Social disappointment and partner presence affect long-tailed macaque refusal behaviour in an “inequity aversion” experiment

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ABSTRACT

Inequity aversion plays a central role in human cooperation. Some animals similarly show frustration and become demotivated when rewarded more poorly than a conspecific, which has been taken as evidence of inequity aversion. An alternative explanation - social disappointment - shifts the cause of frustration from the unequal reward to the human experimenter who could – but elects not to – treat subject and partner equally. This study investigates whether social disappointment could explain frustration patterns in long-tailed macaques, *Macaca fascicularis*. We tested twelve monkeys in a novel inequity aversion paradigm. Subjects had to pull a lever and were rewarded with low-value food; in half of the trials a partner worked alongside the subjects receiving high-value food. Rewards were distributed either by a human or a machine. In line with the social disappointment hypothesis monkeys rewarded by the human refused food more often than monkeys rewarded by the machine. Our study extends previous findings in chimpanzees and suggests that both social disappointment and food competition drive refusal patterns.

KEY WORDS

Social disappointment – Inequity aversion – long-tailed macaques – *Macaca fascicularis*

Humans attend keenly to resource division (Loewenstein et al., 1989). We routinely compare our own pay-offs with those of the people around us, and from a young age we show a strong preference for fair resource division (Blake & McAuliffe, 2011). A number of principles govern how we divide resources (Deutsch, 1975). In some contexts we value equality, in others we accept merit- or need-based resource distribution (e.g. Sigelman & Waitzman, 1991). When we consider resources to have been unfairly or mis-allocated, we display inequity aversion – a behaviour thought to have played a role in stabilising cooperation in humans (Brosnan & de Waal, 2014; Brosnan, 2011a; Fehr & Schmidt, 1999; Fehr & Fischbacher, 2004).

Motivated by the fact that non-human species – like humans – profit from cooperation (e.g. Boesch, 1994; Mendres & de Waal, 2000), scientists have set out to investigate disadvantageous inequity aversion in animals. A widely used way to probe inequity aversion is the token exchange paradigm developed by Brosnan and de Waal (Brosnan & de Waal, 2003). In this experimental set-up, two conspecifics – a subject and partner – alternately interact with a human experimenter. The monkeys take turns to hand a token to the experimenter and receive a food reward. In an inequality condition, subjects receive low-value food for their work, while observing that the partner receives high-value food. In a control equality condition, the two monkeys both receive the same quality of food. Brosnan and de Waal reported that in capuchin monkeys, subjects rejected food rewards more often in the inequality as opposed to the equality condition. This pattern of behaviour has now been demonstrated in a number of primate (Brosnan et al., 2005; Hopper et al., 2013; Massen et al., 2012) and non-primate species (Range et al., 2009; Wascher & Bugnyar, 2013). While the pattern of refusal behaviour appears robust, its interpretation is less clear.

The initial interpretation was that these animals showed inequity aversion, thus challenging the uniqueness of inequity aversion in humans (Brosnan & de Waal, 2003, theoretical considerations refined in Brosnan, 2011a). The inequity aversion hypothesis contends that subjects track and compare their reward scheme with that of the partner. Subjects have expectations about which food they should receive after observing a conspecific

receiving high-value rewards for the same work, and, as a form of protest, they refuse low-value rewards. In line with the inequity aversion hypothesis, a number of species that do not share resources such as territory, food, or support during conflict (e.g. orangutans (*Pongo pygmaeus*), squirrel monkeys (*Saimiri* spp.), and cleaner fish (*Labroides dimidiatus*) also do not show refusal behaviour akin to that shown by capuchin monkeys (Brosnan et al., 2011b; Talbot et al., 2011; Raihani et al., 2012;). Brosnan and de Waal's 2003 conclusion has nonetheless proven contentious (Henrich, 2004; Wynne, 2004), and a number of studies have failed to reproduce Brosnan and de Waal's findings (e.g. Bräuer et al., 2009; McAuliffe et al., 2015), while others have put forward alternative hypotheses to explain subjects' refusal behaviour in the token exchange paradigm.

Two alternative explanations revolve around food; the food expectation hypothesis and the frustration hypothesis. The food expectation hypothesis contends that the mere sight of high value food in the inequality condition is sufficient to elicit refusal behaviour (Wynne, 2004). The sight and proximity of a coveted reward leads monkeys to form expectations about receiving these rewards. Support for the food expectation hypothesis has been mixed; the hypothesis has had its proponents (Bräuer et al., 2006; Dubreuil et al., 2006) but also its challengers (Brosnan et al., 2010; van Wolkenten et al., 2007). The frustration hypothesis contends that a subject's past experience in receiving a preferred reward for a task creates an expectation to receive this reward (Roma et al., 2006). As with the food expectation hypothesis, evidence in support of the frustration effect has faced criticism (Brosnan & de Waal, 2006; Hopper et al., 2014; van Wolkenten et al., 2007).

Recently, Engelmann and colleagues put forward a third explanation - the social disappointment hypothesis (Engelmann et al., 2017). This hypothesis highlights the role of the human experimenter. It shifts the cause of frustration away from social comparison with the partner and onto the relationship the animal has with the human who allocates the rewards. The social disappointment hypothesis contends that subjects compare how they are treated, with how they could be treated. By refusing to take the reward in the unequal condition, the

subject is expressing its dissatisfaction with the human who gives low-value instead of high-value rewards. Engelmann and colleagues investigated the social disappointment hypothesis in chimpanzees using a tool-exchange task. Subjects inserted a tool into an apparatus in order to obtain a food reward. Either a human or a machine - technically, an out-of-view experimenter operated the apparatus by pulling strings - rewarded the subject for a successful exchange. Subjects worked either alone or next to a partner alternately engaged in the same task. Chimpanzees that interacted with the human rather than the machine refused food more frequently. A secondary finding was that partner presence resulted in fewer rather than more food refusals compared to the no-partner condition, a converse pattern to that expected under the inequity aversion hypothesis. This experiment was the first study to systematically manipulate the nature of the distributor in a token exchange paradigm and provide clear support for the social disappointment explanation.

