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Social disappointment explains chimpanzees' behaviour in the inequity aversion task

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Chimpanzees' refusal of less-preferred food when an experimenter has previously provided preferred food to a conspecific has been taken as evidence for a sense of fairness. Here, we present a novel hypothesis—the social disappointment hypothesis—according to which food refusals express chimpanzees' disappointment in the human experimenter for not rewarding them as well as they could have. We tested this hypothesis using a two-by-two design in which food was either distributed by an experimenter or a machine and with a partner present or absent. We found that chimpanzees were more likely to reject food when it was distributed by an experimenter rather than by a machine and that they were not more likely to do so when a partner was present. These results suggest that chimpanzees' refusal of less-preferred food stems from social disappointment in the experimenter and not from a sense of fairness.

1. Introduction

One key challenge in sustaining cooperation lies in distributing collaboratively acquired resources so that everyone is satisfied and motivated to collaborate in the future [1–5]. To resolve situations in which individuals with conflicting interests have to agree on resource distribution, humans use a variety of fairness principles such as merit, authority, need and equality [6–10]. Humans' sense of fairness is most clearly expressed in a strong aversion to inequity, which culminates in the often costly punishment of unfair behaviour, even by third parties that do not personally suffer from inequity [11–14]. According to some theorists, sensitivity to fairness has played a key role in stabilizing cooperation during human evolution [1,2,12]. However, as other animals also engage in stable patterns of cooperation [4,15–22], there is considerable debate about the extent to which a sense of fairness and a concomitant aversion to inequity is uniquely human [23–33].

A variety of experimental designs (e.g. the ultimatum game) have been used to examine sensitivity to equity [34–36]. The best evidence for a sense of fairness in non-human animals comes from an ingenious experimental paradigm first developed for capuchin monkeys by Brosnan & de Waal [23], known as the inequity aversion task. The prototypical version of this task comprises a series of exchange interactions involving three agents: an experimenter, an advantaged recipient and a disadvantaged recipient. The two recipients engage in the same effortful task (e.g. handing back a token), but while the first receives preferred food from a human experimenter, the second recipient is offered less-preferred food. The main finding is that individuals from various species of primates reject the less-preferred food (food that they would otherwise readily accept) if a conspecific gets better food for the same effort [28]. A similar pattern of behaviour has recently been demonstrated in various species outside the primate taxa, such as domestic dogs, rats, and possibly crows and ravens [37–42]. The question from a psychological point of view is: how are rejections of the less-preferred food to be interpreted.

One hypothesis is the inequity aversion hypothesis. Brosnan & de Waal [23,28], for example, interpret food rejections in the inequity aversion task as indicative of social comparison and thus ultimately of a burgeoning sense of fairness. They argue that when individuals see that a conspecific gets better food for the same effort, they feel that they are treated unfairly and protest by refusing to accept the food offered to them. Thus, according to the inequity aversion hypothesis, individuals' refusals of less-preferred food are all about the partner: subjects react negatively to receiving less than a partner. However, a number of subsequent studies have failed to replicate these original results and provided additional data that pointed to an alternative explanation for food refusals: the food expectation hypothesis [25,26,29,43,44]. According to this hypothesis, recipients simply see the preferred food or observe a conspecific receiving preferred food and expect that they will receive the preferred food as well. When individuals then receive the non-preferred food, this expectation is violated, and they subsequently react by refusing to accept the less-preferred food. One version of the food expectation hypothesis is the frustration hypothesis [45–47]. The well-known frustration effect (also known as contrast effect) typically occurs in situations where subjects first receive a preferred reward, followed by a less-preferred reward. Individuals' rejection of the less-preferred food in such cases is linked to the change of food quality experienced by the subject and not to the subject expecting to receive preferred food because her partner received preferred food. According to the food expectation and the frustration hypotheses, individuals' behaviour in the inequity aversion paradigm is all about the food: subjects react negatively to receiving the less-preferred food because they expect preferred food.

