Report

Current Biology

Chimpanzees Trust Their Friends

Highlights

- We investigate whether chimpanzees trust their friends more than their non-friends
- An observational phase is followed by an experimental investigation of trust
- Results show that chimpanzees place special trust in their friends
- Trust within close relationships is not unique to humans

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In Brief

Engelmann and Herrmann investigate whether chimpanzees place greater trust in their partner when interacting with a friend compared to a non-friend. Results of a modified version of the trust game show that chimpanzees place special trust in their friends. Trust within close relationships, therefore, is not a uniquely human characteristic.

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Report

Chimpanzees Trust Their Friends

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SUMMARY

The identification and recruitment of trustworthy partners represents an important adaptive challenge for any species that relies heavily on cooperation [1, 2]. From an evolutionary perspective, trust is difficult to account for as it involves, by definition, a risk of non-reciprocation and defection by cheaters [3, 4]. One solution for this problem is to form close emotional bonds, i.e., friendships, which enable trust even in contexts where cheating would be profitable [5]. Little is known about the evolutionary origins of the human tendency to form close social bonds to overcome the trust problem. Studying chimpanzees (*Pan troglodytes*), one of our closest living relatives, is one way of identifying these origins. While a growing body of research indicates that at least some of the properties of close human relationships find parallels in the social bonds of chimpanzees [6–10] and that chimpanzees extend favors preferentially toward selected individuals [11–14], it is unclear whether such interactions are based on trust. To fill this gap in knowledge, we observed the social interactions of a group of chimpanzees and established dyadic friendship relations. We then presented chimpanzees with a modified, non-verbal version of the human trust game and found that chimpanzees trust their friends significantly more frequently than their non-friends. These results suggest that trust within closely bonded dyads is not unique to humans but rather has its evolutionary roots in the social relationships of our closest primate relatives.

RESULTS

Economics commonly defines trust as follows: individual A trusts individual B if A voluntarily places resources at the disposal of B without any legal agreement. Trust is embedded in A's expectation that the act will pay off in terms of her goals, so if B proves trustworthy, A is better off than if the resources were not offered, whereas if B proves untrustworthy, A is worse off than if the resources had been kept [3, 15].

Trust is thus inherently uncertain as it involves the risk of exploitation by cheaters who fail to prove trustworthy. One solution to this problem is the formation and maintenance of close and long-term social relationships, i.e., friendships [5, 16]. Human friendships are commonly characterized by preferential attitudes and intentions to trust, help, support, and share within intimate social relations [17, 18]. In keeping with this definition, much evidence indicates that human friendships have evolved especially robust forms of trust that are relatively immune to the contingencies of a volatile and ever-changing environment [17, 19]. While nothing is known about trust in closely bonded chimpanzee dyads, a recent experimental study found evidence suggesting that chimpanzees show spontaneous trust in members of their social group and flexibly adjust their level of trust to the trustworthiness of their partner [20].

In the current study, we investigated whether chimpanzees trust their friends more than their non-friends. In a first step, we observed the social interactions of a group of 15 chimpanzees at Sweetwaters Chimpanzee Sanctuary, Kenya, for a period of 5 months (see Table S1). Using scan sampling [21], the following behaviors were recorded: grooming, contact, arm's reach, and co-feeding. Observers also noted whether a given individual was present (i.e., could be seen) or not. Then, based on 352 hr of data, we calculated the composite index of sociality (CSI) for each dyad [22]. To determine friends and non-friends, we selected as friend the chimpanzee that exhibited the highest CSI with a given individual and as non-friend the chimpanzee that exhibited the lowest CSI with the same individual (see Table S2).