At present, the social disappointment hypothesis has only been tested in chimpanzees. Motivated to provide a broader comparative perspective, our study aimed to extend those findings. We tested the social disappointment hypothesis in a catarrhine monkey, the long-tailed macaque, *Macaca fascicularis*. Although a despotic species (Thierry, 2000), long-tailed macaques display a number of cooperative behaviours (see Massen et al., 2012). They form defensive coalitions (van Noordwijk & van Schaik, 1985), for instance, and reciprocate beneficial grooming behaviour (Gumert & Ho, 2008). Long-tailed macaques have been tested in an inequity aversion paradigm and subjects refused food more often under inequality as opposed to equality conditions (Massen et al., 2012). We set out to investigate whether such refusal behaviour could be explained by social disappointment.

Our study design is conceptually faithful to the Engelmann et al. study, including details of the experimental design. However, as our monkeys are not great tool users, we had to devise a different experimental set-up. Subjects had to pull a lever and in exchange they received a food reward. Either a human or a machine rewarded the subject for pulling the lever (implemented as a between-subject factor) and the subject either worked alone or next to a

partner engaged in the same task (within-subject factor). In contrast to the chimpanzee study, our subjects additionally experienced a control condition in which the partner monkey received the same low-value food as the subject.

This study allowed us to contrast the different predictions derived from the theoretical considerations outlined above. If long-tailed macaques refuse food rewards because of inequity aversion, then the distributor should be irrelevant and monkeys should refuse food most often in the test conditions where the well-rewarded conspecific is present. If long-tailed macaques refuse food rewards due to food expectations, in contrast, they should refuse low-value food equally often in all test conditions. Finally, if long-tailed macaques refuse food rewards because of social disappointment, then monkeys assigned to the human distributor condition should refuse food more often than those assigned to the machine distributor condition, irrespective of partner presence and treatment. A control condition was included to distinguish between these different accounts using additional evidence. Inequity aversion predicts no refusals when both individuals receive the same low value food, irrespective of distributor. The food expectation hypothesis predicts refusal in all conditions where high-value food is visible, which is the case for both control conditions. The social disappointment hypothesis predicts more refusals in the human distributor control condition compared to the machine control condition.

MATERIAL AND METHODS

Subjects

Fourteen monkeys took part in the study, twelve as subjects (1.8 - 7.0 years, 7 females) and two in the role of partner monkey (6.3 - 6.4 years, both male). The monkeys were housed in a social group of 37 individuals at the German Primate Center in Göttingen. All twelve test subjects completed the test conditions and ten of the original twelve subjects also completed

the control condition. Participation in the study was voluntary and dependent young often remained with their mothers during testing. For detailed information about subjects and condition assignment, refer to Table S1 of the electronic supplementary material (ESM).

Materials

A table apparatus was attached to the subject's test compartment (ESM, Figure S1). A red light was fixed to the table, and there was a lever within reach of the monkey. Two red carousels were positioned on a plexiglass platform in front of the red light. On top of each carousel was a transparent cylinder which was used to display food. Each carousel had small compartments which could hold food. An identical apparatus was attached to the neighbouring test compartment which either held a partner monkey or was empty (as per condition requirements). In test conditions the subject's apparatus was not accessible to the partner monkey and vice versa. The subject had an unobstructed view of the partner's table.

Design

We implemented the same 2 x 2 factorial design used in the Engelmann *et al.* 2017 study (Figure 1). *Distributor* (human/machine) was a between-subject factor and *partner presence* a within-subject factor. In addition to the original conditions, we ran a control condition where both monkeys received low-value food. The subjects proceeded through five stages during the course of the study: (1) food preference test, (2) lever-training, (3) a 4-step familiarisation procedure, (4) the original test conditions, and (5) the additional control condition. Information about steps (1) to (3) can be found in section 4 of the ESM. Stages (4) and (5) are described below.

Figure 1. The experimental design. A - D depict test conditions: A) *Human distributor/Partner present*, B) *Human distributor/Partner absent*, C) *Machine distributor/Partner present* and D) *Machine distributor/Partner absent*. Circles containing “H” represent a pool of high-value food and those containing “L”, a pool of low-value food.

METHODS

Test conditions

At the start of the familiarisation procedure, subjects were assigned a distributor (human or machine) and they remained with this distributor for the duration of the study. Seven subjects were assigned to the human distributor (three males) and five subjects to the machine distributor (two males; for details see ESM, Table S1). Each subject experienced two types of test conditions, a *Partner present* and a *Partner absent* condition (ABAB presentation, order counterbalanced and in total four sessions per condition). Subjects could undergo just one session per day, with twelve trials comprising a session (see ESM Table S2 for exceptions due to technical failures or drop-outs). Note that in each test condition, both high-value (HV) and low-value (LV) food was on display and the food item offered to the monkey became clear only

after s/he had pulled the lever. The subject and partner interacted alternately with their respective tables. Each time a monkey pulled its lever, a carousel rotated. In machine distributor conditions, food from the carousel was deposited onto a platform and conveyed toward the monkey. In human distributor conditions, an experimenter placed food on the platform as it was conveyed toward the monkey.

Human distributor/Partner present condition (Figure 1A; for video exemplar see ESM Video S1). Prior to each *Human distributor/Partner present* condition, Experimenter 1 (E1) filled one transparent cylinder on each table with LV food and one with HV food (side counterbalanced between sessions). E1 left the room and Experimenter 2 (E2) entered to stand behind the partner's table. E1 monitored the activity in the test room via video and switched the light on the partner's table to on via remote control. If the partner pulled the lever within 120 s after the light went on, the cylinder containing the HV food rotated and the platform on the conveyor belt moved towards the partner. E2 took an item of HV food from the cylinder and placed it on the moving platform. Once the platform reached the end of the track, the monkey had 2 s to take the food before the platform travelled back to the start position. If the monkey refused to take the food it was mechanically swept off the platform into a bag under the table. Once the platform had returned to the start position, E2 moved to stand behind the subject's table and the same procedure was carried out for the subject with the exception that this monkey was only ever offered LV food. If the lever was not pulled within 120 s, the light on the table went out and E2 moved to service the other table. E2 alternated between the two tables until each monkey had completed twelve trials.

Human distributor/Partner absent condition (Figure 1B; ESM Video S2). No partner was present in this condition. This aside, the sequence of events was identical to those of the *Human distributor/Partner present* condition. Given that no monkey was present to take the HV food in the partner's compartment, the partner's platform returned to the start position laden with food which was mechanically swept into the bag under the table. E2 alternated between the partner and the subject table until the subject had completed twelve trials.

