The Psychological Mechanisms Underlying Reciprocal Prosociality in Chimpanzees (*Pan troglodytes*)

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In both the wild and captivity, chimpanzees engage in reciprocal patterns of prosocial behavior. However, the proximate mechanisms underlying these patterns are unclear. In the current study, we investigated whether chimpanzees prefer to act prosocially toward conspecifics who have directly benefited them (perhaps based on an affective bond) or whether they simply observe the prosocial behavior of others in general (including indirectly to third parties) and preferentially interact with and behave prosocially toward the most prosocial individuals. We found good evidence for direct reciprocity but little evidence for a general (indirect) preference for prosocial individuals. These results suggest that cooperative reciprocity in chimpanzees may be based mostly on social–affective processes and direct interactions.

Keywords: cooperation, prosocial behavior, chimpanzees, reciprocity, proximate

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Like many animals, chimpanzees in their natural habitats engage in a variety of cooperative behaviors; for example, they hunt together, share meat with each other, and support one another in fights (Mitani & Watts, 2001; Muller & Mitani, 2005). Captive chimpanzees collaborate in a variety of experimental tasks and even recruit the best collaborators as partners (Hirata & Fuwa, 2007; Melis, Hare, & Tomasello, 2006). Captive chimpanzees are also successful in "stag hunt games" (Skyrms, 2004), in which they are required to forego small rewards to join efforts with

conspecifics to collaborate for larger rewards, even when they had to risk getting nothing (Bullinger, Wyman, Melis, & Tomasello, 2011; Duguid, Wyman, Bullinger, Herfurth-Majstorovic, & Tomasello, 2014; see also Brosnan et al., 2011). Because in all of these examples all partners immediately benefited in a mutualistic manner, these behaviors can be explained by selfish motivations.

Cooperative behaviors are more difficult to explain when they do not result in immediate benefits for all parties. One central mechanism proposed as a solution to this problem is reciprocity: the exchange of favors over time whereby the costs of cooperation are recouped at a later date. A prerequisite for such cooperation to evolve is that cooperators need to be able to identify and preferentially interact with other cooperators (Stevens & Hauser, 2004). This can be achieved by any one of two main proximate mechanisms. First is for individuals to bond emotionally (form "friendships") with other individuals who have benefited them—and friends benefit friends (in both directions). This has been called attitudinal reciprocity (Brosnan & de Waal, 2002). Second is for individuals to determine through observation which individuals are generally cooperative (including to third parties) and then interact preferentially with them, assuming that they will continue to be cooperative to all of their interactants. When that interaction is a prosocial behavior, we can call this mechanism indirect reciprocity. Another possibility is that individuals keep track of favors given and received, but there is little evidence for this kind of calculated reciprocity in nonhuman primate species (Brosnan & de Waal, 2002).

There is much evidence that chimpanzees in the wild and in captivity behave prosocially toward one another in a reciprocal

manner. For example, support in conflicts and meat is exchanged for mating opportunities at a later date, long-term exchange rates of grooming show reciprocal patterns, and prior grooming results in higher rates of subsequent passive food sharing (de Waal, 1997; Duffy, Wrangham, & Silk, 2007; Gomes & Boesch, 2009; Gomes, Mundry, & Boesch, 2009; Schino & Aureli, 2009, 2010). Similar forms of reciprocity have been observed in a number of different species from vampire bats to rats (Axelrod & Hamilton, 1981; Carter & Wilkinson, 2013; Rutte & Taborsky, 2007; Suchak & de Waal, 2012; Trivers, 1971; Wilkinson, 1984). These behavioral patterns in chimpanzees have been mostly observed over long-term contexts and have been proposed to be supported primarily by affective mechanisms such that cooperative partners form close emotional bonds that motivate them to benefit each other prosocially (Brosnan & de Waal, 2002; Engelmann & Herrmann, 2016; Jaeggi, De Groot, Stevens, & Van Schaik, 2013; Schino & Aureli, 2009), although more calculated strategies cannot be fully excluded.

