Fig. 4), and they were more aroused by theft than by loss ($T^+ = 59.00, n = 11, P = 0.018$). However, they were not significantly more aroused by theft than outcome disparity ($T^+ = 49.00, n = 11, P = 0.175$) nor by outcome disparity than by loss ($T^+ = 25.00$, $n = 11$, $P = 0.078$). Within each of the conditions analyzed separately, chimpanzees were more likely to collapse the table when aroused (baseline $r_M = 0.547, n = 11, P < 0.001$; loss $r_M = 0.579, n = 11, P < 0.001$; outcome disparity $r_M = 0.558, n = 11, P < 0.001$; theft $r_M = 0.578, n = 11, P < 0.001$). These results suggest that anger mediated the chimpanzees' collapsing of the table, but it is not clear how arousal was influenced by a feeding conspecific in the different experimental conditions. Because acts of aggression are frequently directed at the appropriate target (2), and because displays in this study were frequently directed toward the conspecific partner, it is most probable that the collapsing of the table was not just the unintended byproduct of arousal.

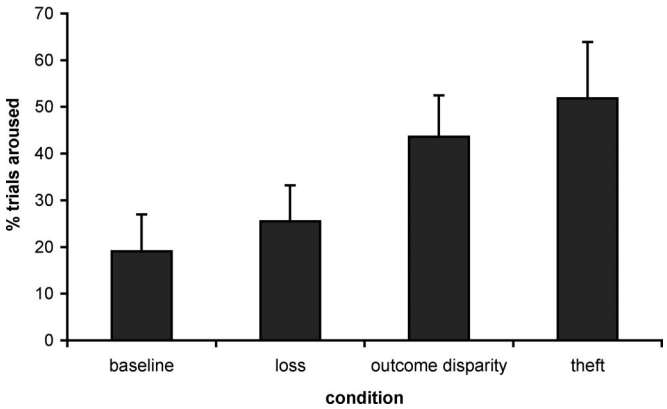

Fig. 4. Mean percentage of trials (±SEM) in which arousal (displays and tantrums) was exhibited by actors in Study 2 in response to nonfood items (baseline), losing food (loss), losing food to a conspecific (outcome disparity), and having the food stolen (theft).

The studies presented here suggest that chimpanzees are vengeful but not spiteful. Chimpanzees are retaliatory, in that they are negatively reciprocal (34), at least on a very short time scale, consistent with retribution as a means of discipline in animal societies (2, 22–24). Retribution did not enforce cooperative behavior through reciprocity in the current experiments likely due in part to the fact that subjects switched roles only once and only after engaging with all others. Furthermore, the benefit of stealing outweighed the costs of suffering retribution in the long run, so perhaps it is not surprising that, in this context, retribution declined with time, and stealing increased. Chimpanzees are not spiteful, in that they did not appear to have the decrease in welfare of conspecifics as an end in itself in either of the two experiments. Spitefulness may thus be a peculiarly human phenomenon. Further studies that attempt to distinguish vindictive motives from spiteful motives in humans and other animals are needed to validate this claim.

Humans who punish noncooperators with no expectation of personal gain may be motivated either to correct personally disadvantageous outcomes (8, 9) or to reciprocate according to perceived intentions (10–13) or both (35). For instance, in studies such as the ultimatum game when unfair proposals are generated randomly (36) or constrain a proposer to unfair options (37, 38), people still reject unfair offers, although at a lower rate, suggesting that both outcomes and intentions influence their perception of unfairness. Chimpanzees recognize negative intentions in others (39), and so it is conceivable they reacted to the harmful intent behind thefts in the current study. That chimpanzees were sensitive to harmful behavior and/or intent, but not to simple disparity over which the partner had no control, is consistent with intention-based models of fairness (10–13) but not with outcome-based models (8, 9). Although altruistic punishment (7) appears to be a key feature supporting sociality on the scale exhibited by humans because it stabilizes cooperation, even in sizable groups in which altruistic rewarding by itself cannot (1), it remains to be shown whether non-human animals will punish noncooperative behavior for no material benefit, and whether such behavior will stabilize cooperation within groups. Although punishment, spitefulness, retribution, revenge, envy, and *Schadenfreude* are often seen as blemishes in human nature, the propensity of people to compare their

fortunes to those of others and to punish those more fortunate, regardless of how those different fortunes arose, may be a characteristic of specifically human cooperation.

