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Chimpanzees trust conspecifics to engage in low-cost reciprocity

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Many of humans' most important social interactions rely on trust, including most notably among strangers. But little is known about the evolutionary roots of human trust. We presented chimpanzees (*Pan troglodytes*) with a modified version of the human trust game—trust in reciprocity—in which subjects could opt either to obtain a small but safe reward on their own or else to send a larger reward to a partner and trust her to reciprocate a part of the reward that she could not access herself. In a series of three studies, we found strong evidence that in interacting with a conspecific, chimpanzees show spontaneous trust in a novel context; flexibly adjust their level of trust to the trustworthiness of their partner and develop patterns of trusting reciprocity over time. At least in some contexts then, trust in reciprocity is not unique to humans, but rather has its evolutionary roots in the social interactions of humans' closest primate relatives.

1. Introduction

On all levels of social interaction, human cooperation is critically dependent on trust [1,2]. From small-scale cooperative interactions between dyads and small groups of people [3], to the workings of large-scale institutions [4] and markets [5], and even whole nations [6], trust is an essential ingredient for the establishment and maintenance of mutually cooperative relationships.

The benchmark test for empirical investigations of trust is the trust game [7]. In its standard version, two anonymous individuals are assigned the roles of investor and trustee. First, the investor has a choice of two options. The investor can either keep an initial endowment or send it to the trustee. If the investor chooses to send the endowment to the trustee, the initial amount is multiplied by some factor and now the trustee has to choose between two options: keeping the total amount (maximizing his own pay-off but stiffing the investor) or sending half back to the investor. Traditional economic theory predicts that investors should transfer zero money to the trustee and the trustee, if given the opportunity, should transfer zero money back, but much empirical work shows that this prediction is false [1]. In developing new models to explain such behaviour, economists have highlighted a possibly human-specific concern for the welfare of others, so-called other-regarding social preferences [8].

Although it seems that humans are exceptional, if not unique, in the animal kingdom regarding the extent to which they can establish and maintain trust not only among closely knit groups but also among strangers [9], very little is known about the phylogenetic origins of such skills. Studying primates, and in particular one of human's closest relatives, the chimpanzees, is one way to identify these origins. The fact that chimpanzees show cooperative abilities in a wide range of circumstances is indicative of the possibility that individuals are able to form trusting relationships. This is suggested by research from the field where chimpanzees form coalitions and long-term alliances [10,11], patrol their territory in groups [12], share food with related and unrelated group members [13,14] and engage in group hunts [15,16]. A similar picture emerges from controlled experiments; for example, Melis *et al*. [17] found that chimpanzees cannot only successfully solve a mutualistic food-retrieval task that requires two individuals to simultaneously pull both ends of a rope, but also selectively recruit the more skilful of two potential partners [18]. In addition, chimpanzees have been shown to provide help to human

carers [19] and also to conspecifics [20,21], but evidence for the latter is mixed [22,23].

In addition, many non-human primates, including chimpanzees, cooperate with group mates in reciprocal patterns [24,25]. A common finding is that individuals who support a coalitionary partner on one occasion, are often supported by that partner in return at a later time [26,27]. Moreover, coalition partners are more likely to groom one another [28] and to share meat [29]. de Waal [30,31] argues and presents evidence that these reciprocal patterns of cooperation are not underlain by any kind of calculated reciprocity involving mental scorekeeping, but rather by attitudinal reciprocity in which individuals value emotionally rewarding social relationships and want to maintain them. Recent research has demonstrated that when chimpanzees groom one another or share food with one another, both the one receiving the benefit and the one providing the benefit show an increase in the mammalian bonding hormone oxytocin [14,32]. Because oxytocin has been associated with feelings of trust in humans [33], it is possible that chimpanzees are experiencing trust in these interactions. But oxytocin is associated with many different positive social emotions [34], and so it is unclear whether trust is involved in chimpanzees' cooperative interactions. Another possibility is that chimpanzees show a sense of 'strategic trust', in which they know what it is in the interest of another individual to do—including to cooperate with them in some particular circumstance—and they count on this individual behaving in this self-interested way.