Here, we propose and experimentally investigate a novel hypothesis: the social disappointment hypothesis. This hypothesis postulates that individuals in the inequity aversion task do not object to how they are treated in comparison to how another is treated but simply to how they are treated relative to how they could be treated by the human experimenter [1,48–51]. Chimpanzees are disappointed by the actions of an experimenter who has the ability to reward them with a preferred food item but distributes a non-preferred food item instead. The social disappointment hypothesis is grounded in experimental and observational evidence suggesting that chimpanzee cooperation is mostly regulated through so-called emotional bookkeeping in dyadic social bonds [52–56]. In line with these results, the current hypothesis maintains that chimpanzees' responses in the inequity aversion task reflect a dyadic response to how they are treated by the experimenter—independent of any social comparison with the partner. More specifically, individuals' emotional expressions and refusals to accept the less-preferred reward convey disappointment with the human experimenter for providing a poor piece of food when she could have provided a better one. The social disappointment displayed by individuals in the inequity aversion task is therefore a distinctively interpersonal emotional reaction to being treated worse than one expected to be treated. This implies that the inequity aversion task reveals special expectations of social agents and not fairness considerations. The social disappointment hypothesis thus focuses on a relationship that has received very little attention from other theorists: that between experimenter and disadvantaged recipient. According to this hypothesis, refusals of less-preferred food are all about the experimenter: individuals react negatively to receiving worse treatment than they expected to receive from the human experimenter. The social disappointment hypothesis differs from the inequity aversion hypothesis in that it is dyadic in nature (involving the subject and experimenter) and does not require complex tracking and comparing of relative pay-offs across multiple ongoing social interactions but instead only a fairly straightforward evaluation of how one is treated by the human experimenter (in comparison to how one could be treated). In comparison to the food expectation and frustration hypotheses, it differs in that it is decidedly social in character and expresses disappointment with social content.

We tested the social disappointment hypothesis in chimpanzees and compared our results with other explanations for refusals in the inequity aversion task. In order to do so, we combined the central elements of each hypothesis. The key variable for the social disappointment hypothesis is whether an experimenter is present or not. In the current set-up, food was thus distributed either by the experimenter or, in the absence of the experimenter, by a machine. The social disappointment hypothesis argues that chimpanzees' negative reactions to receiving the less-preferred food are grounded in interpersonal expectations of social agents (i.e. the human experimenter), and a distributing machine should not elicit such expectations. While such methods, to our knowledge, have never been implemented in studies with non-human primates, it should be noted that a recent study by Brucks *et al*. [57] presents preliminary evidence that dogs react differently—at least on some measures—to unequal distributions that are created by an experimenter versus a machine.

The key to the inequity aversion hypothesis is to manipulate whether a conspecific partner is present or not. Therefore, in our experiment, food was distributed either in the presence or absence of a conspecific partner. In a set-up manipulating these two factors, the social disappointment hypothesis predicts that recipients should be more likely to refuse the less-preferred food when they interact with a human experimenter rather than with a machine, and that their refusal should not be influenced by the absence or presence of a conspecific partner who receives the preferred food. This is in notable contrast with the inequity aversion hypothesis, which predicts that the type of food distributor (human or machine) should have no influence on individuals' refusals and that subjects should be more likely to reject food with a conspecific partner present. The food expectation and the frustration hypotheses both predict that the type of distributor and the absence/presence of a conspecific partner should make no difference to individuals' reactions to receiving the less-preferred food.

Finally, the set-up of our inequity aversion task conformed to the two characteristics highlighted by Brosnan & de Waal [28] as especially relevant to eliciting responses to inequity. First, chimpanzees had to engage in a task in order to receive their rewards: they had to take a tool from an apparatus and reinsert it in order to gain access to food. Second, chimpanzees were seated closely side-by-side, which allowed for clear visibility of the respective rewards (figure 1). Our main measure, based on previous studies [24], was chimpanzees' rate of refusal to exchange their tool for food. As this represents a demanding measure in requiring subjects to reject otherwise palatable food, we also