Machine distributor/Partner present condition (Figure 1C; ESM Video S3). Prior to each session, E1 filled each transparent cylinder on the tables with food (one LV- and one HV-cylinder per table) and then baited twelve carousel compartments with the respective food (presentation side counterbalanced). E1 then left and both E1 and E2 remained outside the room for the duration of the session. The sequence of events which followed was identical to the *Human distributor/Partner present* condition except that now the machine was responsible for loading the platform which travelled within reach of the monkey. E1 alternated via remote control which table was active (indicated by the lamp), until each monkey had completed twelve trials.

Machine distributor/Partner absent condition (Figure 1D; ESM Video S4). No partner was present in this condition. This fact aside, the sequence of events in this condition was identical to that in the *Machine distributor/Partner present* condition. Food on the partner's platform returned to the start position and was mechanically swept into the bag under the table. E1 alternated via remote control which table was active until the subject had completed twelve trials.

Control condition

Following the test conditions, ten of the original twelve subjects were still available to move on to a control condition (one male and one female were deceased by this stage). The control sessions were run after the test sessions so as to match the procedure of Engelmann and colleagues as closely as possible. Each subject remained in his/her pre-assigned distributor group and underwent four *Partner present* sessions. As with the test conditions, subjects could undergo just one session per day, with twelve trials comprising a session (exceptions outlined in ESM, Table S3). The procedure in each control condition was identical to that of the equivalent partner present test condition; the only difference was that the partner monkey was now offered LV rather than HV food for each lever pull.

Coding

Three types of food refusals were coded (*refusal-to-participate*, *refusal-to-take* and *refusal-to-consume* a food item) and pooled during analysis to create a binary response variable (refusal = yes/no). In addition to food refusals, we coded pull-latency behaviour. These pull-latency data were used in an exploratory analysis. 50 test trials and 43 control trials were excluded from analysis at the coding stage (documented in ESM, Tables S2 and S3). In total 1066 test trials and 437 control trials were analysed.

E2 coded all videos and a second coder who was blind to the hypothesis of the study coded 20% of the videos. Inter-observer agreement scores were determined using the *icc* and the *maxwell* functions of the *irr* R package (Gamer et al., 2019). Observer agreement on *refusal* behaviour was very good (Maxwell's correlation coefficient (RE) = 0.994). Agreement on *pull-latency* behaviour was excellent (Intra-class correlation coefficient (R) = 1).

Statistical analysis

We carried out three analyses in R (R Core Team, 2021, version 4.1.1). In analysis one, we tested whether distributor, partner presence and/or their interaction had an effect on monkeys' food refusal behaviour during test conditions. To this end we constructed Model 1A, a Generalised Linear Mixed Model (GLMM; Baayen, 2008; output in ESM Tables S5 and S6). The response variable was food refusal (yes/no), and hence the model was fitted with binomial error structure and logit link function (McCullagh & Nelder, 1989). Model 1A consisted of a two-way interaction between distributor and partner presence, in addition to their fixed main effects and fixed effects of trial number, session number (consecutive numbering across partner present and absent conditions), sex, and counterbalance. Subject ID and subject-session ID were included as random effects. The latter was nested within subject and accounted for potential session to session variation in refusal probabilities. The model included random slopes (Schielzeth & Forstmeier, 2009; Barr et al., 2013) of partner presence, trial number and session number within subject, and trial number within subject-session-ID. We included estimates of the correlations between the random intercept and slopes in the model. For Model 1A we utilised the full dataset; 1066 trials collected in 93 sessions. The data was from 12

subjects tested with 2 partners. To ascertain the (potential interactive) effect of our two factors of interest, we used a likelihood ratio test to compare the full model outlined above with a null model lacking the interaction term and their main effects.

Given that we utilised two partner monkeys in the course of the experiment, we fitted a second, identical model – Model 1B - using just the data obtained with partner identity 1, in order to check whether partner identity had an obvious effect on the outcome. For Model 1B we utilised 597 test trials collected in 52 sessions. The data came from 12 subjects tested with 1 partner. For more detail and to see the output of Model 1B see ESM Tables S7 and S8.

In a second analysis we considered the control condition data. Here we tested whether the value of the partner's reward had an effect on monkeys' food refusal behaviour in the two distributor conditions. More specifically, we tested whether the subjects were more or less motivated to accept the LV reward in the human distributor as opposed to the machine distributor condition. To this end we constructed another GLMM - Model 2 (output in ESM Table S9). The response variable was food refusal (yes/no). The model comprised the fixed effects of distributor, trial number, session number, and sex. Subject ID and subject-session ID were included as random effects and random slopes of trial number and session number within subject and trial number within subject-session ID were included. The same monkey was the partner in all control conditions and we therefore did not need to consider partner ID in the model. For Model 2 we used 437 control condition trials. The trials were collected in 40 sessions and the data came from 10 subjects with 1 partner. To ascertain the effect of our factor of interest (distributor), we used a likelihood ratio test to compare the full model outlined above with a null model lacking the term.

In a third analysis we explored the pull-latency data to establish whether the time it took a monkey to pull the lever differed as a function of distributor and partner presence. Here we fitted a survival analysis – Model 3 (documented in ESM, Tables S10 and S11). The response variable was time in seconds, determined as when the subject pulled the lever or when the trial ended. Distributor and partner presence were included as an interaction term (in addition

to their main effects), and trial number, session number, sex, and counterbalance were included as fixed effects. Subject ID and subject-session ID were included as random effects. Random slopes of partner presence, trial number and session number within subject were included, in addition to the random slope of trial number within subject-session ID. Model 3 used the full dataset of 1066 trials; of these, 119 trials were *refusal-to-participate* (i.e. “timeout”) events. To ascertain the potential interactive effect of distributor and partner presence on pull-latency, we conducted a likelihood ratio test, comparing the full model with a null model lacking the interaction term and their main effects.

Where appropriate, we checked model stability and collinearity (inspected Variance Inflation Factors; Field, 2005). Confidence intervals, where reported, were derived using the *bootMer* function of the *lme4* package. More details on the statistical analyses can be found in the ESM (section 7).

