Chimpanzees return favors at a personal cost

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Humans regularly provide others with resources at a personal cost to themselves. Chimpanzees engage in some cooperative behaviors in the wild as well, but their motivational underpinnings are unclear. In three experiments, chimpanzees (*Pan troglodytes*) always chose between an option delivering food both to themselves and a partner and one delivering food only to themselves. In one condition, a conspecific partner had just previously taken a personal risk to make this choice available. In another condition, no assistance from the partner preceded the subject's decision. Chimpanzees made significantly more prosocial choices after receiving their partner's assistance than when no assistance was given (experiment 1) and, crucially, this was the case even when choosing the prosocial option was materially costly for the subject (experiment 2). Moreover, subjects appeared sensitive to the risk of their partner's assistance and chose prosocially more often when their partner risked losing food by helping (experiment 3). These findings demonstrate experimentally that chimpanzees are willing to incur a material cost to deliver rewards to a conspecific, but only if that conspecific previously assisted them, and particularly when this assistance was risky. Some key motivations involved in human cooperation thus may have deeper phylogenetic roots than previously suspected.

cooperation | prosociality | chimpanzees | reciprocity

The motivation to benefit others even at a cost to the self is commonly seen as a hallmark of human cooperation (1–4). In their natural habitats, chimpanzees—human's closest living evolutionary relatives together with bonobos (*Pan paniscus*) (5)—also engage in a number of cooperative activities, such as teaming up with partners in fights, grooming with others reciprocally, and even sharing meat after successful hunts (6–10). Observational studies with captive animals have shown further that, over the long-term, chimpanzees reciprocally groom and share food with others (11–14). Bonobos also cooperate in a number of contexts (15–18), suggesting that such cooperative tendencies have deep phylogenetic roots.

It is unclear, however, in how far these cooperative acts in chimpanzees are based on prosocial motives in the sense that they are intended to benefit a partner. Coalitions in fights and mutual grooming, for instance, provide immediate benefits to both partners (19), whereas meat sharing most often occurs in response to threats and/or harassment from beggars (20, 21). The psychological mechanisms underlying chimpanzee cooperation and in how far they overlap with those seen in humans is thus currently unresolved (19, 20, 22–26).

Laboratory experiments have attempted to clarify the situation. Numerous studies suggest that when there is no material cost (i.e., solely a small energetic cost), chimpanzees will help both humans and other chimpanzees attain their goals, for example, by fetching out-of-reach objects and tools (27, 28) or by flipping a latch to enable a conspecific to obtain food (29); however, they appear to do this only if they themselves have no chance whatsoever to obtain any food in the situation, and it has been argued that helping rarely occurs in the absence of active solicitation or harassment by the partner (26, 30). A recent study has also argued that experimental design features (e.g., subjects'

motivation to engage with novel tasks) should be considered as potential alternative explanations (31).

Furthermore, several studies have shown that when presented with one option delivering food to both themselves and a conspecific and another option only delivering food to themselves, chimpanzees choose completely randomly between these alternatives, which has been interpreted as suggesting that chimpanzees are indifferent to the welfare of conspecifics even when being prosocial is entirely noncostly (32–34). Although some studies show somewhat more mixed (but not easily interpretable) results concerning cost-free prosocial choices in chimpanzees (35, 36), the picture is very clear when it comes to materially costly prosociality: to date there is no reliable experimental evidence that chimpanzees are willing to deliver resources to conspecifics when doing so entails a cost for themselves.

However, previous experiments may have failed to elicit the kind of social context in which chimpanzee prosociality naturally occurs. One possibility, for instance, is that costly prosocial acts are contingent on others' prior helpful behaviors (37, 38) and therefore could not be detected in experiments stripped of any prior cooperative interaction. Indeed, several studies have suggested reciprocal patterns of sharing behaviors in the animal kingdom (39–42), although the underlying psychological mechanisms are not always clear. Although chimpanzees did not show such reciprocal prosocial patterns in some experiments (43, 44), this can at least partly be explained by the subjects' lack of understanding of experimental setup and the choice contingencies (see refs. 26 and 45 for recent methodological critiques). Others found a slight increase of cooperation with a helpful conspecific in a helping paradigm (46), but chimpanzees did not preferentially favor an individual who had assisted them over one who had not.