To further understand the proximate psychological mechanisms underlying these reciprocal patterns, a number of laboratory experiments have been conducted. Initial experimental studies on immediate reciprocity in captive chimpanzees have yielded mostly negative results (Brosnan et al., 2009; Melis, Hare, & Tomasello, 2008; Yamamoto & Tanaka, 2009), suggesting the possibility that chimpanzees may not possess the cognitive prerequisites to exchange cooperative favors reciprocally over the short term. However, more recently, this conclusion has been challenged (Schmelz, Grueneisen, Kabalak, Jost, & Tomasello, 2017). In a series of experiments, chimpanzees were found to deliver resources to a conspecific actively if that conspecific had just previously assisted them in a cooperative task, and they did this even when returning the favor involved a material cost. They also appeared to distinguish between cases in which the conspecific provided the assistance for selfish or generous reasons, indicating that they took into account their partner's cooperative intentions when deciding whether to reciprocate. One potential reason why chimpanzees were found to repay cooperative acts in this study but not in others might have been the methodological approach that included strict test criteria ensuring thorough understanding of the apparatus (Brosnan, 2018).

But still, in these experiments, it is not clear if the proximate mechanism involved is something like affective reciprocity or more like indirect reciprocity by observing the other to be a generally cooperative individual. Although indirect reciprocity has not been shown in an experimental context, previous studies suggest that chimpanzees might be able to engage in third-party monitoring. Using two different methodologies, chimpanzees from two different populations were shown to preferentially approach and beg for food from a "nice" individual who had previously provided food to a third party compared with a "nasty" individual who had not given food or who had prevented a prosocial act toward a third party (Herrmann, Keupp, Hare, Vaish, & Tomasello, 2013; Russell, Call, & Dunbar, 2008; see also Subiaul, Vonk, Okamoto-Barth, & Barth, 2008). However, it is unclear whether chimpanzees actually chose to interact with the "nice" individuals or just avoided the "nasty" ones after their bad experience. Moreover, although the ability to distinguish cooperators from noncooperators represents a key prerequisite for indirect reciprocal exchanges, the demonstrated approach behaviors may have been entirely motivated by selfish concerns (i.e., the motiva-

tion to receive food from the nice individuals). Whether observing prosocial acts toward third parties also elicits the motivation to benefit individuals committing those acts is currently an open question.

In the current study, therefore, we used a variation of the paradigm successfully demonstrating costly reciprocal cooperation in chimpanzees (Schmelz et al., 2017) and added an indirect third-party element to investigate the proximate psychological underpinnings of the observed behaviors experimentally. Specifically, we were interested in the two alternative potential mechanisms that might underlie the identification of good cooperators: (a) The direct experience of prosocial behavior of a conspecific may have informed subjects of the partner's cooperative intentions toward themselves, and this may have motivated them to act prosocially toward that particular individual in return, possibly mediated via positive emotional responses. This would be consistent with the view that cooperation in primates is primarily based on affective mechanisms and bonding (Engelmann & Herrmann, 2016; Schino & Aureli, 2009; Tomasello, 2016; Wittig, Crockford, Langergraber, & Zuberbühler, 2014). (b) Alternatively, chimpanzees might generally and nonspecifically be motivated to interact with and act prosocially toward good cooperators. When they observe a conspecific acting cooperatively, they may be willing to cooperate with this individual prosocially in return regardless of whether the initial act of cooperation was directed at themselves or at another individual. Whereas the first explanation relies more on direct interpersonal experiences with cooperation partners, possibly because this strengthens their emotional bonds, the second explanation is based on a more general motivation to identify and interact with good cooperators.

In Experiment 1, subjects could choose whether to act prosocially toward a conspecific partner who had just before either acted prosocially by releasing some food to the subject (direct condition) or to an otherwise noninvolved third-party conspecific (indirect condition). In Experiment 2, we added a control condition in which the partner did not act at all prior to the choice of the subjects to clarify the findings of Experiment 1. Together, the two experiments were aimed at shedding light on the mechanisms of partner choice underlying chimpanzees' reciprocal cooperation. More prosocial choices in the direct condition as compared with the indirect and control condition would support the hypothesis that social bonding better accounts for the reciprocal cooperative patterns observed in chimpanzees than a preference for good cooperators in general.

Experiment 1

Method

Subjects. We initially started the experiment with 15 chimpanzees (three roles: 12 potential test subjects, two potential partners, one third-party individual) living in a social group at the Wolfgang Köhler Primate Research Center in Leipzig, Germany. Five subjects did not pass the open door criterion before experiment 1 and one did not pass the open door postcriterion after experiment 1 (see Procedure below), leaving six subjects to be included in experiment 1 and experiment 2 (two females and four males, average age = 13 years 8 months, age range = 6 years 11 months to 23 years 0 months, all ages at the beginning of data collection). One chimpanzee was dropped as partner due to un-

willingness to participate, leaving one female partner (36 years 4 months) and one female third-party individual (39 years 8 months).