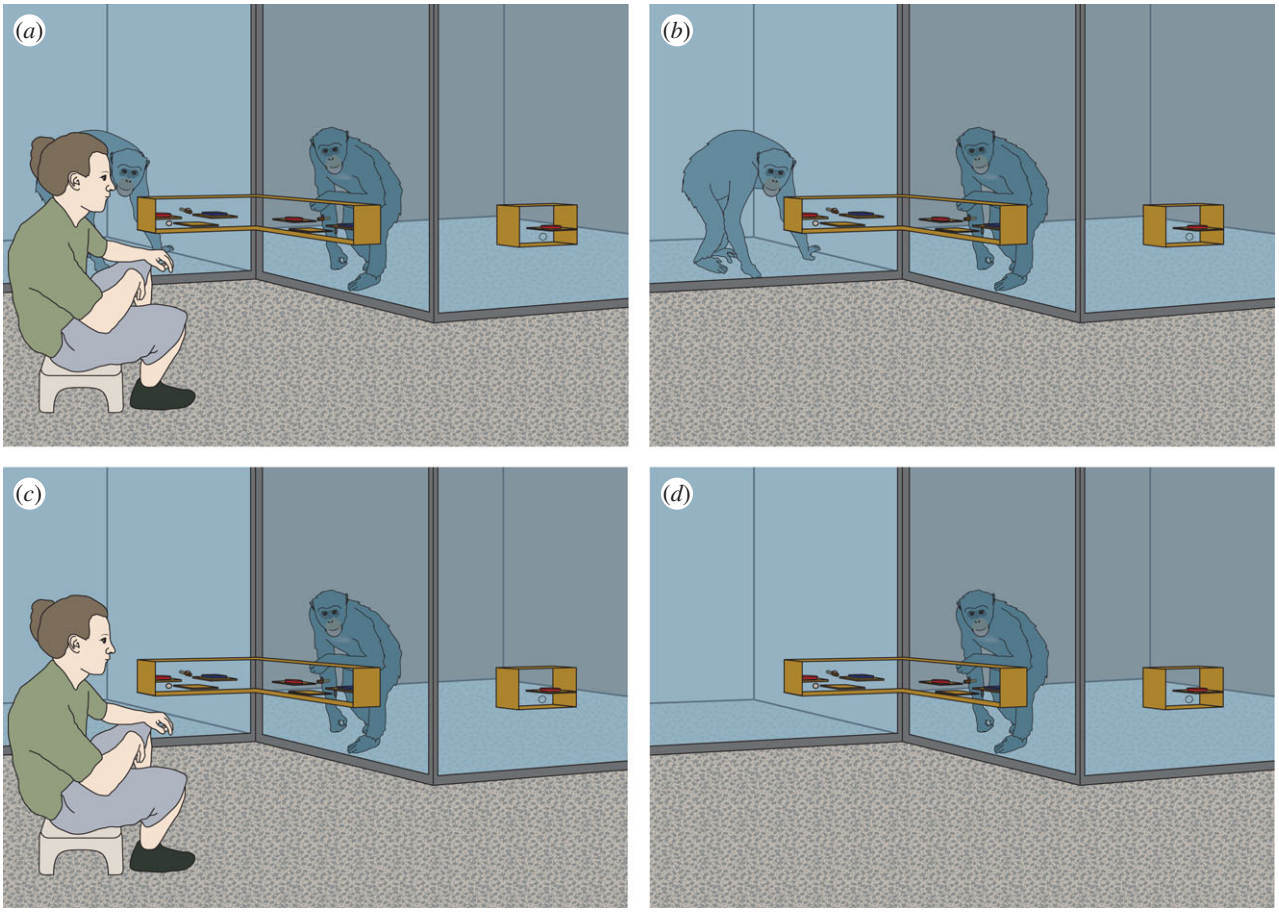

Figure 1. Experimental set-up. The main apparatus is the yellow structure accessible to both chimpanzees, the opt-out apparatus is the structure on the right. Note that for purposes of clarity, the food trap in the main apparatus is not shown. Blue items represent high-value foods and red items represent low-value foods. By removing the tool (located in-between the two food platforms) and re-inserting it in the hole next to the food table (located below the two food platforms), chimpanzees could access the food that had been distributed by either the experimenter or the machine. The different images depict each condition of our 2 × 2 design: (*a*) human/partner present, (*b*) machine/partner present, (*c*) human/partner absent and (*d*) machine/partner absent. (Online version in colour.)

included an additional, non-costly option to reject the experimenter's (or the machine's) distribution, which we called the opt-out possibility. Following previous work [29], subjects thus had the possibility to reject a given distribution without having to give up access to food.