RESULTS

Effect of distributor and partner presence

To establish whether distributor, partner presence and/or their interaction affected refusal behaviour (see Test conditions, Figure 2) we constructed a GLMM, Model 1A. Comparison of the full with the null model revealed a significant difference (likelihood ratio test: $\chi^2_3 = 14.226$, $p = 0.003$). As the interaction between distributor and partner presence was a trend ($p = 0.075$), we report the output of this interactive model. In addition, we fitted a reduced (additive) model (output in ESM Table S6).

The refusal behaviour varied with the distributor condition and was modulated by partner presence: Monkeys in the human group rejected food in on average 24.0 % of the food within a session when a partner was present, and 32.1 % when a partner was absent. Monkeys in the machine group rejected food in on average 5.2 % of the time when a partner was present and 16.6 % of the time when a partner absent. Aside from our key factors of interest, we found

a trend for sex ($p = 0.068$) and evidence of a significant effect of counterbalance ($p = 0.001$). Male monkeys were more likely to refuse food than females. Male monkeys in the human distributor condition refused on average 45.8% of the food within a session compared to females who refused on average just 13.5% of the food within a session. Male monkeys in the machine distributor condition refused on average 14.4% of the food within a session compared to females who refused on average 8.5% of the food within a session. With regard to counterbalance, monkeys that experienced the *Partner present* condition first were significantly more likely to refuse food (refusing on average in 29.0% of the trials) compared to those which experienced the *Partner absent* condition first (8.2%).

Control condition

To test whether there was an effect of distributor when the partner received the same food as the subject (Figure 2, Control conditions) we fitted Model 2. A full-null model comparison revealed no significant difference between the two models (likelihood ratio test: $\chi^2_3 = 0.000$, $p = 0.984$).

Figure 2. White data points show the mean proportion of food refused per subject, according to distributor and (in the test conditions) partner presence (Test conditions: $N_{Human} = 7$, $N_{Machine} = 5$, Control condition: $N_{Human} = 5$, $N_{Machine} = 5$). Black points show the group mean. Vertical

lines show interquartile range.

Pull-latency

To explore whether subjects' pull-latencies varied according to test condition we fitted a survival analysis – Model 3. A full-null model comparison revealed a marginally non-significant difference between the two models (likelihood ratio test: $\chi^2_3 = 6.871$, $p = 0.076$). As the interaction between distributor and partner presence was not significant ($p = 0.392$), we removed the interaction from the model and proceeded with the reduced additive model. The reduced model revealed a significant effect of partner presence on pull-latency (Figure 3). Monkeys were significantly faster in pulling the lever in the partner present as opposed to the partner absent conditions (estimate $\pm$ se = 0.553 ± 0.217 , $p = 0.013$). The median pull-latencies in the human and machine partner present conditions were 2.04 s and 2.52 s respectively, whereas in the human and machine partner absent conditions, the median pull-latencies were up at 2.76 s and 4.22 s.

Figure 3. Average pull-latency (time in seconds) between the table light coming on and the subject pulling the lever; each monkey was given 120 seconds to pull the lever - if the monkey refused to participate within this time, the experimenter turned the light off and blocked the lever. In total there were 119 *refusal-to-participate* events. Figure 3 therefore displays 947 of 1066 pull-latencies. White data points show the mean pull-latency per subject in the respective partner presence conditions ($N_{Human} = 7$, $N_{Machine} = 5$); black points show the group mean. The vertical lines show interquartile range.

DISCUSSION

We report an interactive effect of distributor and partner presence on food refusal behaviour. The data is compatible with the social disappointment hypothesis, which predicts that monkeys in the human distributor condition expect to be provided with high-value food. In contrast to predictions of the social disappointment hypothesis, however, there was no evidence for an effect of distributor in the control condition, where refusal rates were low in both conditions. The low refusal rate in the human distributor control condition may be due to a slight difference between the human test and control conditions: in the test conditions, the experimenter reached to take food from the partner's high-value cylinder. Seeing this could have triggered the subject's expectation of receiving high-value food. In contrast, in the control condition, the experimenter only ever reached for the low-value food.

Because of the small sample size, the results need to be interpreted with caution. Given that some of the effects were quite strong, we felt that reporting was nevertheless warranted. Note that we opted against a full within-subject repeated measures design to emulate the design of the original Engemann et al. (2017) study as closely as possible. Note that their study also only included nine subjects. In what follows, we make a number of suggestions what the results may imply, fully aware of the limitations in light of the small sample size – which is unfortunately typical in our field.

At first glance, our findings do not support either of the food-centred hypotheses. The food expectation hypothesis predicts that subjects should refuse low-value food in conditions where high-value food is visible (Wynne, 2004). In our study subjects saw both high- and low-value food in each condition. If they only behaved according to the food expectation hypothesis, then the refusal rates should have been equally high in all four test conditions; this was not the case. The frustration hypothesis predicts that subjects should refuse low-value food after having received high-value food. In steps three and four of the familiarisation procedure, subjects had experienced that “work” (pulling the lever) could lead to a high-value reward. If this experience was enough to induce a “contrast effect” (Reynolds, 1961), then subjects’ frustration should have affected refusal rates similarly in all four experimental conditions; as stated, this was not the case. Yet, anecdotal observations from the partner’s behaviour suggest that a contrast effect might appear after a higher number of trials: our partner, who was used to receiving high-value food during the test trials, was extremely difficult to motivate to participate in the control trials, where both monkeys received low-value food. Future studies might look into the induction of the contrast effect in more detail.

Our data do not provide support for the inequity aversion hypothesis. If inequity-averse, subjects in both distributor groups should have fixated upon their partner’s pay-off and refused food more often in the presence of a partner. Engelmann and colleagues reported a trend whereby chimpanzees in the human distributor condition refused less often when a partner was present compared to when alone in the test cage (2017). The authors surmised that this effect was due to competition over food, i.e., that watching a conspecific consume food may influence a subject’s resolve or inhibitory control and heighten competitive arousal (Engelmann et al., 2016, 2017). Ample evidence demonstrates that nonhuman primates increase food intake when in social as opposed to alone conditions (Harlow & Yudin, 1933; Koomen & Herrmann, 2018), and the sight and sound of a monkey consuming food nearby is thought to activate a similar motor program in an observing monkey (Ferrari et al., 2005). While we did not find evidence of an effect of partner presence on refusal behaviour, our pull-latency data indicates underlying food competition and/or social facilitation effects may indeed be

modulating the subjects' behaviour. Our monkeys were significantly faster to pull the lever in the partner present as opposed to the partner absent conditions.