Ethical note. 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 not deprived of food or water and could participate or show unwillingness to participate in the study.

Apparatus. We designed an apparatus in which subjects could choose between a prosocial and a nonprosocial option. To test the role of direct and indirect reciprocity, the three chimpanzees subject, partner, and third-party individual were located in three different rooms. Between room 1 on the left side, room 2 on the far side, and room 3 on the right side, a table (96 × 68 cm) was placed in a booth that could be accessed from all three rooms through mesh panels on their respective sides (Figure 1). On the mesh panel of room 1, the release box (ca. 12 × 12 × 12 cm) was attached and could be operated by sliding a release mechanism sideways. This caused a valued piece of food (banana pellet) on top of a plastic slide clearly visible from room 2 and room 3 to slide down. Depending on the condition, the attached slide either led to room 3 (88 cm in length, 10 cm in width; Figure 1a and 1b) or room 2 (73 cm in length, 10 cm in width; Figure 1c and 1d) so that the food could be retrieved in the respective room. In room 2, the banana pellet was directly accessible through a hole in a transparent access window (33 cm in width, 13 cm in height), and in room 3, it entered into an opaque reward box (13 cm in width, 13 cm in depth, 11.5 cm in height) attached to the mesh that could be accessed by moving up a vertical sliding door (Figure 1b). The release box also included a small opaque compartment that could only be seen and accessed from room 1 and was opened by operating the release mechanism. When the partner was in room 1, a piece of food was placed into this compartment so that she reliably operated the release box. There was never any food in the hidden compartment when a subject was in room 1. Subjects therefore never saw or experienced the possibility of food being present in this compartment and only knew the release box as a mechanism to slide down the food and never as a food source in itself.

On the front half of the table, the prosocial choice task was presented. This included two reward options, option 1 and option 2, that each held two round cups (diameter = 8 cm) out of reach from both sides (Figure 1a and 1c). By sliding a horizontal sliding door (decision window) either to the left or the right, either option 1 or option 2 could be chosen from room 3, and an attached string could be pulled so that one of the two cups moved toward room 1 and the other one toward room 3 (Figure 1b and 1d). Throughout the methods, we will refer to rewards located 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 3 (from where it was chosen) and the second number to the cup accessible from room 1. Once one option was chosen, access to the other was blocked, so that only one option could be chosen per trial. Both the vertical sliding door allowing access to the reward box and the decision window allowing access to the choice between options 1 and 2 were blocked until the release box was operated from room 1. As soon as this happened, the experimenter first unblocked access to the reward box and as soon as the subject opened the vertical sliding door from room 3, the experimenter also unblocked the access to the decision window. The chimpanzees learned during the prerequisite conditions that the reward box could only be accessed when the release mechanism had been operated and the decision window could only be accessed when the reward box had been opened. This predetermined the order of possible actions during the experimental conditions.

Procedure. In all conditions, different trial types and 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 highly valued banana pellets. Trials always started with the experimenter removing a Perspex panel in room 1 to allow access to the release box.
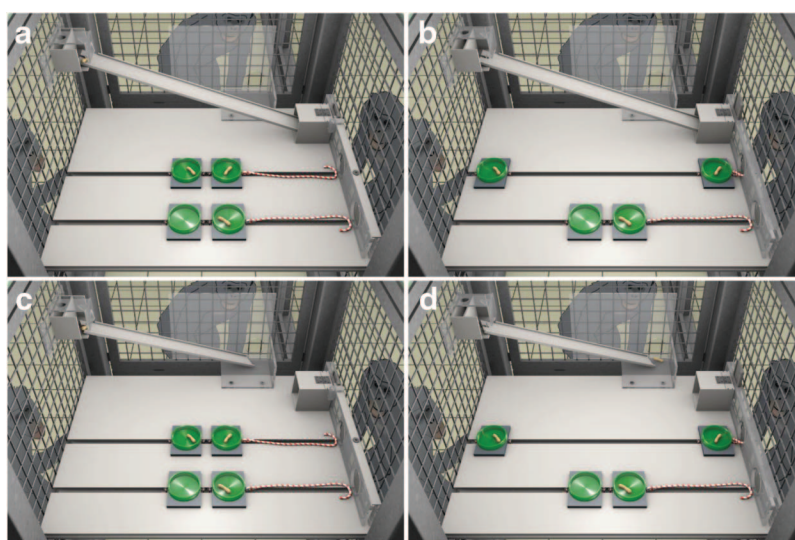

Figure 1. Experimental setup/apparatus. (a) Starting position of the direct condition. (b) End position of the direct condition. (c) Starting position of the indirect condition. (d) End position of the indirect condition. See the online article for the color version of this figure.