2. Material and methods

(a) Subjects

Nine chimpanzees (five males and four females) ranging in age from 7 to 42 years ($M = 17.2$ years) participated in the study (see the electronic supplementary material, table S1). The subjects were housed in two social groups at the Wolfgang Köhler Primate Research Center in the Leipzig Zoo (Leipzig, Germany). Of the participants, four acted solely as subjects ($M = 13.3$ years) and five acted as both the partner and the subject ($M = 20.4$ years; see the electronic supplementary material, table S2). Two of the subjects were nursery-reared, six were mother-reared and one (Frederike) is without a documented rearing history (see the electronic supplementary material, table S1).

Chimpanzees had access to a large outdoor enclosure during the day and received regular daily feedings, daily enrichment and water ad libitum. Subjects voluntarily participated in the study and were never food or water deprived.

(b) Materials

Two apparatuses were used during testing: the main apparatus and the opt-out apparatus. The main apparatus consisted of two identical units that mirrored each other when affixed to the mesh. One unit was attached to the partner's room and the other was attached to the subject's room. Each participant could only access their portion of the apparatus (figure 1). In the upper section of each unit, there were two food platforms and a slot where subjects could take the tool. In the middle section, there was a food trap that was hidden from both participants' view. The lower portion comprised a food table and a tool reinsertion hole. Food from the food table could only be accessed when the tool was inserted into the hole (in the default position the food was blocked by a window). Importantly, participants could no longer access tools after they had been fully reinserted. The sides of the apparatus flush with the mesh were transparent, which allowed each participant to clearly see each other's food on the food platforms and the food on the food tables following distribution. Thus, the main apparatus functioned as follows: once participants removed the tool from the main apparatus, food pieces were distributed either by the experimenter or the machine (depending on condition). The distributor placed one piece of food on the food table (where food could be accessed) and the other piece of food in the food trap (where foods could not be accessed). If participants chose to reinsert the tool into the main apparatus, they thereby gained access to the food placed on the food table.

Alternatively, during the test phase, participants could decide to insert the tool (once they had removed it from the main apparatus) into the opt-out apparatus. The opt-out apparatus was attached outside of the mesh on the wall of the subject's room running along the hallway (figure 1). The opt-out consisted of a food table and a tool reinsertion hole.

As with the main apparatus, a Plexiglas window sat flush against the mesh and would drop when the tool was completely reinserted. If subjects inserted the tool into the opt-out apparatus, they could access the food from the food table.

(c) Procedure and design

(i) Design

We employed a 2×2 design with distributor (human versus machine) as a between-subjects factor and partner presence (partner present versus partner absent) as a within-subjects factor. The procedure consisted of three consecutive steps: a food preference test (see the electronic supplementary material), a familiarization phase (see the electronic supplementary material) and the test phase.

(ii) Test phase

In a mixed design, subjects completed four test sessions (each comprising 24 trials) on four days in the same distribution groups (human or machine) as they were assigned during familiarization. Subjects were tested for two consecutive sessions with a partner and two consecutive sessions without a partner. Whether the subject started testing with a partner or without was counterbalanced (for details on subjects, partners and counterbalancing see the electronic supplementary material, table S2). At the beginning of each trial, a second experimenter baited the partner's food platforms and the subject's food platforms with both high-value food (HV) and low-value food (LV), and the opt-out apparatus with LV food. During the test phase, the first experimenter (E1) made the tools accessible to the chimpanzees (either directly in the human condition or from outside the testing room in the machine condition) and the second experimenter was responsible for resetting and rebaiting the apparatus (for details, see the electronic supplementary material). Below, each of the four conditions is described in detail.