In the current studies, we presented chimpanzees with a modified, non-verbal version of the trust game. Chimpanzees had a choice between pulling a no-trust rope (resulting in immediate access to low-quality food) and a trust rope (thereby allowing a partner access to high-quality food, which he could then send a part of—a part he himself could not access—back). Regarding its pay-off structure, the current version of the trust game is thus distinct from the human version in one main aspect: partners could not access all of the high-quality food, thereby decreasing the partners' incentive for exploiting subjects' trust. In line with the human research, trust was operationalized as a decision by the 'investor' to send the high-quality food to the partner. In Study 1, we investigated whether chimpanzees show spontaneous trust in conspecifics in a novel context. Study 2 investigated whether chimpanzees selectively adapt their trusting behaviour to the trustworthiness of their partner. And, finally, Study 3 explored chimpanzees' ability to establish and maintain a trusting relationship without any experimental manipulation.

2. Study 1

(a) Method

(i) Subjects and materials

Fifteen chimpanzees, living at Sweetwaters Chimpanzee Sanctuary, Kenya, participated in this study (see the electronic supplementary material). Subjects were tested in dyads with nine chimpanzees solely acting as subjects and six chimpanzees exclusively as partners.

In Study 1, subjects had a choice between pulling one of two ropes (figure 1). Pulling the no-trust rope resulted in immediate access to low-quality food for the subject only (one piece of lemon and one piece of orange). Pulling the trust rope resulted in a small vehicle moving along a track to the partner. The vehicle consisted of two compartments, each containing high-quality food (a mix of bananas and apples). The partner could eat the food from one compartment only and then either send the vehicle (with the second compartment still baited) back by pulling a small rope (prove trustworthy) or not send the vehicle back (prove untrustworthy) to the subject. The partner did not have access to both food compartments.

(ii) Procedure and design

Familiarization. All subjects were individually introduced to the experimental set-up (see the electronic supplementary material).

Study. In a within-subjects design, subjects engaged in a control and a test condition. Specifically, subjects first engaged in one session of three control trials, then in six test sessions of one trial (each with a different partner), and at the end again in one control session consisting of three trials. The procedure of control and test trials was identical except for the absence of a partner in room 3 during control trials. However, during control trials, a chimpanzee was present in room 4 in order to rule out any effects based on the presence of a conspecific alone. At the beginning of both conditions, control and test, chimpanzees were in room 1 and the following procedure was applied. In counterbalanced order, experimenter 1 (E1) baited the two apparatuses, calling the subjects name while doing so. Next, E2 opened the door between rooms 1 and 2. Chimpanzees then entered room 2 and chose one of the two ropes. E3 removed the other rope once subjects had started pulling either rope. During control and test conditions, if subjects pulled the no-trust rope, the trial ended once subjects had stopped eating the low-quality food. If subjects pulled the trust rope in the control condition, the trial ended after 30 s. If subjects pulled the trust rope in the test condition, the partner, located in room 3, was given 90 s to send the food back. If the partner did not send the food back, the trial ended after 90 s. If the partner sent the food back, the trial ended once subjects had finished eating.

It was coded whether subjects pulled the trust rope (for full coding, refer to the electronic supplementary material).

(b) Results

Figure 2 presents the average rate of pulling the trust rope for each individual in the control and test condition in Study 1. A Wilcoxon matched-pairs exact test revealed a significant difference between the control (Mdn = 0.33) and test condition (Mdn = 0.833), ($n = 9$), $z = -2.25$, one tie, $p = 0.004$. Chimpanzees thus pulled the trust rope significantly more often in the test condition as compared with the control condition.

Regarding the partners' behaviour, trusting decisions by chimpanzees were reciprocated in 32% of all trials.

3. Study 2

In a second study, using the same basic set-up, we investigated whether chimpanzees are simply prone to blind trust or whether, alternatively, they flexibly adjust their level of trust to the trustworthiness of their partner.