The second step of the current investigation consisted of an experimental investigation of chimpanzees' trust in friends and non-friends. Chimpanzees participated in a modified, non-verbal version of the human trust game (see Figure 1). Subjects had a choice between pulling a no-trust rope (resulting in immediate access to less-preferred food) and a trust rope (thereby allowing a partner access to preferred food, which he could then send a part of—a part he himself could not access—back). In a within-subjects counterbalanced design, subjects engaged in 12 trials with their friend and 12 trials with the non-friend. In line with the human research, trust was operationalized as a decision by the "investor" to send the preferred food to the partner.

We ran a generalized linear mixed model (GLMM) to examine whether subjects trusted their friends more than their non-friends. We included as fixed effects condition, trial number, sex, and counterbalance (whether chimpanzees started as subjects or partners) in the model. The results revealed no effect of sex (χ^2 = 0.96, degrees of freedom = 1, p = 0.32), trial number (χ^2 = 1.16, df = 1, p = 0.28), or counterbalancing (χ^2 < 0.001, df = 1, p = 0.99), but a highly significant effect of condition (χ^2 = 8.22, df = 1, p = 0.004), showing that subjects were more likely to trust their friends than their non-friends (see Figure 2 and Table S2).

We ran a second GLMM to test whether any of the two types of partners (friends and non-friends) were more likely to reciprocate

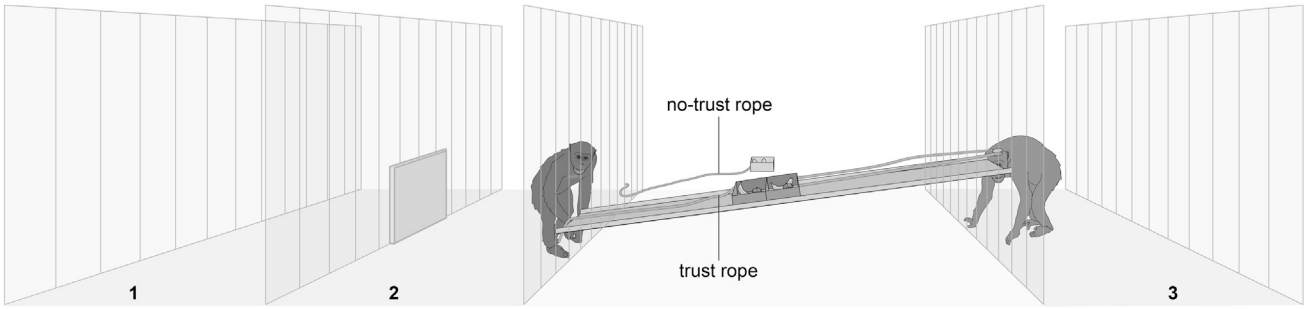

Figure 1. Experimental Setup
In the modified version of the human trust game, subjects (situated in room 2) had a choice between pulling the trust rope and the no-trust rope. The gray box between rooms 1 and 2 depicts a door that allowed subjects to move between rooms.

trust by sending the preferred food back. This included condition, trial number, counterbalancing, and sex as fixed effects. The results revealed no effect of sex (χ^2 = 0.07, df = 1, p = 0.79), trial number (χ^2 = 2.80, df = 1, p = 0.09), and condition (χ^2 = 0.66, df = 1, p = 0.41), showing that friends and non-friends were equally likely to reciprocate trust (see Figure 3). Finally, in a third GLMM, we investigated whether friends were more likely than non-friends to request food but did not detect any evidence for this (χ^2 = 0.24, df = 1, p = 0.62). For details on all models, see Supplemental Experimental Procedures.

DISCUSSION

The current results demonstrate that chimpanzees trust their friends more than their non-friends. In line with the economic definition of trust, chimpanzees were significantly more likely to voluntarily place resources at the disposal of a partner, and thus to choose a risky but potentially high-payoff option, when they interacted with a friend as compared to a non-friend. This finding provides evidence that chimpanzees, like humans, evolved robust forms of trust toward their close social partners, which might allow them to forge cooperative relationships even in contexts where threats of defection by cheaters loom large.