Human/partner condition (figure 1*a*; electronic supplementary material, video S1). In this condition, the experimenter distributed the pieces of food. First, the tool was made accessible to the partner (E1 did so by pulling a concealed rope). Once the partner removed the tool from the slot in her portion of the main apparatus, E1 distributed the food placing the HV food onto the food table and the LV food in the food trap. Next, the partner inserted the tool into the apparatus and obtained and consumed the HV food. Then, it was the subject's turn. E1 made the tool in the subject's portion of the main apparatus accessible approximately 10 s after food distribution for the partner (or, if the partner took longer, once the partner had accessed the HV food). The procedure for the subject was exactly the same as for the partner except that LV food was now placed on the food table and HV food went in the trap. In all four conditions, subjects could only see the food distribution after they had removed the tool. Also in all four conditions, the trial ended once the subject completed the exchange by re-inserting the tool into the main apparatus and consumed the food, inserted the tool into the opt-out or refused to exchange the tool (see the Coding section).

Human/no partner condition (figure 1*c*; electronic supplementary material, video S2). This condition was identical to the *human/partner* condition except for the absence of a partner: the subject was the only chimpanzee present. Both the partner's and the subject's portion of the main apparatus were still baited with LV and HV food. First, E1 distributed the foods on the partner's side of the main apparatus, placing the HV food onto the food table and the LV food in the food trap. Approximately 10 s after this food distribution, E1 made the tool available to the subject. The remaining part of this condition was identical to the *human/partner* condition.

Machine/partner condition (figure 1*b*; electronic supplementary material, video S3). In this condition, the experimenter was outside of the room. Both chimpanzees, subject and partner, were present. First, to make the partner's tool accessible, E1 pulled a rope from outside the testing room. When the partner took the tool, food was distributed automatically (as a result of the partner removing the tool): HV food fell onto the food table and LV food fell into the food trap. Approximately 10 s after the automatic food distribution for the partner (or once the partner had accessed the HV food), E1 made the subject's tool accessible (again by pulling a rope from outside the testing room). The procedure for the subject was the same as for the partner, except the subject received LV food (HV food fell into the food trap and LV food fell onto the food table).

Machine/no partner condition (figure 1*d*; electronic supplementary material, video S4). In this condition, the subject was the only chimpanzee present in the testing room. First, E1 pulled a rope from outside the testing room to make the partner's tool accessible. Then, since there was no partner chimpanzee to remove the tool, E1 pulled a second rope that allowed for the platforms to automatically tilt and distribute the food. The remaining part of this condition was identical to the *machine/partner* condition.

(d) Coding

All trials were videotaped with two cameras. We coded all trials live as well as after testing from video. For our analysis, we only included trials in which subjects initiated the trial by removing the tool from the apparatus within 30 s of it being made available and thus saw the distribution of foods (see electronic supplementary material, table S3). After subjects took the tool, their behaviour was coded in one of three ways: refusal to exchange; choice of opt-out apparatus; completed exchange with the main apparatus.

(i) Refusal to exchange

Our main analysis was based on refusals to exchange. Cases in which the subject chose not to insert the tool into either apparatus within 30 s of the tool's removal were coded as refusals to exchange. Refusal to exchange included behaviours such as moving to the corner of the room with the tool (see the electronic supplementary material, video S2), dropping the tool on the floor or throwing the tool out of the room (see the electronic supplementary material, video S1).

Initially, we further divided refusals to exchange into (i) active and passive refusals (active refusals to exchange included instances in which the subject expelled the tool from the testing room while passive refusals to exchange included instances in which the tool stayed in the testing room for the 30 s duration/refusal window); and (ii) refusals to consume (if the subject reinserted the tool into the main apparatus but did not consume the distributed food within 30 s, a refusal to consume was coded). However, because both active refusals to exchange and refusals to consume were extremely rare (subjects showed active refusals to exchange in only 1.6% of trials and refusals to consume in 1.1% of trials), we collapsed the data into one category: refusal to exchange.

(ii) Choice of opt-out apparatus

Our secondary analysis was based on the opt-out apparatus. If the subject chose to insert the tool into the opt-out apparatus, the choice was coded as 'opt-out'.