The social disappointment hypothesis implies that monkeys refuse food because they hold certain expectations toward the human as an intentional agent, while monkeys in the machine group attribute no such intentionality to the inanimate distributor. The attribution of intentionality fits with studies which show that nonhuman primates, including catarrhine species, differentiate between different intentional stances (Call et al., 2004; Call & Tomasello, 1998; Canteloup & Meunier, 2017; Phillips et al., 2009). For example, chimpanzees and orangutans differentiate between intentional and accidental events (Call & Tomasello, 1998). Chimpanzees and capuchin monkeys differentiate between an experimenter who is unwilling as opposed to unable to deliver a food item (Call et al., 2004; Phillips et al., 2009), and Tonkean macaques, *Macaca tonkeana*, become more attentive and engage more often in gaze alternation when faced with a distracted as opposed to an unwilling experimenter (Canteloup & Meunier, 2017).

Our results tentatively suggest that an intentional stance, in combination with food competition (or social facilitation) effects, explains the refusal behaviour of the monkeys in the human distributor group. We suggest that the monkeys expect to be treated in a certain way because they understand that the experimenter is an intentional agent; particularly, in the current study she was someone the monkeys have interacted with previously and with whom they have a positive relationship. In follow-up studies it would be interesting to manipulate the experimenter – subject relationship to see whether subjects' disappointment levels fluctuate systematically. For example, they might hold stronger expectations about being treated well towards familiar researchers who have frequently provided high value food in the past, than towards novel researchers, and might consequently refuse low-value food more often when it's provided by the familiar experimenter. A number of studies have investigated non-human primate sensitivity to reputation (Subiaul et al., 2008; Herrmann et al., 2013) and to reliability of the humans they interact with (e.g., Brosnan & de Waal, 2009) and have shown that the

subjects can take social information about different people into account: they prefer nice over mean and reliable over unreliable experimenters. It would be interesting to contrast how animals responded to the familiar human, with how they would respond to a neutral human or a human they view negatively. In addition, animals with more test experience should have stronger expectations around being treated with concern compared to more naïve monkeys. Studies such as these would help to illuminate how the monkeys form expectations.

In summary, the long-tailed macaques' behaviour in the current study can be best explained by a combination of social disappointment in an intentional agent and a certain degree of food competition and/or social facilitation. The response patterns resemble previous findings in chimpanzees and thus extend the social disappointment account as one important facet in refusal behaviour beyond the ape lineage to a catarrhine species.

Data, code and materials

Supporting material is supplied in electronic form. The Electronic Supplementary Material, datasets and R code which accompany this paper are available at OSF:

https://osf.io/fu6j4/?view_only=f076ef4272464947abfd52bf8b9dab63

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Authors' contributions

Contributions following CRediT: Conceptualization, R.T., J.F. and S.K.; Methodology, R.T., S.K., T.H.; Formal analysis: R.T.; Investigation: R.T. and C.T.; Resources: T.H.; Writing – original draft, R.T. and C.T.; Writing – review and editing, R.T., H.S., J.F. and S.K.; Visualization, R.T.; Supervision S.K. and J.F.; Funding acquisition, S.K., J.F., and H.S.

Animal welfare note

This non-invasive behavioural study was approved by the ethics committee of the Animal Welfare Body of the German Primate Center (permit number E7-18_4-17).

Declarations of interest: none

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[Supplementary information]

Social disappointment explains long-tailed macaque behaviour in an “inequity aversion” experiment

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1. Subjects and condition assignment

Subjects lived in an enclosure with both indoor and outdoor space (190 m²). These monkeys had participated in previous cognitive tests, however, none had experience with an inequity aversion paradigm, and none had prior experience with the apparatus we employed. The group was fed daily at regular intervals and water was available *ad libitum*. In an effort to control motivation due to fluctuating hunger levels over the course of the day, all test and control sessions took place prior to the midday feed (between 10am and 12.30pm).

Table S1 lists the monkeys which took part in the study. There is information about which distributor group each monkey was assigned to (Human or Machine) and the conditions each subject took part in (Mars died before he could take part in the control condition and Sambia before she could complete the test conditions). Table S1 displays which monkey took on the partner role when a partner's presence was required and for how many of the sessions each partner monkey was in this role. Information about subject sex and age (at the time the study commenced) is provided.

Table S1*Information about subjects*

Subject	Distributor group	Condition(s) experienced	Partner (number of sessions)	Sex	Age (years)
Lukas	Human	test <i>control</i>	Ilja (2), Linus (2) <i>Linus (4)</i>	male	4.1
Mars*	Human	test	Ilja (4)	male	5.3
Mila	Human	test <i>control</i>	Ilja (2), Linus (2) <i>Linus (4)</i>	female	7.0
Mona	Human	test <i>control</i>	Ilja (1), Linus (3) <i>Linus (4)</i>	female	2.0
Moritz	Human	test <i>control</i>	Ilja (3), Linus (1) <i>Linus (4)</i>	male	2.7
Sambia**	Human	test	Ilja (2)	female	4.2
Sherry	Human	test <i>control</i>	Ilja (2), Linus (2) <i>Linus (4)</i>	female	2.7
Mara	Machine	test <i>control</i>	Linus (4) <i>Linus (4)</i>	female	3.4
Max	Machine	test <i>control</i>	Linus (4) <i>Linus (4)</i>	male	6.3
Meiwi	Machine	test <i>control</i>	Ilja (3), Linus (1) <i>Linus (4)</i>	female	3.4
Smilla	Machine	test <i>control</i>	Ilja (2), Linus (2) <i>Linus (4)</i>	female	3.1
Simon	Machine	test <i>control</i>	Ilja (2), Linus (2) <i>Linus (4)</i>	male	1.8

* Mars was deceased before he could take part in the control sessions.