Methods

Study 1. Chimpanzees were tested at the Wolfgang Köhler Primate Research Centre (Leipzig, Germany). Three chimpanzees from each of two groups were partners (passive role), and nine from the A group (seven females and two males, mean age 20 years) and four from the B group (four females, mean age 10 years) were the actors (test subjects). The actor faced the partner across a 1-m space (booth). The actor occupied the cage to the left, giving her two approaches to the booth. The partner could occupy the cage across from the booth. The apparatus was a 20-cm-wide table the length of the mesh panel (86 cm). It had three legs, the most distal one being hinged. A rope attached to it made the table collapse when pulled, causing anything on it to fall beyond the reach of the chimpanzees.

Chimpanzees were first given two familiarization sessions of two trials, alone with the apparatus baited with nonfood objects. During testing, there were first two baseline conditions, actor-accessible and -inaccessible, in which inedible pieces of bamboo and plastic were put onto the table by the experimenter before inserting the rope. The partner's cage was unoccupied. In the control and test conditions, counterbalanced for order, 12–15 g of dry food (pellets, raisins, almonds, and peanuts) was put onto the table. In the self-feeding control condition, the table was accessible only to the actor, and the partner was in the opposite cage. In the nobody-feeding control condition, no partner was present, and the table stood on the partner's side of the booth. In the partner-feeding test, the partner was in the cage across the booth from the actor. All trials lasted 2 min or until the actor collapsed the table. The experimenter was outside of the sleeping room during testing, and all trials were videotaped.

Coding of actor's choice, whether the table was collapsed or not, was done *in situ* by the first author; interobserver reliability coding was done on 20% of videotaped trials, randomly chosen, by an observer blind to the study's design (Cohen's $\kappa = 0.926$). Friedman's nonparametric and planned Wilcoxon's signed rank analyses were applied to the data. All analyses were two-tailed.

Study 2. Twelve chimpanzees from the A group were tested (nine females, three males, mean age 21 years). One female was excluded from analysis due to interference by one of her offspring. Each chimpanzee was in the roles of both actor and partner once with each of the others, giving a total of 110 trials. Each individual interacted only once in a single role with each other individual before roles were reversed. As in Study 1, actor and partner faced each other across a booth (Fig. 2). A table fully occupied the space. It had two hinged legs with wheels that caused it to collapse when the actor pulled the rope attached to it. On the table was a sliding platform (30 cm wide) that could be moved across the booth. The partner could pull this platform when the partner's rope was made available.

Chimpanzees were first given one familiarization session with three trials, two with food on the platform (one in which they could use the partner's rope to pull the food closer, and one with only the actor's rope) and one with plastic pieces. During test sessions, the first trial was the baseline condition in which pieces of plastic were placed on the platform beyond the actor's reach; the partner was not in the partner's cage. In all other conditions, counterbalanced for order, 12–15 g of food was put on the platform, which was slid to the actor's side of the booth. The actor was allowed to eat for 30 s. In the loss condition, the experimenter then came back into the room and slid the platform to the empty partner's cage. In the outcome disparity condition, after 30 s had passed, the experimenter let the partner into the partner's cage before sliding the food platform to her. In the theft condition, once the 30 s had elapsed, the experimenter let the partner into the partner's cage; the partner could then pull a rope attached to the platform, drawing it away from the actor to within her own reach. Only those trials in which the partner actually stole the food from the subject, 74% of all trials, were used in the analyses. (In all three followup trials, all individuals but one pulled the food platform away from the empty actor's cage toward themselves in the partner's cage suggesting that the absence of theft, with one exception, was not due simply to an inability or unwillingness to pull the partner's rope.) Trials ended after 2 min or when the actor collapsed the table. All trials were videotaped.

K.J. live-coded all trials. Twenty percent of the trials were coded by the second author for choice, namely, whether the table was collapsed (Cohen's $\kappa = 1.0$), whether the partner stole the food (Cohen's $\kappa = 1.0$), and whether the actor was aroused (Cohen's $\kappa = 0.81$). Nonparametric Friedman's and planned Wilcoxon's signed rank tests were used, in addition to Mantel's matrix correlations and a linear regression for session effect. All analyses were two-tailed.

After testing, each dyad was tested in two sessions of feeding tolerance as a measure of rank. A food platform (75 cm across) was placed in front of a mesh panel outside of the cage and baited with two and one-half bananas cut into slices. A pair of chimpanzees was then allowed into the cage. Chimpanzees were considered food-tolerant and assigned a score of one each if both individuals cofed, such that each individual ate at least 20% of the food. Dyads were considered intolerant if one individual ate >80% of the food while cofeeding; the "winner" was given a score of two and the "loser" a score of zero. Twenty percent of the trials were coded by an observer blind to the study's design (Cohen's $\kappa = 1.0$).