(iii) Completed exchange with the main apparatus

If the subject successfully took the tool, reinserted the tool into the main apparatus, and then consumed the distributed food,

the trial was coded as a completed exchange (see the electronic supplementary material, videos S3 and S4).

A research assistant naive to the study design and the hypothesis independently coded 25% of the trials. Interrater agreement was excellent (Cohen's $\kappa = 0.97$).

Finally, for one-quarter of all trials, we also coded any form of arousal shown by chimpanzees. This is generally taken as a measure for anger/frustration, and we coded for any of the following behaviours: displaying, begging, hitting the apparatus, throwing the tool, foot stomping and handclapping. However, as behaviours that fit one of these categories appeared in only 5.2% of coded trials, we did not code the full sample.

3. Results

We ran a generalized linear mixed model to examine whether the distributor (human or machine) or partner presence (yes or no) had an effect on chimpanzees' refusal to exchange. We included the two-way interaction between distributor and partner presence as well as trial, session, sex and chimpanzee group (subjects were recruited from two different groups, see the Material and methods section) as test predictors in the model. To control for potential effects of the sequence which subjects were tested (with or without partner first), we also included counterbalance as a fixed effect into the model. To test the effect of the test predictors, we compared the deviance full model with that of the reduced model (comprising all terms except for the test predictors) using a likelihood ratio test. Overall, the full model was highly significant when compared with the null model (likelihood ratio test: $\chi^2_3 = 27.44$, $p = <0.001$). Specifically, we found a significant interaction between distributor and partner presence (estimate $\pm$ s.e. $= 3.08 \pm 1.51$, $z = 2.04$, $p = 0.01$). To further investigate the interaction between distributor and partner presence we conducted post hoc pairwise comparisons. Both conditions involving the human experimenter were significantly different from the conditions involving the machine (*human/no partner* and *machine/no partner*: $p = <0.001$; *human/no partner* and *machine/partner*: $p = <0.001$; *human/partner* and *machine/partner*: $p = 0.012$; *human/partner* and *machine/no partner*: $p = 0.006$), revealing that subjects were more likely to refuse to exchange when food was distributed by a human experimenter rather than by a machine (figure 2).

In addition, we found a significant difference between the *human/no partner* and the *human/partner* conditions ($p = <0.001$), indicating that when the human distributed food, the chimpanzees refused to exchange more when there was no partner. There was no difference when comparing the *machine/no partner* and the *machine/partner* conditions ($p = 0.84$). Finally, there was no effect of trial (estimate $\pm$ s.e. $= -0.63 \pm 0.58$, $z = -1.09$, $p = 0.27$), session (estimate $\pm$ s.e. $= -1.82 \pm 1.32$, $z = -1.37$, $p = 0.18$), sex (estimate $\pm$ s.e. $= -0.97 \pm 0.84$, $z = -1.16$, $p = 0.22$) and chimpanzee group (estimate $\pm$ s.e. $= -0.49 \pm 0.91$, $z = -0.54$, $p = 0.58$).

In a second model, we examined whether the distributor or presence of a partner had an effect on chimpanzees' choosing to opt-out. As in the first model, we included the two-way interaction between distributor and partner presence as well as trial, session, sex and chimpanzee group as test predictors in the model. To control for potential effects of the sequence in which subjects were tested (with or without partner first), we also included counterbalance as a fixed effect into the model. To test the effect of the test predictors, we compared the deviance full model with that of the reduced model (comprising all terms except for the test predictors) using a likelihood ratio test. The comparison between the full and null model was not significant (likelihood ratio test: $\chi^2_3 = 4.00$, $p = 0.26$), suggesting that the tested effects did not have a significant effect on the chimpanzees' selection of the opt-out. Please refer to the electronic supplementary material for details on both models.