** Sambia was deceased before she could complete all of the test sessions (36 test trials are missing).

2. Set-up

The set-up consisted of two identical tables (Figure S1) and a central tethered remote controller. There were two main mechanisms per table, a remotely lockable lever that could be pulled by the monkey and two identical food-dispensing carousels with moving platforms. Each of those subsystems was controlled by an Arduino that communicated with the central controller over a serial I2C protocol.

The lever used a standard hobby servo to manipulate a locking pin that prevented the lever from being pulled if the pin was in the extended position. A micro switch was used to monitor the state of the lever to ensure the lever was locked correctly. See Figure S2b for a detailed view of the mechanism. Additionally, an electronically controlled light indicated the locking state to the monkey, allowing the monkey to determine the state of the lever without continuously trying to pull it.

The food dispensing mechanism used two identically geared DC motors with encoders to drive the carousel and the platforms. The platform was attached to a belt and pulley mechanism, while the carousels were mounted directly to the shaft of the motor. Both motors were connected to the Arduino via a commercially available motor driver shield. A custom motor control library enabled closed-loop control of the motor position, allowing for accurate and reliable positioning of the carousels and the platforms. The design of the carousels allowed for the automated dispensation of twelve items of food per carousel without human intervention. See Figure S2c for a detailed view of the platform and carousel mechanisms.

Figure S1. An overview of the experimental set-up; from the viewer's perspective, the table on the left-hand side was used by the partner monkey and the table on the right-hand side by the subject.

Figure S2. A schematic of the electronics and mechanical components; Diagram a shows how the different components were connected - blue lines indicate data communication connections and orange lines indicate motor control signals. Diagram b shows the lever mechanism. The locking pin (red) is manipulated by the servo motor (black). The lever was pulled into its default position (shown) by a spring. Diagram c shows the carousel (red) and moving platform (green) mechanism. The carousel dropped food onto the platform which then moved as indicated by the arrow to deliver the food to the monkey.

Video S1: *Human distributor/Partner present condition*

Video S2: *Human distributor/Partner absent condition*

Video S3: *Machine distributor/Partner present condition*

Video S4: *Machine distributor/Partner absent condition*

3. Technical difficulties & trial discounts

Issues with the electronics intermittently arose in the machine distributor sessions (in both test and control conditions). For example, if the monkey did not release the lever before the platform had travelled back to the start position the red light on the table no longer lit up. This meant that a human (*not* E2, the designated human distributor) at times had to enter the room between trials to reset the machine. This fault occurred 4 times during the test sessions and 7 times during the control sessions.

A number of trials were marked for exclusion from subsequent analyses (see Tables S2 and S3). We scored when technical failure resulted in no food or a double-load of food on a platform, and when the subject accidentally dropped the food. Technical failures could have had an influence on the subject's motivation to refuse or take the food on offer, for instance the subject could have been more motivated to take a double LV food load. When food was dropped, it was safest to discount the trial as we could not be certain whether, even if the subject had taken the food, it would have subsequently consumed or discarded it.

Table S2 documents test condition (*inequality*) trials which were marked for discount at the coding stage. In total 50 test trials were discounted.

Fitting one of the following criteria meant that a trial was discounted:

(a) A technical failure/table malfunction occurred with the consequence that:

- i.* the subject's platform travelled empty, or
- ii.* the subject's platform travelled with a double load, or
- iii.* the partner's platform travelled empty immediately prior to the subject's trial, or
- iv.* the partner's platform travelled with a double load immediately prior to the subject's trial

(b) Subject accidentally dropped food

(c) Experimenter mistake resulted in trial not being conducted

(d) Machine malfunction resulted in trial not being conducted

Table S2

Information about discounted test trials

Subject	(a)				(b)	(c)	(d)	Trials discounted
	<i>i.</i>	<i>ii.</i>	<i>iii.</i>	<i>iv.</i>				
Lukas	-	-	-	-	-	2	-	2
Mars	-	-	-	-	-	-	-	0
Mila	-	-	-	-	-	-	-	0
Mona	-	-	-	-	-	-	-	0
Moritz	-	-	-	-	1	-	-	1
Sambia	-	-	-	-	-	-	-	0
Sherry	-	-	-	-	-	-	-	0
Mara	-	-	-	-	7	-	-	7
Max	-	-	1	-	-	-	-	1
Meiwi	11	4	-	-	2	-	-	17
Smilla	4	2	2	-	-	-	1	9
Simon	4	-	1	-	8	-	-	13
Total								50

Table S3 documents control condition (*equality*) trials which were marked to be discounted at the coding stage. In total 43 control condition trials were discounted. The criteria according to which these trials were discounted are the same as those outlined in the Table S2 preamble.

Table S3

Information about discounted control trials

Subject	(a)				(b)	(c)	(d)	Trials discounted
	<i>i.</i>	<i>ii.</i>	<i>iii.</i>	<i>iv.</i>				
Lukas	-	-	-	-	1	-	-	1
Mila	-	-	-	-	1	-	-	1
Mona	-	-	-	-	-	-	-	0
Moritz	-	-	-	-	1	-	-	1
Sherry	-	-	-	-	1	-	-	1
Mara	3	-	1	-	3	-	-	7
Max	1	1	3	3	-	-	-	8
Meiwi	6	3	1	-	-	-	-	10
Smilla	7	2	-	-	-	-	-	9
Simon	1	-	-	-	4	-	-	5
Total								43

4. Details about food preference tests, lever-training and the familiarisation procedure

Food preference test

Each subject was tested to establish an individual food preference. Food preference testing took a minimum of four separate sessions, each of which lasted for ten trials. In the first three sessions, the monkey was offered the choice of two food types. In each trial an item of each food type was placed in a petri dish and these were simultaneously slid toward the monkey. The experimenter simultaneously held both food items up and the monkey selected and received his/her food of choice. The non-selected item was removed from sight before the next trial commenced. The side on which the food items were placed (left or right) was random but evenly distributed among the trials of a session. The food type which was chosen in at least 70% of the trials for three consecutive sessions was classified as high-value (HV). In session four, the monkey was presented with an item of the previously non-selected food type ten times. If subjects consumed the food in at least 90% of the trials this food was classified as low-value (LV). Nine subjects consumed the LV food in all ten trials and three subjects took the LV food in nine of the ten trials. For eight subjects, the LV food was fennel. For one subject, it was capsicum and for another, a half raisin. For two subjects, the LV food was Haferfleks® cereal. For eleven of the twelve subjects, grape was the HV food and for one subject it was blueberry.