In the current study, we therefore aimed to create a situation in which chimpanzee subjects thoroughly understood the experimental setup and clearly recognized whether a conspecific

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Significance

There are many examples of costly cooperation in humans. Although other great apes have been shown to engage in a number of cooperative behaviors, there is no reliable experimental evidence that they will sacrifice resources to benefit others. Here, we show that chimpanzees (*Pan troglodytes*) return favors to conspecifics who have previously assisted them in acquiring food; crucially, they even do this at a material cost to themselves and especially when the conspecific incurred a risk in providing the assistance. Chimpanzees are thus capable of engaging in materially costly reciprocal interactions commonly considered unique to humans.

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partner had previously assisted them to access food; subsequently, they had the opportunity to return that favor by providing their partner with resources. In each of three experiments, subjects ($n = 6$) always chose between a prosocial option that equally benefited both themselves and a conspecific partner and an option that only benefited themselves. What differed between conditions was that this choice was either made available to the subject by a prosocial act of the partner or without her assistance.

In the risky assistance condition (RA) of experiment 1, the partner first rejected an option (option A; Fig. 1A) that would have terminated the trial while delivering two pieces of food to herself and leaving the subject empty-handed (unbeknownst to the subject, the partner was trained to always reject option A). Instead, the partner pulled on a rope which—while precluding her from directly accessing any food—unhinged a latch whereby the aforementioned choice was opened up for the subject (options B and C; Fig. 1B). Before the test, subjects had extensive experience with the apparatus and demonstrated in several training steps that they were sensitive to the payoffs associated with each choice as well as the apparent choices available to the partner. Hence, from the subject's perspective the partner risked getting nothing for herself but instead assisted the subject in obtaining food. In the no-assistance condition (NA), the partner was present but did not act at all. The experimenter unhinged the latch and the subject faced the same choice as in RA but without having received assistance from the partner. In both conditions, subjects faced the choice between a prosocial 2/2 option (subject's payoff/partner's payoff) and a 2/0 option benefitting only the subject (Table 1).

Results

Chimpanzees chose the 2/2 option in 76.4% of trials in RA and in 50.7% of trials in NA ($P = 0.031$, exact Wilcoxon signed-rank
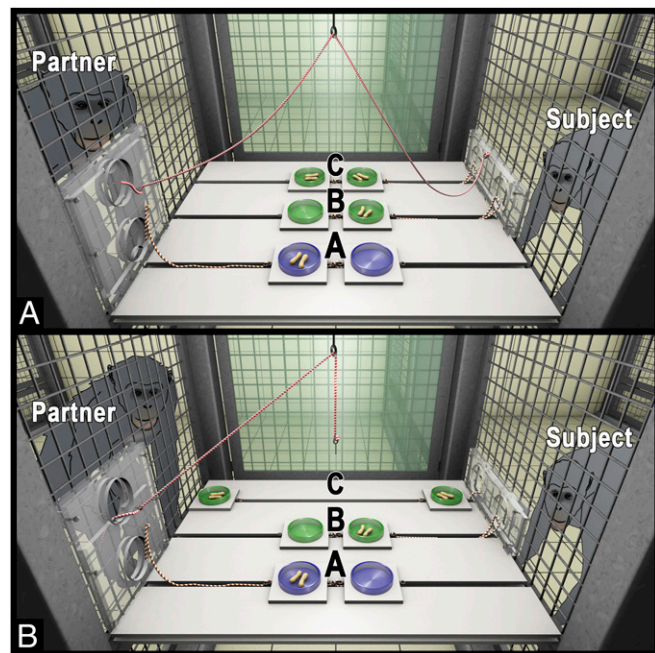
Fig. 1. Experimental setup/apparatus. (A) Starting position of the apparatus. From the subject's point of view, the partner can either choose option A (delivering two pieces of food to the partner and nothing to the subject) or pull a rope to make the choice between options B and C available to the subject. (B) End position. The partner has made options B and C available for the subject. The subject has chosen option C, thereby delivering two pieces of food to both the partner and herself. The location of the prosocial option was randomized and counterbalanced so that it was equally often in location B and C.