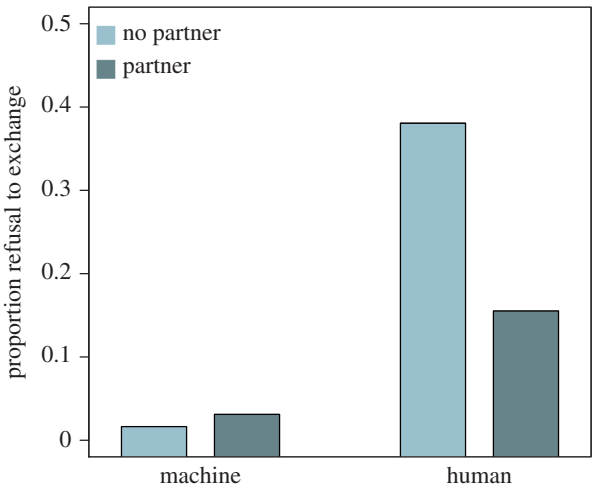

Figure 2. Proportion of refusal to exchange in the four conditions. (Online version in colour.)

4. Discussion

The current results provide support for the social disappointment hypothesis: chimpanzees' reactions to receiving less-preferred food in the inequity aversion task are grounded in specific expectations of the experimenter. When chimpanzees received less-preferred food from a human experimenter, they refused to accept the food in more than a quarter of trials (26.1%), while their average refusal rates tended towards zero when food was distributed by a machine (2.4%). In addition, seeing a partner receive the preferred reward for the same effort did not increase rates of refusal. On the contrary, chimpanzees were most likely to reject less-preferred food when a partner was absent and food was distributed by the human experimenter. Chimpanzees' reactions to receiving the less-preferred food from the human experimenter ranged from active protests, such as those observed in capuchin monkeys in the original Brosnan & de Waal study [23] (e.g. throwing the tool at the experimenter, see the electronic supplementary material, video S1), to more passive forms of protest, which comprised the great majority of refusals (e.g. simply dropping the tool on the ground and moving to a corner of the room, see the electronic supplementary material, video S2).

The current results provide no support for the inequity aversion hypothesis [23,28]. If chimpanzees engage in social comparison and show a concern for relative pay-offs, they should refuse food more often in the presence of a partner regardless of whether the food was distributed by a human experimenter or a machine. In addition, the current results also do not support the food expectation hypothesis [25] which argues that chimpanzees' negative reactions to receiving the less-preferred food are rooted in expectations for

receiving the preferred food. Chimpanzees should have expected the preferred food in all conditions equally because it was always present and clearly visible in the apparatus. Alternatively, subjects might have expected preferred food specifically in conditions in which partners were present and received the preferred food, but we did not find that chimpanzees were more likely to reject food in these situations either. During stages 4 and 5 of the familiarization, just before they started the test phase, subjects received the preferred food. The current study thus also allows for a test of the frustration hypothesis [47] or the idea that subjects react negatively to a lesser reward after having just received a better reward (contrast effects). However, this hypothesis predicts equal rates of rejection in all conditions, which we did not find. Subjects were much more likely to reject less-preferred food when they interacted with an experimenter rather than with a machine.

An alternative interpretation of this finding is that chimpanzees rejected more food in the human conditions not as a consequence of disappointment with the experimenter, but with the single goal of changing the experimenter's behaviour during the trial or in future trials. This line of argument suggests that subjects did not protest against the machine's distribution because they did not expect to be able to modify the machine's current or future behaviour. On one level, chimpanzees' negative responses to poor treatment in a cooperative dyad can of course be understood as an attempt to modify their partner's future behaviour. However, the pattern of behaviours shown by chimpanzees in the current study makes it very unlikely that chimpanzees refused to exchange more in human conditions with only the instrumental aim of changing the experimenter's behaviour (and without any corresponding feelings of disappointment). First of all, chimpanzees showed active refusals (such as throwing the tool at the experimenter) in less than 2% of all trials. Active protest directed at the experimenter such as displaying, foot stomping, or hitting the apparatus, also occurred very rarely, in approximately 5% of trials. Finally, subjects' begging for the preferred food from the experimenter was virtually non-existent. If subjects were simply attempting to change the experimenter's behaviour one would expect much more active forms of refusal and protest. The majority of trials included passive refusals to exchange the tool (see the Coding section) in which subjects moved away from the apparatus to sit in a corner of the testing room, sometimes even dropping the tool on the floor while doing so.