A number of researchers have investigated the adaptive benefits of friendship in various primate species and found that well-integrated individuals with stable social bonds show fitness gains in the form of increased offspring survival and longevity [23–27]. To date, relatively little attention has been paid to proximate mechanisms underlying primates' social relationships (for an exception, see [28]). The current study extends this line of research by showing that increased levels of trust characterize close social bonds in chimpanzees.

An alternative interpretation of the current results might be that it was not trust that influenced the subjects' choices but simply increased prosociality toward friends. However, the two main paradigms used to investigate prosociality in chimpanzees, the prosocial choice task [29] and instrumental helping tasks [30, 31], yielded mixed results. In the prosocial choice task, chimpanzees showed no signs of prosociality. In instrumental helping tasks, chimpanzees showed prosociality only in situations in which they could not access any food themselves or did not have to give up any of their own food. Crucially, pulling the trust rope in the current study does necessitate that subjects give up valued food (accessible using the no-trust rope). Furthermore, requests by potential recipients have been shown to be crucial to eliciting prosociality in instrumental helping tasks [30], but we did not find increased requests by friends compared to non-friends in the current study. Therefore, we believe that the more likely interpretation of chimpanzees' behavior is trust in their friend rather than prosociality.

A second finding of the present study was that both friends and non-friends reciprocated trust in more than two-thirds of all trusting events and were thus equally likely to prove trustworthy. A potential explanation for this finding is that reciprocation in the current setup is low cost. While proving trustworthy in the classic human version of the trust game is costly and requires trustees to give up part of a resource (usually money) that they possess, chimpanzees in the current setup prove trustworthy by sending back part of a resource that they cannot access themselves. Research on human relationships has shown that friends can tolerate inequalities and are largely unconcerned with immediate reciprocation [10, 32], and there is limited evidence for this in chimpanzees [33, 34] and bonobos [35] as well. One possibility is that chimpanzees in the current study were less concerned with immediate reciprocation when they interacted with closely bonded partners and continued to trust friends at higher levels even though they did not reciprocate more than non-friends. Future research is necessary to conclusively show that closely bonded chimpanzee dyads, like human friends, tolerate inequalities and do not rely on strict forms of contingent reciprocity. As a corollary, the fact that friends and non-friends were equally likely to reciprocate trust precludes explanations of the current findings exclusively in terms of payoff structures. These results suggest that the chimpanzees' decisions about whom to trust and whom not to trust are grounded in decidedly social factors, namely the specific identity of a given partner.

The current results extend the findings of a previous study on trust in chimpanzees [20]. While the previous study revealed that chimpanzees show basic trust in members of their social group, the current study highlights the relevance of close social relationships to trusting attitudes. In addition, while the previous results were interpreted as "strategic trust," the current results might be more appropriately explained in terms of "emotional trust" [36–38]. Rather than basing their decision to trust on calculated and strategic computations of short-term levels of reciprocation, chimpanzees might experience trusting a closely