We are grateful to the keepers at the Leipzig Zoo, Katrin Riedl, Sara Macellini, Nicole Diekmann, and Martin Schmelz, for help with the studies and to Roger Mundry for statistical advice. We thank three anonymous reviewers for helpful comments. This research was supported by the Max Planck Society for the Advancement of Science.

1. Boyd R, Gintis H, Bowles S, Richerson PJ (2003) *Proc Natl Acad Sci USA* 100:3531–3535.
2. Clutton-Brock TH, Parker G (1995) *Nature* 373:209–217.
3. Batson CD (1991) *The Altruism Question: Toward a Social-Psychological Answer* (Erlbaum, Hillsdale, NJ).
4. Trivers R (1985) *Social Evolution* (Benjamin/Cummings, Menlo Park, CA).
5. Hamilton WD (1970) *Nature* 228:1218–1220.
6. Wilson EO (1975) *Sociobiology: The New Synthesis* (Harvard, Cambridge, MA).
7. Fehr E, Gächter S (2002) *Nature* 415:137–140.
8. Fehr E, Schmidt KM (1999) *Q J Econ* 114:817–868.
9. Bolton GE, Ockenfels A (2000) *Am Econ Rev* 90:166–193.
10. Rabin M (1993) *Am Econ Rev* 83:1281–1302.
11. Levine D (1998) *Rev Econ Dyn* 1:593–622.
12. Dufwenberg M, Kirchsteiger G (2004) *Games Econ Behav* 47:268–298.
13. Charness G, Rabin M (2002) *Q J Econ* 117:817–869.
14. Brosnan SF, de Waal FBM (2003) *Nature* 425:297–299.
15. Brosnan SF, Schiff HC, de Waal FBM (2005) *Proc R Soc London Ser B* 272:253–258.
16. Dubreuil D, Gentile M, Visalberghi E (2006) *Proc R Soc London Ser B* 273:1223–1228.
17. Roma PG, Silberberg A, Ruggiero AM, Suomi SJ (2006) *J Comp Psychol* 120:67–73.
18. Brosnan SF, Freeman C, de Waal FBM (2006) *Am J Primatol* 68:713–724.
19. Bräuer J, Call J, Tomasello M (2006) *Proc R Soc London Ser B* 273:3123–3128.
20. Silk JB, Brosnan SF, Vonk J, Henrich J, Povinelli DJ, Richardson AS, Lambeth SP, Mascaro J, Schapiro SJ (2005) *Nature* 437:1357–1359.
21. Jensen K, Hare B, Call J, Tomasello M (2006) *Proc R Soc London Ser B* 273:1013–1021.
22. Hauser M (1992) *Proc Natl Acad Sci USA* 89:12137–12139.
23. de Waal FBM, Luttrell LM (1988) *Ethol Sociobiol* 9:101–118.
24. Silk JB (1992) *Curr Anthr* 33:318–325.
25. Zizzo DJ (2003) *Econ Lett* 81:263–266.

26. Kummer H, Cords M (1991) *Anim Behav* 42:529–549.
27. Tomasello M (1996) *Social Learning in Animals: The Roots of Culture*, eds Galef J, Heyes C (Academic, New York), pp 319–346.
28. Crawford MP (1937) *Comp Psychol Monogr* 14:1–88.
29. Melis AP, Hare B, Tomasello M (2006) *Anim Behav* 72:275–286.
30. Trivers R (1971) *Q Rev Biol* 46:35–57.
31. Pillutla M, Murnighan J (1996) *Organ Behav Hum Decis Proc* 68:208–224.
32. Goodall J (1986) *The Chimpanzees of Gombe* (Harvard, Cambridge, MA).
33. Nishida T, Kano T, Goodall J, McGrew WC, Nakamura M (1999) *Anthr Sci* 107:141–188.
34. Fehr E, Gächter S (2000) *J Econ Perspect* 14:159–181.
35. Falk A, Fischbacher U (2006) *Games Econ Behav* 54:293–315.
36. Blount S (1995) *Organ Behav Hum Decis Process* 63:131–144.
37. Güth W, Huck S, Müller W (2001) *Games Econ Behav* 37:161–169.
38. Falk A, Fehr E, Fischbacher U (2003) *Econ Inq* 41:20–26.
39. Call J, Hare B, Carpenter M, Tomasello M (2004) *Dev Sci* 7:488–498.