Partner training. We trained the partner to always operate the release box as soon as a trial started. As this only involved opening the hidden compartment to access a piece of food for herself (which was the same mechanism that sent down another piece of food down the slide), the partner immediately performed this action reliably without extensive training.

Prerequisite conditions. Subjects first had to pass the open door criterion to show full apparatus understanding. Here they had access to all three rooms and had to maximize their food payoffs by first operating the release box, collecting the released food in either room 2 or room 3, opening the reward box to unblock the decision window, and finally choosing the [1/1] option over the [1/0] option to receive both pieces of food on both sides. The next step was the chance criterion to ensure that the subjects did not generally prefer the [1/1] option over the [1/0] option. Here they only had access to room 3 and had to first open the (empty) reward box to unblock the decision window and then choose between the [1/1] and the [1/0] option. The chimpanzees had to understand that it did not matter which option they chose, as they only received the one piece of food on their side either way. Subjects passed the chance criterion when they showed no statistical preference for the [1/1] option. Finally, to experience what the task looked like from the perspective of the partner and the third-party individual, subjects received one session each of dependence experience 1, 2, and 3. In these sessions, the chimpanzees experienced the possible actions and payoffs when being restricted to rooms 1, 2, and 3, respectively, and that it depended on the actions and choices of another individual—a human test helper in this case—whether they would receive food in each location (see the online supplemental materials for more details on all prerequisite conditions).

Experimental conditions. There were two experimental conditions: direct and indirect. Half of the subjects (randomly chosen) received two sessions of eight trials of the direct condition first and then two sessions of eight trials of the indirect condition. The other half started with indirect and then received direct. Between the different experimental conditions, there was a test break of 10 to 11 days to avoid carryover effects and one more session of dependence experience 3 at the end of the break as a reminder of the partner's role.

Direct. The chimpanzee partner was in room 1, the third-party chimpanzee was in room 2, and the subject was in Room 3. The slide that led to room 3 was attached to the release box with a food reward on top held by the release mechanism. The third-party individual could not do anything in room 2 and did not receive any food during trials in this condition. When the trial started, the partner operated the release mechanism to access hidden food for herself, without subjects being able to see this action behind the opaque release box. This resulted in the seemingly prosocial action of the food reward sliding down toward subjects into the reward box. The experimenter unblocked the reward box and, when subjects had opened it and taken the piece of food, the experimenter also unblocked the decision window so that subjects could make a choice. In half of the trials, option 1 was baited with [1/1] and option 2 with [1/0] and vice versa in the other half of trials.

Indirect. The setup was identical as in direct, except that the slide attached to the release box led to room 2. When the trial started, the partner released the food to slide toward room 2 where the third-party individual could access it. The trial only started once subjects were sitting at the mesh, so that they were able to watch the third party receiving the food and eating it. The experimenter then unblocked the reward box, which was already secretly baited with an additional piece of food that subjects could only see once they had opened the box. This was done so that subjects always received the same amount of food in each condition, as differential rewarding might have influenced their subsequent choice. When subjects had opened the reward box and taken the piece of food, the experimenter unblocked the decision window so that subjects could make a choice.

Open door postcriterion. After the experimental conditions, subjects once more had to pass the open door criterion (see prerequisite conditions) to ensure that they still paid attention to the payoffs and understood the contingencies. If subjects failed to choose the [1/1] option consistently in this condition, their results were dropped from further analysis. One potential subject had to be dropped at this stage, all other subjects passed the criterion (see Table S1 in the online supplemental materials for details).

Data analysis. To analyze the data, we used a generalized linear mixed model (Baayen, 2008). The response variable was whether subjects chose the prosocial [1/1] option, and the only test predictor was the experimental condition (direct vs. indirect). We controlled for session and trial number and included the random intercept of subject ID. To keep Type I error rates at the nominal level of 5%, we included all possible random slope components (i.e., condition, session, and trial number nested within subject ID; see Schielzeth & Forstmeier, 2009). To test for the effect of condition, we used a likelihood ratio test comparing the full model with a reduced model that was identical except that it did not include the experimental condition as a predictor. This analytic approach has the advantage that it allows the residuals of the response measure to be non-normally distributed (in this case, to follow a binomial distribution), that it can handle complex random effect structures (e.g., to have multiple observations from the same individual), and that it allows testing the effect of specific test predictors while controlling for the influence of several potentially confounding variables.