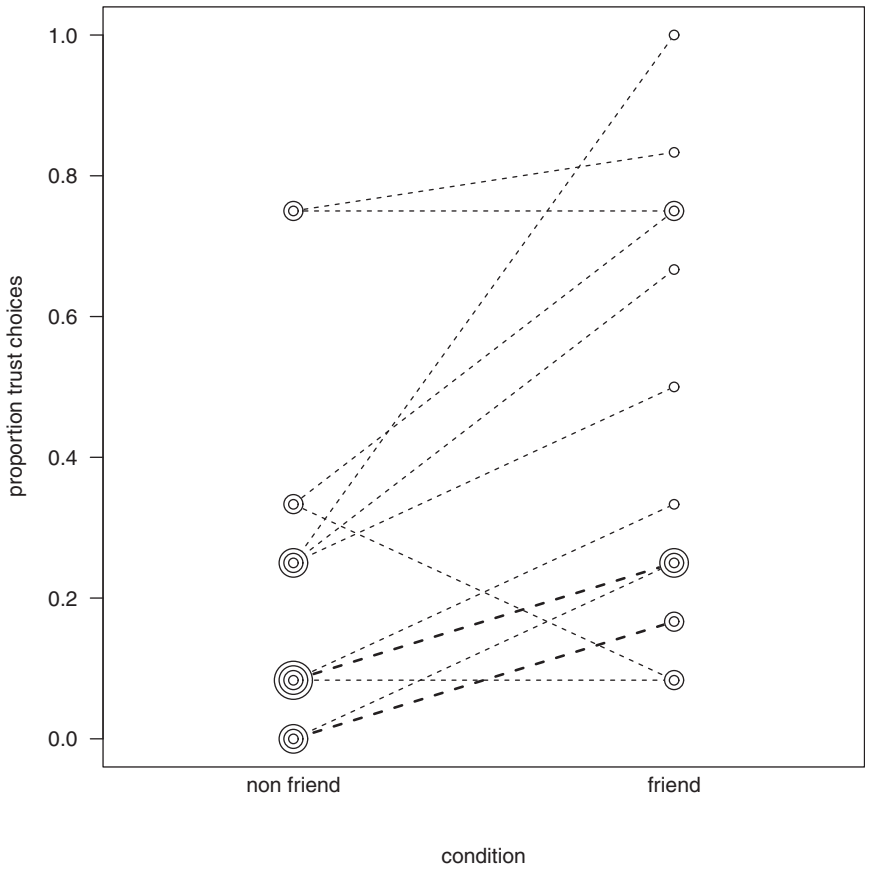

Figure 2. Proportion of Trust Choices for Each Individual in the Friend and Non-friend Conditions

Each circle represents the average behavior of one individual across 12 trials. Multiple circles at a given trust rate indicate that several subjects showed that score. Dashed lines connect the behavior of a given subject in the non-friend and friend conditions. Thicker dashed lines indicate that two subjects showed a given change across conditions.

bonded partner as emotionally rewarding [28]. In that case, trust serves as a mechanism to maintain and reinforce valued relationships.

Taken together, the current findings support the view that social relationships of primates in general, and chimpanzees in particular, are key to explaining individual behavior in a variety of situations [39–41]. Social interactions among dyads and larger associations of animals cannot be accurately understood by examining the individual characteristics of involved parties alone and must take ongoing social relationships into account. The current study investigated one such component of social relationships, trust, and found that chimpanzees extend trust selectively to their friends, a behavior that likely plays an important role in their cooperative activities including food sharing, grooming, and coalition formation.

EXPERIMENTAL PROCEDURES

Part 1: Observational Phase

Subjects

In this phase, the observed social group consisted of 15 chimpanzees (8 females and 7 males), ranging in age from 9 to 28 years (mean = 20.3 years) and living in Sweetwaters Chimpanzee Sanctuary, Kenya. Except for two chimpanzees, who joined the group in 2013, all individuals had lived in the group since the mid-to-late 1990s (see Table S1). The group included one mother-daughter dyad. Over the course of this study, group composition was stable, and none of the females were pregnant or lactating. Chimpanzees spend the day in a large outdoor enclosure (29 ha) with regular feedings, daily enrichment, and water ad lib.

Chimpanzees are fed three times during the day (morning, noon, evening), and observational data collection always took place during the hour leading up to feeding. Animal husbandry and research complied with the "PASA Primate Veterinary Healthcare Manual" and the policies of Sweetwaters Chimpanzee Sanctuary, Kenya.

Materials and Procedure

Four research assistants collected observational data between December 2014 and May 2015 using a Samsung tablet equipped with CyberTracker software (version 3.389). In total, 352 hr of observational data were collected. During each observation, scan samples were collected for 60 min. Every 10 min, observers conducted a scan, noting the activities of each group member in the same predefined order. These activities included grooming (observers noted who the focal animal groomed and/or who she was groomed by), contact (any two body parts of two individuals touching in an affiliative manner), arm's reach (two individuals sitting at a distance that would allow them to have contact if both extended their arms), and co-feeding (two individuals eating while sitting within arm's reach).