Lever training

Each subject was presented with an incomplete version of the apparatus; tables fitted only with a lever and a light. These tables were attached to the “subject” and “partner” test compartments and a separator panel was removed so the monkey could roam between the two compartments according to which table’s light was on. The lever training gave each monkey the opportunity to associate the light-on status with the fact the lever could be pulled. This association was trained to ensure subjects understood the relevance of the lights and would limit the time they spent interacting with their lever when their light was off, thereby increasing the likelihood that they would attend to the partner’s activity during test sessions. E2 and an assistant rewarded the monkeys for interacting with an unblocked lever with small pieces of banana chips, raisins and dried apricot. Subjects proceeded to the next stage once they had learned to pay attention to the light, moving between the two cages depending on the on/off status of the light and reliably not attempting to operate a table’s lever when the light was off. There was variation in how quickly the monkeys understood the light-lever association, and unlike in the following familiarisation stages, we applied a flexible protocol which suited the individual monkey’s needs (e.g. by focusing on drawing attention to the light, or working towards the monkey feeling

comfortable moving between the two cages). Each subject received at least six lever training sessions.

Familiarisation procedure

This procedure closely follows the familiarisation protocol of Engelmann et al (Engelmann et al., 2017). Here subjects were presented with the complete apparatus. Each subject underwent one session per day and the familiarisation procedure was broken down into four steps. The LV food of the respective subject was used in steps 1 and 2 and the HV food in steps 3 and 4. Subjects were pseudo-randomly divided into groups prior to step 1; half of the monkeys were assigned to the human distributor condition and the other half to the machine distributor condition. The monkeys remained in these two groups for the entirety of the study. Here “pseudo-randomisation” refers to the fact that the random assignment of individuals to group was altered to balance kin, age and sex ratios between the two groups as best as possible.

Step 1 - Subjects were familiarised with the table apparatus from the designated ‘subject’ test cage. For subjects from the human distributor group, once the monkey pulled the lever, E1 pressed a remote control from outside the test room, a carousel rotated and a platform began to move towards the monkey. E2 removed a piece of LV food from the cylinder on top of the food carousel and placed it on the platform as it was conveyed toward the monkey. For the subjects from the machine distributor group, prior to the beginning of the session, E1 baited the food carousels with 12 items of food before leaving the room. E2 remained outside of the test room for the entirety of the baiting time and the session. Once the monkey pulled the lever, E1 pressed a remote control from outside the test room and the food carousel rotated, depositing an item of food on the platform which moved towards the monkey. There were twelve trials in a session. A trial was considered successful if the monkey pulled the lever and consumed the item of food delivered. Subjects moved onto the next stage if eight of twelve items of food were consumed in two consecutive sessions. The platform on which food was conveyed to the subject was alternated (side counterbalanced) so that all subjects were able to experience that low-value food was conveyed on the left-hand platform and on the right-hand platform.

Step 2 - Subjects were familiarised with the table apparatus from the designated ‘partner’ test cage. This fact aside, the procedure followed in step 2 was identical to Step 1, subjects experienced that LV food could be delivered via both the left and the right-hand platforms on the partner’s table.

Step 3 - Subjects were placed in the ‘subject’ test cage. The procedure followed in Step 3 was also identical to Step 1 except that now HV food was used. This step was important as

here subjects experienced that it was possible to receive HV food in the subject's cage. Subjects that pulled the lever and took the food item 8 from 12 times moved onto the fourth and final stage.

Step 4 - Subjects were placed in the 'partner' test cage. Subjects received 4 trials with HV food. This step provided subjects with the experience that HV food could be obtained in the partner cage. Subjects that pulled the lever and took the food item in 4 from 4 trials were ready to move on to the test stage.

5. Test conditions and coding

Subjects experienced a total of four sessions per test condition (i.e. one presentation order was AABBAABB). A subject could undergo one session per day. Food displayed on the partner's table was identical to that of the subject's table (i.e. if the HV food was displayed in the left cylinder on the subject's table, the same HV food was displayed in the left cylinder on the partner's table).

Test and control sessions were videotaped from multiple perspectives (two front and two side). These perspectives were merged using *Techsmith Camtasia* software (version 9.1) to create one video file per test session. Videos were coded using the *Mangold Interact* software (version 9.0.7).

Three types of refusal behaviour were coded. A *refusal-to-participate* event was coded if the subject did not interact with the lever within 120 seconds of the table's light being switched on. A *refusal-to-take* event was coded if the subject permitted a food-laden platform to return to the start position on the table. A *refusal-to-consume* event was coded if a monkey discarded (i.e. threw, dropped or spat out) food which had been picked up from the platform. Care was taken when coding 'spitting' behaviour. Some monkeys 'spit out' the skin of certain food items (e.g. capsicum) when eating; this behaviour is normal and was not classed as a refusal-to-consume. In addition to refusal events we identified accidental discards. This was where the monkeys pushed food out of reach but it was clearly not their intention to have done so and they continued to expend energy trying to reach the food item.

6. Refusal behaviour

Table S4 documents the proportion of trials which ended in food refusal. At the coding stage refusal behaviour was split into three categories (*refusal to participate*, *refusal to take* & *refusal to consume*) and all refusal data was later pooled to create a binary response variable (refused = 1, accepted = 0). Refusal categories were not analysed separately as some refusal behaviours occurred only rarely. The proportion of test condition trials which ended in refusal appear first in each cell and the proportion of control condition trials follows (in brackets). All

proportions have been rounded to 2 decimal places. NA (not applicable) indicates that the animal was deceased and did not experience the condition. For an overview of an individual's behaviour see the *Total* column, the proportions listed here sum up the proportions associated with each refusal category. The abbreviations *H* and *M* in column one, refer to the distributor condition to which the subject was assigned.