The model was fitted in R (R Core Team, 2013) using the function "glmer" of the R-package lme4 (Bates, Maechler, Bolker, & Walker, 2014). We ran several model diagnostics (model stability, checks for influential cases, variance inflation factors), which were all unproblematic (see the online supplemental materials for detailed model output). In addition, we compared subjects' choices in the two conditions with chance using one-sample *t* tests. Finally, to ensure confidence in the current results, we also ran our main analyses using a more conservative bootstrapping likelihood ratio procedure using the function "PBmodcomp" of the R package "pbkrtest" (Halekoh & Højsgaard, 2014). This practically yielded identical results (see the online supplemental materials).

Results and Discussion

Subjects chose the prosocial option significantly more often in the direct than in the indirect condition, $\chi^2 = 4.46$, $df = 1$, $p = .035$, marginal R^2 (variance explained by the fixed effect) = 0.10, conditional R^2 (variance explained by the fixed and random effects) = 0.45 (see Figure 2). The tendency to choose prosocially did not change over experimental sessions ($\chi^2 = 0.06$, $df = 1$, $p = .814$) or over trials within sessions ($\chi^2 = 0.00$, $df = 1$, $p = .935$).
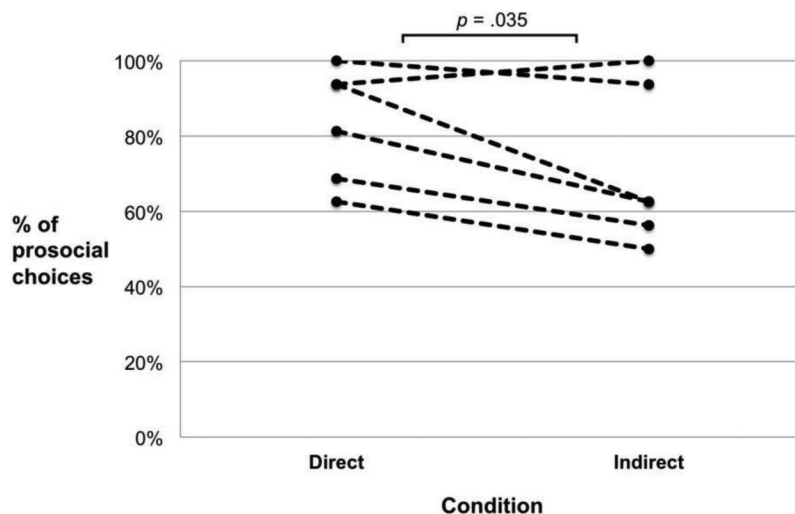
Figure 2. Percentage of prosocial choices per individual in the direct and indirect conditions.

Furthermore, subjects chose the prosocial option significantly above chance in the direct condition, $M = 13.33$ out of 16 trials, chance level $= 8$, $t(5) = 5.39$, $p = .003$. There was also a nonsignificant trend toward higher prosociality than chance in the indirect condition, $M = 11.33$, $t(5) = 5.39$, $p = .058$.

These results show that chimpanzees were more willing to reward prosocial acts directed at themselves than ones directed at the third-party individual. However, we also found an intriguing but nonsignificant trend that subjects rewarded a prosocial act directed at the third-party chimpanzee more than expected by chance. This could potentially mean that they were willing to reward prosocial acts directed at third parties. To follow-up this possibility, we ran a second experiment. This was identical to experiment 1, except that we included an additional control condition in which the subject's choice was not preceded by any prosocial act by the partner. This provided a baseline of subjects' prosocial choices that could be compared with their choices in the direct and indirect conditions.

Experiment 2

Method

Experiment 2 was identical to experiment 1 regarding subjects, apparatus, ethical statement, procedure, and data analysis, except that we added a third experimental condition, the control condition, and a further pairwise comparison between conditions. All six subjects received the three experimental conditions in a different order (assigned randomly). Between the different experimental conditions, there were test breaks of 10 to 28 days to avoid carryover effects and one more session of dependence experience 3 at the end of the breaks as a reminder of the partner's role.

Procedure. In the control condition, the partner was in room 1, the third-party individual was in room 2, and the subject was in room 3. There was no slide attached to the release box, there was no food in the hidden compartment for the partner, and the release box had already been operated (see Figure 3). The partner and the third party could not do anything in this condition. When the trial started, the experimenter waited for a few seconds and then unblocked the reward box, which was baited with a piece of food (to keep the reward structure constant across conditions) that subjects could only see once they had opened the box. When subjects had opened the reward box and taken the piece of food, the experimenter unblocked the decision window so that the subjects could make a choice. In half of the trials, option 1 was baited with [1/1] and option 2 with [1/0] and vice versa in the other half of trials.