Analysis of Observational Data

We first calculated the frequency with which each individual was grooming, in contact, at arm's reach, or co-feeding with all other individuals. The frequencies of the four activities were positively correlated within dyads and consequently cannot be considered independent sources of information about relationship quality. Following Silk, Cheney, and Seyfarth [22], we calculated the CSI for each dyad using the following formula:

$$CSI_{xy} = \frac{\sum_{i=1}^{4} \frac{f_{ixy}}{\bar{f}_i}}{4}$$

In this equation, f_{ixy} is the rate of behavior i for dyad xy, and $\bar{f}_i$ is the mean rate of behavior i across all dyads. The rate of a given behavior i for dyad xy was calculated by dividing the number of interactions i between x and y by the number of times that both x and y were present. Since the CSI involves the division of the rate of a given behavior within a dyad (f_{ixy}) by the average of that behavior across all dyads ($\bar{f}_i$), its outcome describes the extent to which a particular dyad deviates from the average of all dyads. Dyads with a high score are more closely bonded than the average dyad, and, conversely, dyads with a low score are less closely bonded than the average dyad.

Coding

To determine friends and non-friends, we selected as friend the chimpanzee that exhibited the highest CSI with a given individual and as non-friend the chimpanzee that exhibited the lowest CSI with the same individual (see Table S2). In doing so, we strictly adhered to the results of the CSI computations and did not, for example, selectively focus on same-sex dyads. While both male-male [11, 42] and female-female [43] bonds are common in chimpanzees, recent work by Langergraber and colleagues [44] suggests that bonds between sexes also exist. The one exception to this general rule was kinship. Since we were interested in social bonds among unrelated partners, we