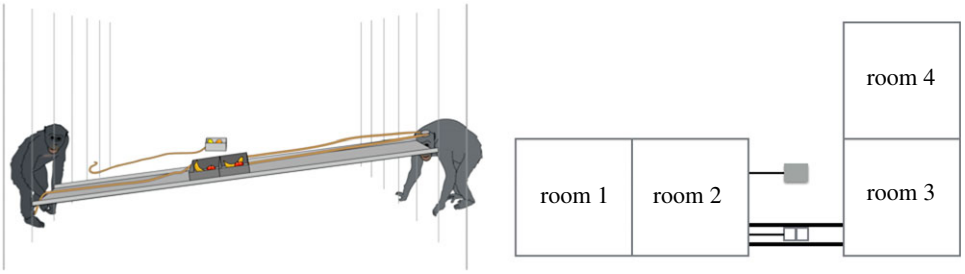

Figure 1. Experimental set-up. In all studies, subjects (situated in room 2) had a choice between pulling the trust-rope or the no-trust rope. (Online version in colour.)

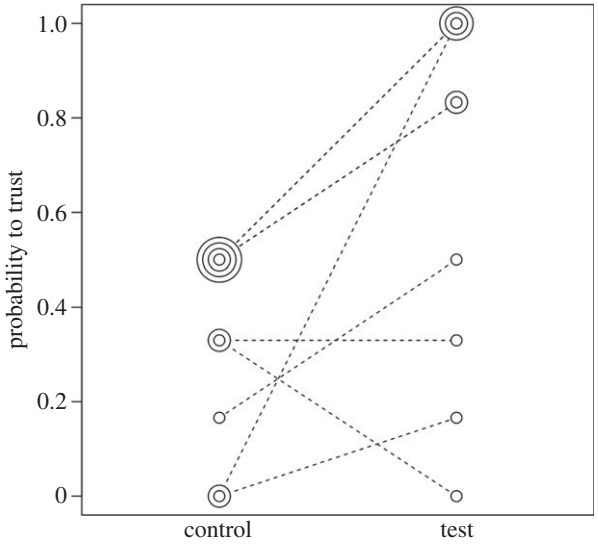

Figure 2. Results of Study 1. Probability to trust for each individual in the test and control condition. Each circle represents the average behaviour of one individual.

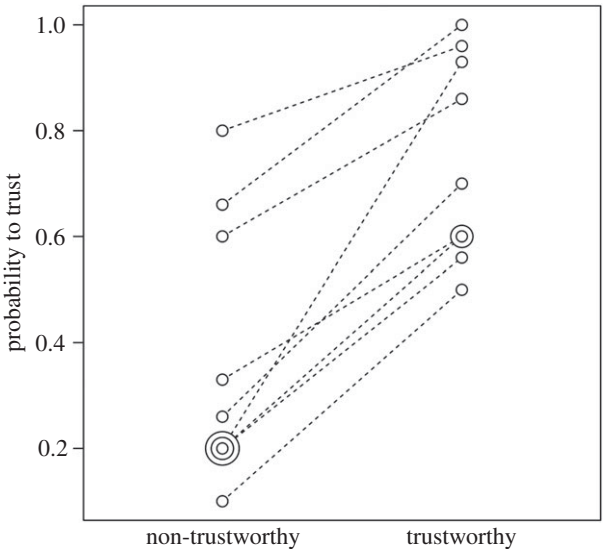

Figure 3. Results of Study 2. Probability to trust for each individual when confronted with a trustworthy and a non-trustworthy partner. Each circle represents the average behaviour of one individual.

(a) Method

(i) Subjects and materials

The same subjects as in Study 1 participated in Study 2. Subjects were again tested in dyads with the same nine chimpanzees acting as subjects and the same six chimpanzees acting as partners as in Study 1. In addition, identical apparatus was used.