Table 1. Payoff structure of the three experiments

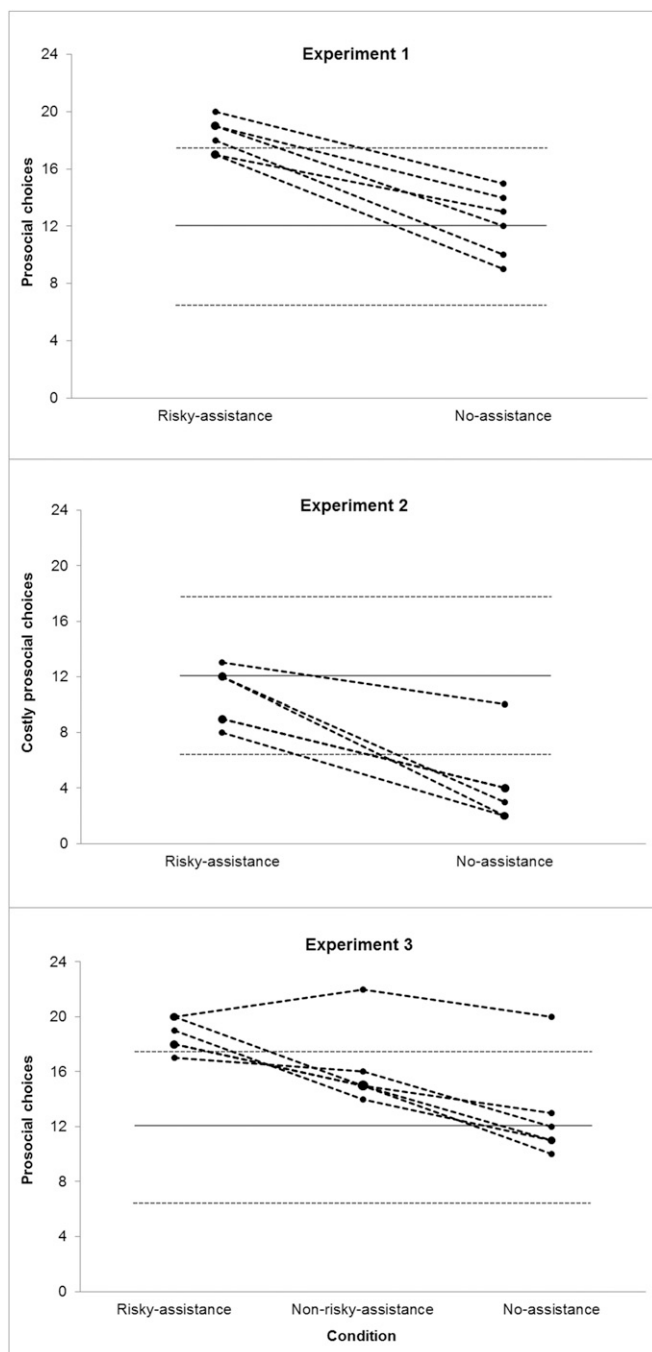| Experiment/condition	Option	Subject's payoff	Partner's payoff
Experiment 1	A		••
	B	••	
	C	••	••
Experiment 2	A		•••
	B	••••	
	C	•••	•••
Experiment 3 RA and NA	A		••
	B	••	
	C	••	••
Experiment 3 NRA	A		
	B	••	
	C	••	••

Dots represent pieces of food.

test, $V = 21$, $n = 6$; Fig. 2; all Wilcoxon signed-rank tests were two-tailed). Moreover, in RA, four of six subjects chose the 2/2 option significantly above chance ($P < 0.05$), whereas no subject did so in NA (chance comparisons were based on two-tailed binomial tests that were corrected for multiple testing using false discovery rates to keep type 1 error rates at the nominal level of 0.05) (47).

Experiment 2 was identical to experiment 1 except that choosing the prosocial option was now costly for the subject—that is, after the partner made the choice available to the subject, the subject chose between a prosocial 3/3 option and a selfish 4/0 option (Table 1), which meant that they had to give up one piece of food to deliver a benefit to their partner. Chimpanzees chose the 3/3 option in 43.8% of trials in RA compared with 17.4% of trials in NA ($P = 0.031$, exact Wilcoxon signed-rank test, $V = 21$, $n = 6$). In a preference test before and after experiment 2, subjects further demonstrated that they clearly discriminated between three and four pieces of food and showed a strong and stable preference for the higher quantity. This finding indicates that subjects often went against their preference in RA and were willing to give up 25% of their payoff to reward their partner's cooperative effort.