Data analysis. We used the same analytic approach to test for the overall effect of condition as in experiment 1. In addition, we ran pairwise comparisons between the three conditions.

Results and Discussion

Overall, there was no significant effect of condition ($\chi^2 = 4.31$, $df = 2$, $p = .116$, marginal $R^2 = 0.10$, conditional $R^2 = 0.20$). However, the comparison of the direct and the control condition revealed a significant effect ($\chi^2 = 4.24$, $df = 1$, $p = .040$, marginal $R^2 = 0.16$, conditional $R^2 = 0.26$), suggesting that subjects chose
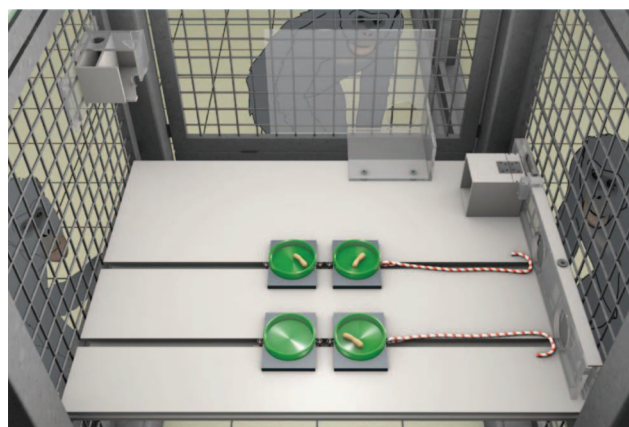

Figure 3. Experimental setup/apparatus in the control condition (starting position). See the online article for the color version of this figure.

the prosocial option more often if their partner had previously assisted themselves than when no assistance preceded their choice. There was no significant difference between the indirect condition and the control condition ($\chi^2 = 0.57$, $df = 1$, $p = .444$, marginal $R^2 = 0.03$, conditional $R^2 = 0.15$) and between the indirect condition and the direct condition ($\chi^2 = 1.67$, $df = 1$, $p = .196$, marginal $R^2 = 0.06$, conditional $R^2 = 0.17$).

Furthermore, subjects chose the prosocial option significantly above chance in all three conditions—direct condition: $M = 12.00$, $t(5) = 4.30$, $p = .008$; indirect condition: $M = 10.67$, $t(5) = 3.51$, $p = .017$; control condition: $M = 9.83$, $t(5) = 3.84$, $p = .012$ (see Figure 4). As in experiment 1, the tendency to choose prosocially did not change over experimental sessions ($\chi^2 = 2.01$, $df = 1$, $p = .156$) or over trials within sessions ($\chi^2 = 0.44$, $df = 1$, $p = .505$). Moreover, the number of prosocial choices did not differ significantly between the two experiments ($\chi^2 = 0.18$, $df = 1$, $p = .667$, analysis comparing prosocial choices in experiments 1 and 2 while controlling for condition, but excluding the control condition of experiment 2), suggesting a high consistency in subjects' prosocial tendencies overall.

General Discussion

Experiment 1 indicates that chimpanzees were more willing to reward prosocial acts directed at themselves than ones directed at a third party. This is in line with previous findings indicating that chimpanzees are prosocially inclined toward individuals who had previously assisted them in acquiring food (Schmelz et al., 2017). Although we found a nonsignificant trend that subjects also rewarded a prosocial act directed at a third party more than expected by chance, the results do not provide strong support for the hypothesis that chimpanzees are generally motivated to prosocially benefit cooperative individuals.

To investigate the nonsignificant trend further, we conducted experiment 2, a replication of experiment 1 with an added control condition. Although there was no overall main effect of condition, pairwise comparisons confirm that—in line with prior work

(Schmelz et al., 2017)—chimpanzees tend to benefit others who have assisted them directly, and they do so more than when no assistance preceded their choice (i.e., in the control condition). A similar effect was not found when comparing the indirect and the control condition. experiment 2 thus also does not provide support for the hypothesis that chimpanzees are generally motivated to benefit cooperators.