(ii) Procedure and design

In Study 2, in a within-subjects design, subjects interacted with three trustworthy partners (i.e. partners that always sent the vehicle back) and three untrustworthy partners (i.e. partners that never sent the vehicle back). Thus, in contrast to Study 1, the trustworthiness of partners was systematically manipulated. In each session, subjects interacted for 10 trials with one partner. The trustworthiness of partners as well as their sequence was counterbalanced across subjects. The same general procedure was applied as during study 1. Subjects started in room 1 and had the choice between pulling the trust rope or the no-trust rope in room 2. If subjects pulled the no-trust rope, E1 removed the trust rope and the chimpanzee moved back to room 1 once she had finished eating. If subjects pulled the trust rope, E3 removed the no-trust rope. Partners in the trustworthy condition then had 30 s to send the vehicle back. If the partner did not release the mechanism, E1 released the mechanism by pulling a transparent rope from outside the subject's visual field (this was done while the partner was still manipulating the apparatus to access his food, so as to give the impression that the partner had sent the vehicle back). In the partner untrustworthy condition, the small rope that allowed partners to send the vehicle back was removed (subjects could not see this rope from their vantage point). Thus, partners could not send the food back. Again, once subjects had finished eating their food (in the trustworthy condition) or after 60 s (in the untrustworthy condition), subjects moved back to room 1. Then the next trial started.

For coding, refer to the electronic supplementary material.

(b) Results

Figure 3 presents the average rate of pulling the trust rope for each individual with the trustworthy and untrustworthy partners. Chimpanzees showed significantly more trust in trustworthy partners (Mdn = 0.7) than in non-trustworthy partners (Mdn = 0.26) as revealed by a Wilcoxon matched-pairs exact test, ($n = 9$), $z = -2.67$, zero ties, $p = 0.002$. In addition, we ran a logistic generalized linear mixed model (GLMM) to examine whether subjects' probability to trust was influenced by trial and partner, by including these two predictors as well as their interaction (to test whether there was a different temporal pattern depending on the partner's trustworthiness),

and controlling for day (for a full description of the model, refer to the electronic supplementary material). We found no effect of day ($\chi^2 = 0.06$, d.f. = 1, $p = 0.81$) and that increasing trial number influenced subjects' levels of trust differently depending on trustworthiness of the partner ($\chi^2 = 9.29$, d.f. = 1, $p = 0.002$), showing that subject's probability to trust increased over trials if the partner proved trustworthy compared with when the partner proved untrustworthy (figure 4).

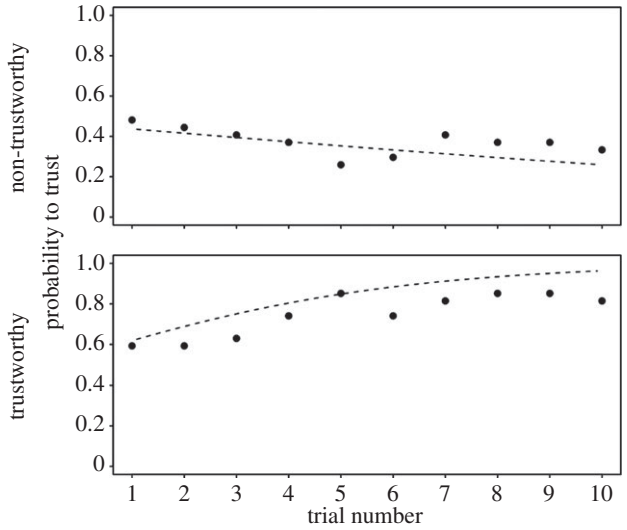

Figure 4. Interaction between trust level and trial number. Subjects' probability to trust when faced with a trustworthy or non-trustworthy partner as a function of trial number.

4. Study 3

Study 2 showed that chimpanzees are not simply prone to blind trust but rather flexibly adjust their levels of trust to the trustworthiness of their partner, with this effect increasing over time. In a third study using the same set-up, we investigated whether chimpanzees who had already learned the trust game could spontaneously establish and maintain a trusting relationship on their own.