In experiment 3 we examined further whether subjects appreciated that their partner's assistance was potentially costly. RA and NA conditions were virtually the same as in experiment 1, but in a new nonrisky assistance condition (NRA), the partner provided assistance without having to forego any resources (i.e., there was no food present in the rejected option A; Table 1). Hence, from the subject's point of view, the partner had no choice but to provide assistance to obtain any food. The new NRA condition thus provides an especially subtle contrast because the partner assisted the subject just as in the RA condition—only without incurring any material cost or risk to do so.

The number of 2/2 choices differed significantly between conditions [$P = 0.011$, Friedman test, $\chi^2(2) = 8.96$]. Subjects chose the 2/2 option in 77.8% of trials in RA and in 53.5% of trials in NA—virtually replicating the results from experiment 1 with the exception of one subject (Fig. 2). The proportion of 2/2 choices in NRA (67.4%) was intermediate as would be expected if nonrisky assistance was interpreted as less costly than risky assistance but still more worthy of reward than if no assistance was given. Indeed, post hoc pairwise comparisons revealed a significant difference between choices in NRA and NA ($P = 0.031$, exact Wilcoxon signed-rank test, $V = 21$, $n = 6$). The difference between the RA and NA as well as the difference between RA and NRA approached statistical significance (exact Wilcoxon signed-rank test, $V = 15$, $n = 6$, $P = 0.063$ and $V = 19$, $n = 6$, $P = 0.094$, respectively). Moreover, five of six subjects chose the 2/2 option significantly above chance in RA, whereas only one subject—who

Fig. 2. Subjects' prosocial choices in the different conditions of the three experiments. The horizontal lines indicate the 50% chance level (continuous line) and significance levels above and below chance (dashed line). Note that in experiment 2, subjects had a stable preference for the non–prosocial option (see preference tests) so that the 50% chance level is not a meaningful baseline. The dot sizes correspond to number of subjects.

predominantly chose the prosocial option regardless of condition— did so in the other two conditions (Fig. 2).

To test for potential order effects, we fitted a generalized linear mixed model for each experiment (see *SI Materials and Methods* for detailed model descriptions), which revealed that neither the test predictors session and trial number nor the interaction of these predictors with the experimental condition significantly affected subjects' tendency to choose the prosocial option in any of the three experiments: experiment 1, $\chi^2(4) =$

5.71, $P = 0.222$; experiment 2, $\chi^2(4) = 5.31$, $P = 0.257$; experiment 3, $\chi^2(6) = 6.13$, $P = 0.409$.

Discussion

The tendency to engage in costly behaviors aimed at benefiting others is a central component of human cooperation. The findings of the current study demonstrate experimentally that under some circumstances chimpanzees are also motivated to deliver benefits to conspecifics. In the absence of any prior interaction (NA conditions), chimpanzee subjects' behavior was consistent with previous studies finding no prosociality in chimpanzees in similar prosocial choice paradigms (32–34). Indeed, when choosing the prosocial option was materially costly, subjects' prosocial choices in the NA condition were close to zero (Fig. 2). In contrast, however, after they had received assistance from a partner, subjects provided their partner with resources in return, even at a material cost to themselves. Across the three experiments, subjects tended to reward risky assistance most often, nonrisky assistance somewhat less, and no assistance least often, suggesting that they understood the other's motivation and distinguished genuine prosociality from potentially self-serving behaviors.

We found material reciprocation where other researchers have not (43), most likely because we made sure before testing that subjects understood everything about the apparatus and the contingencies facing both the partner and themselves (*SI Materials and Methods* and Table S1). Given the careful counterbalancing scheme and as indicated by the session and trial number analysis, our findings cannot be explained by local enhancement, order effects, or learning. Moreover, previous research has demonstrated the importance of stable social bonds in primate cooperation (48–50). In the current experiments, however, increases in prosocial choices after receiving risky assistance were highly consistent across subjects who differed in rank and their social relationship with the partner (Table S2). These results are therefore unlikely to be explained by variation in prior long-term relationships (although future research should look at this more systematically). The current findings thus complement previous work highlighting the long-term nature of chimpanzee reciprocation of social services (14, 51) by showing that chimpanzees can also integrate recent single events into contingent cooperative short-term decisions, even when this involves making a material sacrifice.