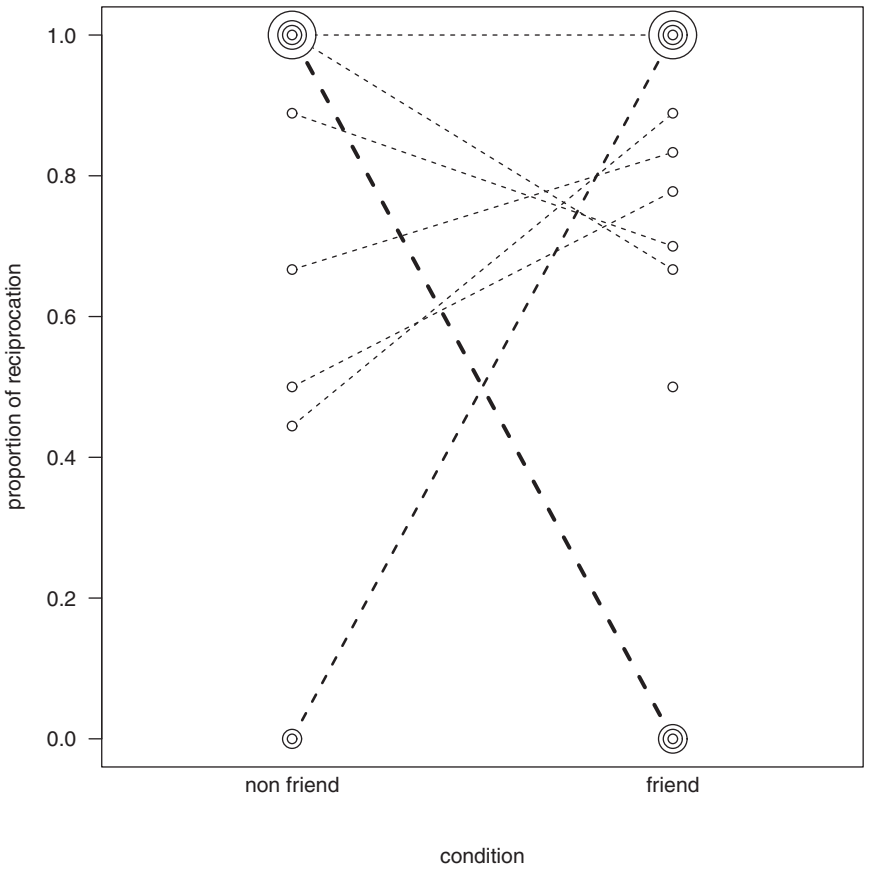

Figure 3. Proportion of Reciprocation as a Function of the Friend and Non-friend Condition

Each circle represents the average behavior of one individual. Multiple circles at a given trust rate indicate that several subjects showed that score. Dashed lines connect the behavior of a given subject in the non-friend and friend conditions. Thicker dashed lines indicate that two subjects showed a given change across conditions, and the thickest dashed lines indicate that three subjects showed a given change across conditions.

selected as friend for the one mother-daughter dyad in our sample not the individual with the highest CSI (which would have been the mother for the daughter and vice versa) but the individual with the second-highest CSI.

Part 2: Experimental Phase

Subjects and Materials

Of the 15 chimpanzees that were observed during the first part of this study, 14 chimpanzees participated in part 2 (one male chimpanzee did not pass criterion on apparatus understanding; see Supplemental Experimental Procedures). Participants were tested in dyads with all but two chimpanzees acting as both subjects and partners (Table S2).

During the experimental phase, subjects had the choice of pulling one of two ropes (Figure 1). Pulling the no-trust rope resulted in immediate access to less-preferred food for the subject only (two pieces of banana; for results of the food preference test, please refer to the Supplemental Experimental Procedures). Pulling the trust rope resulted in a small vehicle moving along a track to the partner. The vehicle consisted of two compartments, each containing preferred food (three pieces of banana and three pieces of apple). 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.

Procedure and Design

Familiarization. All subjects first underwent a food preference test and were then individually introduced to the experimental setup (see Supplemental Information).

Study. In a within-subjects design, subjects engaged in a friend condition and a non-friend condition. The order of conditions was counterbalanced across subjects. In each condition, subjects participated in six trials on two consecutive days, amounting to a total of 12 trials per condition. Since all but two of the participants acted as both subjects and partners, we also counterbalanced whether participants started as subjects or partners. Half of the participants started as subjects and the other half as partners. The design of the friend and non-friend conditions was identical except for the identity of the partner in room 3 (see Figure 1). In friend conditions, the subject's friend (highest CSI) was located in room 3. In non-friend conditions, the subject's non-friend (lowest CSI) was located in room 3. Before each trial and before subjects entered the testing rooms, partners were moved to room 3. At the beginning of each trial, subjects were in room 1, and the following procedure was applied. In counterbalanced order, experimenter 1 (E1) baited the two apparatuses, calling the subject's name while doing so. Next, E2 opened the door between rooms 1 and 2. Entering room 2, chimpanzees chose and pulled one of the two ropes. If subjects pulled the no-trust rope, E1 removed the trust rope, and the trial ended once subjects had stopped eating the less-preferred food. If subjects pulled the trust rope, E3 removed the no-trust rope, and the partner, located in room 3, was given 60 s to send the food back. If after 60 s the partner did not send the food back, the trial ended. If the partner sent the food back, the trial ended once subjects had finished eating. During trials, E1 (who stood 2 m left of the trust rope) and E3 (who stood 2 m to the right of the no-trust rope) remained quiet and stationary, with their heads facing the floor.

We coded whether subjects pulled the trust rope (for full coding, please refer to the Supplemental Information).

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures and two tables and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2015.11.037.

AUTHOR CONTRIBUTIONS

J.M.E. and E.H. designed and conducted the study, analyzed the data, and wrote the manuscript.

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