Previous research with domestic dogs has provided preliminary evidence that the role of the experimenter influences subjects' responses in the inequity aversion paradigm [57], but did not provide evidence that dogs are more likely to reject unequal distributions when the experimenter was present versus absent. Consequently, this is, to our knowledge, the first research to show that individuals are in fact more likely to reject food when it is offered by a human experimenter compared to a machine and suggests that chimpanzees' food refusals are grounded in distinct social expectations of the human experimenter. An important and interesting question is how to best characterize chimpanzees' emotional reaction to receiving the less-preferred food. The prototypical human reaction to being wronged by a cooperative partner is resentment [58,59]. In addition, in closer relationships such as friendships, individuals often experience hurt feelings, including feelings of personal disappointment or betrayal [60]. The social disappointment hypothesis argues that chimpanzees' reactions to receiving the less-preferred food express discontent about receiving worse treatment than one could receive. Future studies should further examine the nature of chimpanzees' emotional responses to being treated without concern, and, for example, study chimpanzees' facial expressions when refusing the less-preferred food. Another interesting question relates to chimpanzees' expectations towards their friends [53–55]: do chimpanzees react more strongly when a close conspecific friend fails to take their well-being into consideration than when a neutral individual does?

In the current study, chimpanzees clearly differentiated between a human distributor and a machine distributor in terms of their refusals to exchange, but not regarding their selection of the opt-out apparatus. By choosing the opt-out apparatus, chimpanzees could protest against a given distribution by the experimenter or the machine without having to give up food. As such, it provided chimpanzees with a second way in which to express dissatisfaction with a given distribution and is closely related to the approach used by Sheskin *et al.* [29] in a study with capuchin monkeys. We thus included the opt-out as an additional, non-costly measure, given that refusal to exchange is a costly behaviour in that it requires chimpanzees to forgo food that they otherwise like to eat (see food preference test during the familiarization phase). However, as the results indicate, chimpanzees actually showed the costly behaviour and gave up access to food by refusing to exchange their tool in the human conditions at a relatively high rate; in fact, the observed average rate in the human conditions is nearly identical to the one observed in previous studies on chimpanzees' behaviour in the inequity aversion task (see Brosnan *et al.*'s inequity test condition [24]). Chimpanzees not only showed more refusals to exchange in the human conditions compared with machine conditions but also particularly high refusal rates when their partner was absent and food was distributed by a human. One potential explanation for this behaviour is that seeing a conspecific consume food elicits food competition [61]. This competition in turn might weaken subjects' inhibitory control, an ability that is necessary in refusing to exchange the tool for food. In any case, the fact that chimpanzees were most likely to refuse food in the *human/no partner* condition does not challenge the social disappointment hypothesis, but rather the social comparison hypothesis.

Very few previous empirical and theoretical studies have stressed the role of the experimenter in the inequity aversion paradigm [57,62]. Van Schaik [62, p. 328], for example, writes that 'The monkey in the token-exchange experiment can be said to signal to the experimenter that this unequal treatment is not acceptable in a social bond'. However, all previous work has accepted the claim that individuals in the inequity aversion task respond to how they are treated compared to how another individual is treated, i.e. that their response is based on social comparison. Here, instead, we have provided, to our knowledge, the first empirical evidence that chimpanzees' rejections in the inequity aversion paradigm are grounded in social disappointment—protesting against the experimenter for treating them worse than she could have treated them—and not in social comparison—what they are getting in comparison with what a conspecific partner is getting. Using Roughley's terminology [49], chimpanzees' behaviour in the inequity aversion task is thus best explained

in terms of dyadic rather than triadic sociality. Nevertheless, reacting negatively to being treated without concern, thereby acting on social expectations of social agents, represents an important and necessary step on the way to a full-fledged moral sense and a concomitant aversion to inequity.

Data accessibility. Data associated with this manuscript can be accessed at http://dx.doi.org/10.5061/dryad.s8d24 [63].

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