One possibility is that chimpanzees strategically chose the prosocial option in RA conditions to motivate their partner to continue to provide assistance on future trials. However, if the prosocial option were only used to motivate future assistance, subjects' behaviors should have been the same in the RA and NRA conditions in experiment 3. A more probable explanation is instead that chimpanzees' choices were mediated by affiliative reactions in response to their partner's cooperative efforts; this would correspond to theoretical accounts suggesting that chimpanzees may engage in some form of "emotional bookkeeping" such that individuals make social decisions based on emotional states associated with particular partners (14, 51, 52), which may also be consistent with empirical findings showing that chimpanzees show elevated oxytocin levels—a hormone involved in social bonding—in response to cooperative interactions (48, 53), and this may mediate individuals' propensity to engage in cooperative activities with particular partners in the future. Hence, in the current experiments, subjects may have interpreted the partner's assistance (and thus her decision to deviate from a payoff-maximizing strategy) as an invitation to contribute to a mutually desirable cooperative outcome (54), triggering positive affect toward the partner and motivating reciprocation.

It should further be noted that in contrast to previous experimental studies on animal reciprocity (39–42), there was a distinct cognitive dimension to the current task—that is, chimpanzees did not merely respond to the outcome of the partner's actions but

rather took into account their partner's decisions (and decision alternatives). This finding is particularly clear in experiment 3 in which the partner's actions and the outcomes of these actions were identical in both assistance conditions, but subjects tended to reward the partner more if they had incurred a risk in assisting them than when the same action could be interpreted as self-serving. This kind of consideration of a partner's decision-making and thus her cooperative intentions as a basis for reciprocal prosocial behavior is a central contribution of the current study.

One limitation of this study was the small sample size; this was the result of the strict prerequisite criteria at training (*SI Materials and Methods*), which, while reducing the number of subjects permitted to the test, ensured that all tested subjects thoroughly understood the test situation and the consequences of their choices. Although the resulting small sample was unfortunate, we think the strict training protocol was a key advantage of the study and the clarity and consistency of the results across three separate experiments further strengthen our confidence in these findings. However, a valuable extension to the current study would be to conduct similar experiments with different groups of chimpanzees and, if possible, with larger samples. Furthermore, similar studies with bonobos—who display greater prosociality than chimpanzees in several contexts (55)—would be highly insightful for our understanding of the evolution of human cooperation and the sociocognitive makeup of humans' last common ancestor with the Pan species.

Finally, the cooperative inclinations of chimpanzees revealed in the current experiments suggest that observed species differences in cooperative propensities between humans and chimpanzees may at least partly be due to factors other than the motivation to reward others' prosocial actions. For example, competition and lack of social tolerance appear to fundamentally constrain chimpanzees' abilities to sustain cooperative interactions in some contexts (56), and it would be important to ascertain in how far these factors also impact their propensity to engage in material reciprocation. Here again, the comparison with bonobos would be instructive given that bonobos show considerably greater social tolerance and less intragroup aggression than chimpanzees (55).

In conclusion, the current findings demonstrate experimentally that chimpanzees are willing to incur a material cost to themselves to deliver a material reward to a conspecific, but they do this only if that conspecific previously incurred a risk to assist them. This finding suggests that some of the key motivations crucial to human cooperation may have deeper phylogenetic roots than previously suspected.

Materials and Methods

Subjects. We initially started the test with 12 socially housed chimpanzees (*Pan troglodytes*) at the Wolfgang Köhler Primate Research Center in Leipzig, Germany. Six test subjects met our prerequisites and advanced to the testing phases of all three studies (two females and four males; average age = 13.1 y; age range = 8.9–21.3 y at the beginning of data collection). For further details, see Table S2. We trained an additional female chimpanzee (age 11.8 y at the beginning of data collection, middle to low ranking) to act as a partner during the test (*SI Materials and Methods*). All subjects have previously participated in studies on cooperation; however, as far as we can ascertain, they have not been paired with the same partner in similar prosocial choice tasks.

Ethical Statement. The study complied with the European and World Associations of Zoos and Aquariums Ethical Guidelines and was approved by the joint ethical committee of the Max Planck Institute for Evolutionary Anthropology and Leipzig Zoo. Chimpanzees were neither food- or water-deprived and could participate or refuse to participate in the study by their own choice.