Taken together, the two experiments confirm that chimpanzees are motivated to benefit a conspecific partner who has directly benefited them immediately before. This is consistent with the hypothesis that prosocial acts among chimpanzees strengthen the emotional bond between individuals as a psychological mechanism for reciprocal prosocial cooperation. It is less consistent with the hypothesis that chimpanzees generally and nonspecifically act prosocially toward individuals they have observed to be good cooperators.

An intriguing finding is that subjects chose the prosocial [1/1] option above chance level in all three experimental conditions even though prior training criteria ensured that, going into the test, subjects did not have a preference for the [1/1] option in a non-social context (that is, when no partner was present). This criterion was included to rule out the potential low-level explanation that prosocial choices in the actual test can be explained by a mere preference for the larger amount of food in one of the options even when subjects cannot access the food on the partner's side. In experiment 1, this preference could be explained with subjects rewarding the partner's prosocial acts directed at themselves but also doing the same (to a lesser degree) when those acts were directed at others. However, this does not explain the prosocial choices in the control condition in experiment 2 in which no prosocial acts by the partner preceded their choice.

One explanation for this finding is that chimpanzees do sometimes show spontaneous prosocial motivations to transfer resources to conspecifics actively. However, although there is now widespread experimental evidence suggesting that chimpanzees are motivated to help conspecifics reach their goals instrumentally,
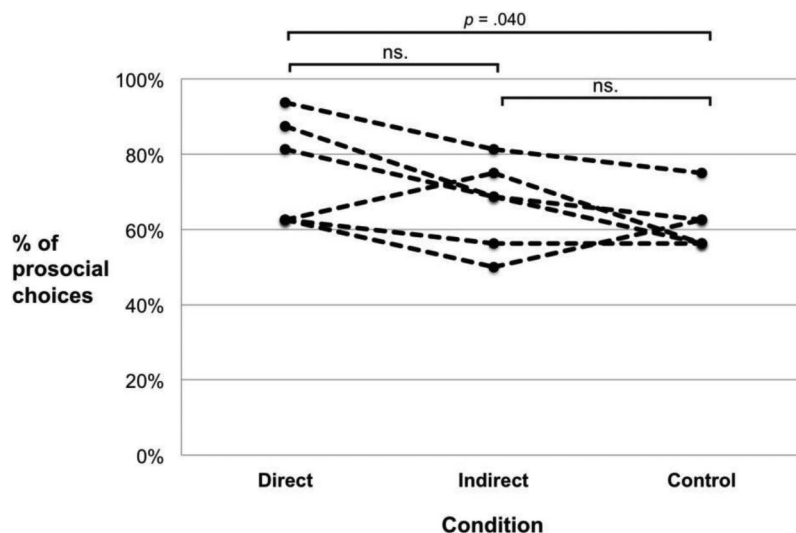

Figure 4. Percentage of prosocial choices per individual in the direct, indirect, and control conditions.

for example, by opening a door so that another individual can access some food (Melis et al., 2011; Warneken, Hare, Melis, Hanus, & Tomasello, 2007; Yamamoto, Humle, & Tanaka, 2012; although this view has recently been challenged: Jensen, 2016; Tennie, Jensen, & Call, 2016), they only appear to do this when they have no chance of accessing any food in the process themselves and when cooperation comes at no or an extremely low physical cost. Although a few studies have reported a certain level of spontaneous prosocial resource delivery in chimpanzees (Claidière et al., 2015; Horner, Carter, Suchak, & de Waal, 2011; House, Silk, Lambeth, & Schapiro, 2014), the effects were small or susceptible to alternative explanations or the claims were not supported by appropriate controls (Heyes, 2012; Jensen, 2016; Schmelz & Call, 2016). Indeed, this explanation would be in stark contrast to several earlier studies (Jensen, 2016; Jensen, Hare, Call, & Tomasello, 2006; Silk et al., 2005) and our own previous study (Schmelz et al., 2017). However, because the partner in the current study was a different individual, this explanation deserves further exploration in the future, particularly with regard to the question whether chimpanzees display partner-specific prosocial preferences. Due to the small sample size, the effect of social and genetic relationships could not be analyzed statistically in the current study. However, if there was an effect on the results, it was not straightforward (see Table S1 in the online supplemental materials for more details).

Another explanation might be that—in contrast to previous studies using this paradigm and to our chance criterion at training—subjects in the current study were provided with food just prior to their choice, either directly supplied by the partner in the direct condition or because it was already present in the reward box in the other conditions. They might have been more inclined to act prosocially due to the positive experience of "discovering" food in the reward box just before their choice (but note that this explanation cannot account for the difference between conditions in the current experiments). Future studies could directly test how contextual factors such as access to food affect chimpanzee's prosocial inclinations.