(a) Method

(i) Subjects and materials

From the pool of nine subjects having participated in Studies 1 and 2, four chimpanzees were randomly selected to act as subjects in Study 3. From the same pool, four chimpanzees were arbitrarily selected to act as partners and were, again randomly, paired with the subjects. Thus, importantly, the chimpanzee dyads participating in Study 3 were novel pairs; they had never been paired in either Study 1 or 2. The identical apparatus as in Studies 1 and 2 was used.

(ii) Procedure and design

The same basic procedure as in Study 2 was implemented in Study 3. In this study, each dyad received 10 trials per session. In total, each dyad received five sessions, resulting in a total of 50 trials. However, in contrast to Study 2, the trustworthiness of the partners was not manipulated in Study 3. Partners were thus free to send the food back (prove trustworthy) or not send the food back (prove untrustworthy).

In Study 3, a trusting relationship was defined as choosing the trust option significantly more often than expected by chance over the course of 5 days and 50 trials. For coding, refer to the electronic supplementary material.

(b) Results

We conducted a GLMM to investigate whether subjects' trusting behaviour changed as a function of trial number (for a full description of the model, see the electronic supplementary material). This analysis revealed no effect of trial ($\chi^2 = 0.25$, d.f. = 1, $p = 0.62$) but a positive and clearly significant intercept (estimate $\pm$ s.e. = 1.12 ± 0.43, $z = 2.62$, $p = 0.008$) indicating a higher than chance probability for the investor to pull the trust rope. This result also holds on the individual level, where three of the four dyads were significantly more likely to pull the trust rope (all three binomial tests, $p < 0.01$). At least some chimpanzee pairs, then, were able to establish and maintain a trusting relationship with a randomly chosen partner over the course of 5 days and 50 trials.

In addition, using a second GLMM (see the electronic supplementary material), we examined whether subjects' behaviour was influenced by the partners' behaviour on the previous trial. We included dyad as a random effect and the probability to pull the trust rope after the partner had behaved trustworthy as fixed effect, and controlled for trial number. This revealed no effect of trial number ($\chi^2 = 2.87$, d.f. = 1, $p = 0.1$), but a significant effect of partner' behaviour at trial $x - 1$ on subjects' behaviour at trial x ($\chi^2 = 4.32$, d.f. = 1, $p = 0.04$).

Regarding the partners' behaviour, trusting decisions by chimpanzees were reciprocated in 58% of all trials.

5. Discussion

The current results demonstrate that chimpanzees can form trusting relationships with unrelated conspecifics in low-cost contexts. In Study 1, subjects showed spontaneous trust in group members in a 'one-shot' situation, although subjects had never interacted with their partners in the current situation before. They also showed that they are not indiscriminately trustful but rather flexibly adjust their trust levels to the trustworthiness of their partner (Study 2). Combining these results, one might argue that chimpanzees show a version of 'generous tit-for-tat' [35,36], that is, they enter a cooperative situation with an initial propensity to trust their partner but then flexibly reciprocate the partner's behaviour. If the partner proves trustworthy, trust levels remain high, but if the partner proves untrustworthy trust levels decrease. And finally, the chimpanzees showed an ability to establish and maintain, to some degree, a trusting relationship over the course of 50 trials with a randomly paired partner (Study 3). In addition, Study 3 found that subject's behaviour at trial x was influenced by their partner's behaviour at trial $x - 1$. This represents an important addition to the literature on animal reciprocity as it suggests that trusting acts are indeed contingent on the partner's previous behaviour, even in the short term [37]. A further interesting point relates to the partner's behaviour. Specifically, while partners reciprocated trusting decisions by subjects in 32% of all trials in Study 1, they reciprocated in 58% of all trials in Study 3. This potentially suggests that partners discriminated between one-shot (Study 1) and repeated (Study 3) interactions, strategically increasing their cooperation in the latter case.

However, as the current studies were not designed to test this question, alternative explanations cannot be ruled out (e.g. partners might have reciprocated more in Study 3 because they had acted as subjects before). Whether chimpanzees indeed distinguish between one-shot and repeated interactions thus represents an interesting avenue for further research.