Apparatus. Between room 1 on the left and the opposite room 2 on the right, a table (70 × 90 cm) was placed that could be accessed from both sides through mesh panels. On the table, there were three different options, A, B, and C, that each held two round cups (diameter 8 cm). At the beginning of all trials in all conditions, all six cups were in the middle of the table, out of reach from the rooms. Each option could be chosen by pulling a string,

resulting in one of the two cups to move toward room 1 and the other one toward room 2 (Fig. 1). Throughout the methods we will refer to rewards in the two cups of each option in square brackets (e.g., [1/0] or [1/1]) with the first number always referring to the cup accessible from room 1 and the second number to the cup accessible from room 2. Only one of the three options could be chosen per trial. Option A could only be accessed from room 1, whereas options B and C could only be chosen from room 2; to emphasize this, the two cups in option A were blue, and the four cups in option B and C were green. To pull the string attached to option A, a transparent vertical sliding door had to be operated. Moving the sliding door upwards made it possible to access option A while simultaneously precluding access to options B and C. If the sliding door was instead moved down, option A was blocked and a rope (the "offer rope"; 4.5 m long) running over a hook at the ceiling to the mesh panel of the opposite room became accessible. The rope was attached to a latch in a transparent horizontal sliding door that blocked access to options B and C from room 2. The latch was in the middle of the door and thus equally distant from both options. When the offer rope was pulled from room 1 long enough the latch was removed, which enabled subjects in room 2 to choose between options B and C (this action will henceforth be called "making options B and C available"). Making available options B and C was very salient: the rope had to be pulled for several seconds, which resulted in the latch conspicuously springing out of the horizontal sliding door and then swinging from the ceiling, and this ensured that a chimpanzee watching from room 2 would clearly see and hear the removal of the latch from the other side. Once subjects chose option B or C, the other option became inaccessible.

In the starting position, the vertical sliding door was in the middle position, the end of the offer rope was in place behind the vertical sliding door in room 1, and the attached latch blocked the horizontal sliding door in room 2 (Fig. 1A). All options, A, B, and C, were thus accessible when the appropriate choices were made on both sides. In room 1, subjects could either choose option A or they could discard option A and instead make options B and C available in room 2. In room 2, subjects could then choose between options B and C (Fig. 1B). Different payoffs of food rewards could be placed into the six cups to manipulate the optimal choices. A trial always started with the experimenter (E) removing a transparent Perspex cover in front of the mesh panel in room 1 to allow access to the vertical sliding door at option A. Access to the horizontal sliding door in room 2 was always unobstructed but with the latch in place, it could not be operated.

Procedure. We used strict prerequisite criteria to ensure that only subjects with a thorough understanding of the apparatus contingencies and consequences of their choices were tested (for detailed descriptions of all prerequisite steps, see *SI Materials and Methods* and Table S1).

In all prerequisite criteria and experimental conditions, different trial types or different payoff locations were randomized and counterbalanced (with the stipulation that there were never more than two identical trials in a row) to preclude local enhancement and order effects. Rewards throughout all conditions were banana pellets. Individual data and number of sessions per subject of all conditions can be found in Table S2. All trials of all conditions were video recorded and live coded.

Basic Training Procedure Before Experiments. We trained a chimpanzee partner (P) to always make options B and C available in room 2. Subjects (S) first experienced all parts of the apparatus and the different actions that could be performed on both sides (*SI Materials and Methods*). Six of 12 initial S managed to operate the apparatus and passed to experiment 1.

Experiment 1.
Prerequisite criteria. S first had to pass the one solution criterion (*SI Materials and Methods*) in which the door between rooms was open so that they had access to both sides of the apparatus. In each trial, there was one piece of food in one of the six food cups, and S had to demonstrate that they understood how to operate the apparatus on both sides to access each of the available cups. The next step was the best solution criterion (*SI Materials and Methods*) in which the cups were baited equivalently to the later experimental conditions. Again, the door between rooms was open so that S could operate the apparatus on both sides. To pass this criterion, S had to demonstrate apparatus understanding by maximizing their food intake. All six S passed these criteria steps. Last, S received dependence experience 1 and 2 (*SI Materials and Methods*). Here, S experienced that whether they received food depended on the choices made by their partner in the opposite room (in dependence experience 1 S was in room 1 and a human partner in room 2, and the reverse was the case in dependence experience 2).