There was no evidence for a difference between the indirect condition and the control condition in experiment 2. The increased level of prosocial choices compared with chance in the indirect condition (that we also found in experiment 1 to a lesser degree) does therefore not seem to reflect any reaction to the partner acting prosocially toward the third-party individual. However, subjects did choose the [1/1] option significantly more often in the direct condition compared with the indirect condition in experiment 1 and significantly more often in the direct condition compared with the control condition in experiment 2. The only evidence for truly prosocial behavior caused by their partner's actions can therefore be found in the direct condition. When looking at only the absolute numbers in experiment 2, one could speculate that chimpanzees potentially showed an increase in prosocial choices across the three conditions: the lowest level in the control condition, a medium level in the indirect condition, and the highest level in the direct condition. However, the heightened prosocial baseline and the small sample size preclude any chance of exploring this intriguing possibility with the current data.

The combined results of experiment 1 and 2 are thus most consistent with the hypothesis that chimpanzees are motivated to reciprocate prosocial behaviors directed at themselves, suggesting that they use direct experience to identify cooperative partners (direct reciprocity). By contrast, the results are less consistent with the hypothesis that they are motivated to benefit individuals prosocially who had behaved prosocially toward others (indirect reciprocity), indicating that the mere observation of cooperative acts is not sufficient to elicit cooperative behaviors in response. This is in line with the bonding hypothesis stating that chimpanzees need to experience a prosocial act personally and directly to connect with their partner and establish cooperation. However, in the current study and in our previous findings (Schmelz et al., 2017), we did not find carryover effects into the control conditions after subjects had directly experienced prosocial acts of their partner; that is, the bond that was established in these interactions did not remain over the test break between conditions. Indeed, there seemed to be no individual differences in the prosocial choices across the counterbalanced subjects that had experienced the experimental conditions in different orders, suggesting that prior experience of the partner's prosocial assistance did not have a lasting effect. It can therefore be argued that the "seed" of bonding that we created artificially would have had to be maintained and fostered more consistently—as would be the case in more naturalistic settings—to have more lasting effects.

The current findings do not preclude the possibility of more calculated behaviors or heuristic decision rules that have also been observed in chimpanzees and other social animals (Calcutt, Proctor, Berman, & de Waal, 2019; Melis et al., 2006; Taborsky, Frommen, & Riehl, 2016). It would be very interesting to see specific tests of the different hypotheses with strict criteria of task understanding in other species. In rats (*Rattus norvegicus*), it has been proposed that females but not males might engage in generalized reciprocity (Rutte & Taborsky, 2007; Schweinfurth, Aeschbacher, Santi, & Taborsky, 2019). Cleaner wrasses (*Labroides dimidiatus*) increased their levels of cooperation in the presence of an image-scoring audience (Pinto, Oates, Grutter, & Bshary, 2011). Which ecological factors play into different aspects of reciprocal behavior is an important question for future research.

It must be noted that the bonding hypothesis that emphasizes affective responses and the hypothesis that chimpanzees more strategically look for good cooperators are not mutually exclusive. For instance, observing a partner prosocially assist a third party could potentially trigger positive emotions and, as a consequence, the inclination to act prosocially toward that partner (although this was not supported by our data). Likewise, we cannot be sure that subjects' responses in the direct condition were devoid of strategic motivations. However, our interpretation is consistent with prior assertions that primate cooperation is to a substantial degree based on affective mechanisms.

One limitation of the current study was the small sample size. However, we stress the need for strict criteria to ensure thorough apparatus understanding, as no inference can be drawn from the subjects' test performance if they cannot be shown to know what consequences their actions have (Brosnan, 2018). With the various criteria in the current study in place, we can confidently state, for instance, that subjects did not experience the partner's prosocial act toward the third party in the indirect condition as a decision of the partner *against* a prosocial act toward themselves. Subjects understood the contingencies of the apparatus, the fixed slides in the different conditions, and the possible actions the partner could perform.

In conclusion, in a series of two experiments, we show that chimpanzees show direct reciprocal responses to a prosocial act of a conspecific partner, although there was little evidence that they show indirect reciprocal responses when the partner prosocially assisted a third party. This indicates that the proximate mechanism of identifying good cooperators to establish reciprocal cooperation in chimpanzees is primarily based on direct experiences with specific individuals—possibly based on emotional bonding—rather than the motivation to generally benefit good cooperators.

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