An alternative explanation of the current results might attempt to describe the chimpanzees' behaviour simply in terms of the frequency of obtained rewards. Such an explanation might claim that chimpanzees pay no attention to the presence or absence (Study 1), or the trustworthiness (Study 2) of a partner, but simply adapt the pulling of the trust rope to the frequency of received rewards. However, we think that such an interpretation is implausible as it is unlikely to account for the full behaviour displayed by chimpanzees in the current studies. First of all, results from the control condition of Study 1 show that chimpanzees did understand that they needed a partner in order to have a chance of receiving the high-quality food in the current set-up; in addition, previous studies have shown that chimpanzees' reinforcement learning from arbitrary cues is slow and usually takes several dozens of trials [38–40], but in the current study subjects received very few trials. Finally, partners' behaviour in Studies 1 and 3 was inconsistent, which would have made it extremely difficult to learn via arbitrary cues which rope consistently resulted in more food. Instead of reinforcement learning based on arbitrary cues, we believe that chimpanzees in the current study evaluated their partners' cooperative tendencies (so-called image scoring) and, based on these evaluations, interacted with trustworthy, but not untrustworthy, partners. Several previous studies have shown that chimpanzees evaluate others based on both direct experience [18] as well as from observing third-party interactions [41–43].

Studies on human behaviour on the one hand reveal commonalities of non-social risk decisions and social trust decisions [44], but also a trust-specific 'betrayal aversion' [45], suggesting that humans differentiate between social risk (i.e. risk imposed by another person) and non-social risk. Further empirical studies are necessary to conclusively show that chimpanzees differentiate between such situations and potentially also experience betrayal aversion.

The current results suggest that trust in reciprocity shows important evolutionary continuities with at least one of our closest living relatives. The non-verbal version of the trust game employed in the current study differed in three aspects from the standard human trust game. First, most human studies use a small and a large amount of the same resource (mostly money) as the non-trusting and trusting option, respectively. In the current studies, we used two different types of food. However, in all trials where chimpanzees did not pull the trust rope, they pulled the low-value rope and ate the associated food, presenting strong evidence that also the low-value food was appealing to the chimpanzees. Second, most studies on the human trust game are one-shot interactions: truster and trustee interact with each other for a single trial only. In the test condition of Study 1, we tried to model a one-shot interaction as closely as possible. Subjects engaged in six trials and each of these trials involved interaction with a different partner. In Studies 2 and 3, we investigated subjects' behaviour over more trials, thereby exploring chimpanzees' trust under more natural assumptions: repeated interactions. Lastly, in the current set-up, subjects and partners had no control over the exact splitting of the endowment. Partners could not keep all of the resource, thus making reciprocation, compared with the human version, low cost. Subjects, however, still had to trust their partner when pulling the trust rope. After all, the partner's decision not to return the food would leave the subject empty handed.

These methodological adaptations have a strong bearing on the interpretation of the current results. Social scientists (e.g. [46]) have differentiated among strategic and moral forms of trust. We think that the chimpanzees' behaviour in the current studies is best explained in terms of strategic trust. Such trust materializes in situations where trusters' and trustees' interests are perfectly or almost perfectly aligned and there is thus little incentive to defect. Just as humans' behaviour in the trust game is influenced by beliefs about the partner's trustworthiness [1], chimpanzees' behaviour in the same game may be influenced by beliefs about the partner's tendencies towards reciprocity. In the current study, investors may realize not only that reciprocating is low-cost for trustees, but also that future interactions are likely, and so reciprocation is probable. It would thus seem that strategic trust is not uniquely human but already characterizes the cooperative interactions of humans' closest living relatives. Whether chimpanzees, like humans, also show moral trust in situations where trustees have a strong incentive to defect and experience associated feelings such as betrayal [45] represents an interesting avenue for further research.

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Data accessibility. Data for this publication can be accessed here: Dryad doi:10.5061/dryad.76v09.

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