RA. In RA, S were in room 2, and the trained conspecific P was in room 1. Option A always contained two food rewards [2/0], and either option B contained four [2/2] and option C two [0/2] or vice versa (B [0/2] and C [2/2]) (Table 1). The vertical door was rigged (see *SI Materials and Methods* for details) so that P could never choose option A. However, this manipulation was invisible to S. With the apparatus in the starting position, P made options B and C available to S in each trial. S could then choose between one option delivering rewards only to themselves ([0/2]) and another option delivering rewards to both herself and P ([2/2]). Hence, S had the opportunity to provide a reward to her partner at no material cost to herself. Option B or C were the prosocial option in half of the trials of each session.

NA. NA was equivalent to RA with regards to the positions of P and S as well as the payoffs. In contrast to RA, however, P did not perform any action. The vertical sliding door was already moved down and the string of option A was removed so that option A could (visibly for S) not be accessed by P. The offer rope was not attached; options B and C were closed with a latch without a rope. At the start of each trial, E waited a few seconds for S to see and assess the situation and then removed the latch from the horizontal sliding door to give S the choice between the [0/2] and the [2/2] option. In both conditions, the time interval between two trials was roughly a little over 1 min.

Subjects received two sessions of 12 trials per condition. Half of the S first received RA and then NA, whereas the other half completed the experiment in the reverse order. Between conditions, there was a test break of 17–20 d (median = 19 d) to avoid carryover effects between conditions. Whether a subject started with RA or NA was assigned randomly.

Experiment 2.
Prerequisite criteria. In experiment 2 the same six S were tested again with the same P. S had to pass the same prerequisite criteria (one solution criterion, best solution criterion, dependence experience 1 and 2) to confirm thorough apparatus understanding. However, unlike in experiment 1, different payoffs were used at test and the best solution criterion was adjusted to match the new test payoffs. In addition, there were quantity preference sessions before and after testing to ensure that S could recognize the difference of four vs. three pieces of food and demonstrated that they preferred the bigger quantity (*SI Materials and Methods*). All six subjects passed all criteria.
RA and NA (Movies S1 and S2). The procedures in both conditions were identical to the procedures in experiment 1 but the payoffs were different: option A always contained three rewards ([3/0]), whereas either option B contained [3/3] and option C [0/4], or vice versa (Table 1); this means that in experiment 2, S had to incur a cost to provide a benefit to their partner (i.e., by choosing [3/3] over [0/4]).

The same three S as in experiment 1 first received the RA and then NA, whereas the other half completed the experiment in the reverse order. Between conditions, there was a test break of 16–19 d (median = 17 d) to avoid carryover effects.

Experiment 3.
Prerequisite criteria. In experiment 3, again the same six S were tested with the same P. S had to pass the same prerequisite criteria with the same payoffs as in experiment 1 (one solution criterion, best solution criterion, dependence experience 1 and 2) to confirm thorough apparatus understanding. There was also an additional attention criterion (*SI Materials and Methods*) between the best solution criterion and dependence conditions in which S had access to both rooms. In some trials S had to choose option A, whereas in the other trials they had to reject option A to make options B and C available to maximize their food intake. S were thus trained to pay additional attention to the payoffs in option A, which was crucial for the subsequent experimental conditions. All six subjects passed all criteria. In addition to RA and NA, there was also a nonrisky assistance condition.
RA. RA was identical in every aspect to RA in experiment 1 (see above).
NRA. NRA was identical to RA with the critical difference that no rewards were present in option A ([0/0]; Table 1). P therefore performed the same actions as in RA but from the point of view of S she did not risk losing food by discarding option A.
NA. NA was identical to NA in experiment 1 (see above) except for one difference: whereas P remained passive, E now made options B and C available to S by mimicking P's actions in RA and NRA. At the start of each trial, E pulled the offer rope himself to remove the latch. Functionally this condition was identical to NA in experiments 1 and 2 (P was only present and could not act at all, whereas E opened up the choice for S). However, the timing as well as the perceptual information that S received in the new NA procedure closely matched the RA and NRA conditions. It thus controlled for the possibility that S had learned (for unspecified reasons) to only choose prosocially (i.e., the [2/2] option) when the offer rope was used to remove the latch.

Each S received the three conditions in a different order, assigned randomly. As previously, test breaks of 15–19 d (median = 16.5 d) were introduced between conditions to avoid carryover effects.

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