Table S4

Proportion of test trials which ended in food refusal (control condition proportions in brackets)

Subject (distr.)	Refusal to participate	Refusal to take	Refusal to consume	Total
Lukas (H)	0.24 (0.00)	0.17 (0.00)	0.03 (0.00)	0.45 (0.00)
Mars (H)	0.60 (NA)	0.11 (NA)	0.02 (NA)	0.74 (NA)
Mila (H)	0.03 (0.00)	0.06 (0.02)	0.06 (0.04)	0.16 (0.06)
Mona (H)	0.04 (0.02)	0.06 (0.02)	0.01 (0.00)	0.11 (0.04)
Moritz (H)	0.00 (0.00)	0.17 (0.02)	0.00 (0.00)	0.17 (0.02)
Sambia (H)	0.00 (NA)	0.00 (NA)	0.00 (NA)	0.00 (NA)
Sherry (H)	0.00 (0.00)	0.22 (0.06)	0.00 (0.04)	0.22 (0.11)
Mara (M)	0.09 (0.00)	0.02 (0.00)	0.00 (0.00)	0.11 (0.00)
Max (M)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Meiwi (M)	0.01 (0.00)	0.03 (0.03)	0.00 (0.03)	0.04 (0.05)
Smilla (M)	0.03 (0.00)	0.08 (0.23)	0.00 (0.00)	0.11 (0.23)
Simon (M)	0.23 (0.00)	0.07 (0.00)	0.00 (0.00)	0.30 (0.00)

7. Analyses

We conducted three confirmatory analyses: Models 1A, 1B and 2 (see subsection 7.1). We conducted one exploratory analysis – a survival analysis, Model 3 (subsection 7.2). Details on the construction and output of each model are documented in individual subsections below. The data and r-scripts used in these analyses have been made available here: https://osf.io/fu6j4/?view_only=f076ef4272464947abfd52bf8b9dab63

7.1. Confirmatory analyses

Model 1A

To estimate the effect of distributor and partner presence on monkeys' food refusal behaviour, we used a Generalized Linear Mixed Model (GLMM; Baayen, 2008). The response (food refusal) was binary (refusal = 1) and so the model was fitted with a binomial error structure and logit link function (McCullagh & Nelder, 1989). The model was comprised of a two-way interaction between distributor and partner presence in addition to their fixed main effects and the fixed effects of trial and session, sex and counterbalance. Trial number and session number entered the model as z-transformed variables with a mean of zero and standard deviation of one. Counterbalance was included to control for any potential effect of monkeys' having experienced the first two sessions in the presence or the absence of a partner monkey. Subject ID was included as a random effect as repeated measures were taken from a small pool of individuals. Subject-session ID was included as a random effect to account for potential session to session variation in refusal probabilities.

In order to keep type I error rates at the nominal level of 0.05 and avoid an 'over-confident' model we included the random slopes of partner presence, trial and session within subject as well as trial within subject-session ID in the model (Schielzeth & Forstmeier, 2009; Barr et al., 2013). In addition, we included estimates of the correlations between the random intercept and slopes in the model. A 'singular fit' message indicated that some of the random effects terms were unidentifiable however, as we were interested in the fixed effects, this message was not a concern.

To establish the overall effect of our factors of interest (distributor and partner presence) and to avoid 'cryptic multiple testing' (Forstmeier & Schielzeth, 2011) we used a likelihood ratio test (Dobson, 2002) to compare the full model as described above with a null model lacking the interaction term and their main effects. This test revealed the two models differed significantly from one another (likelihood ratio test: $\chi^2_3 = 14.226$, $p = 0.003$).

We estimated model stability by dropping the levels of the random effects (one at a time) and comparing the estimates derived from each reduced dataset with those obtained from the full dataset; model stability was fine (see columns *min.* and *max.* in Table S5).

To check whether we should be concerned about collinearity we inspected Variance Inflation Factors (VIF; Field 2005). The largest VIF was 1.01; that is, collinearity was not an issue.

We fitted the model in R (version 4.1.1; R Core Team, 2021) using the *glmer* function from the *lme4* package (version 1.1-27; Bates et al., 2015). To achieve convergence we used the *nLminbwrap* optimizer. To obtain the VIFs we used the *vif* function of the *car* package (Fox and Weisberg, 2011); this function was applied to a linear model lacking the random effects. Confidence intervals were derived using the *bootMer* function of the *lme4* package.

Model 1A utilised the full dataset; the sample size was 1066 trials collected in 93 sessions and the data came from 12 subjects with 2 partners.

The output from the full model revealed a trend for the distributor and partner presence interaction term. The output of the full model is reported in Table S5 and we discuss these findings in the paper. As the significance threshold was not reached, we also fitted a reduced (additive) model. The output from the reduced model is reported in Table S6.

A note on not having controlled for Partner ID in Model 1A; initially we planned to use just one partner monkey for our study. With one partner, it would not have been necessary to include a partner ID term in the model. Unfortunately, the monkey which initially took the role of the partner became ill midway through the study and another monkey took over. With several partners (>5), partner ID can be included as a random effect. However, with two partners, we had to find another way to address a possible effect of partner ID; we conducted a second analysis (Model 1B; see following subsection).

Table S5

Model 1A (full model): Testing the effect of the interaction between distributor and partner presence as well as the fixed effects of trial, session, sex and counterbalance on the probability to refuse low-value food under conditions of inequality (estimates, standard errors, confidence intervals, test results, and minimum and maximum of model estimates obtained after dropping levels of random effects one at a time).

Term	Estimate	SE	CI _{Lower}	CI _{Upper}	LRT	Df	P-value	min.	max.
Intercept	-3.650	0.805	-5.342	-2.222			(1)	-4.460	-3.016
Distributor (machine)	-1.503	0.831	-3.309	0.101			(1)	-2.485	-0.474
Partner presence (yes)	-0.058	0.779	-1.521	1.531			(1)	-0.971	0.412
Trial ⁽²⁾	0.192	0.276	-0.389	0.738	0.450	1	0.502	0.022	0.484
Session ⁽³⁾	0.422	0.357	-0.246	1.273	1.396	1	0.237	0.248	0.627
Sex (male)	1.253	0.613	0.053	2.423	3.332	1	0.068	0.863	2.032
Counterbalance (partner)	2.409	0.587	1.175	3.985	11.825	1	0.001	2.066	3.264
Distributor : Partner presence	-2.133	1.255	-6.669	0.312	3.168	1	0.075	-3.067	-1.030

(1) Not indicated as of limited interpretability

(2) z-transformed to a mean of 0 and a standard deviation of 1; mean and SD of the original variable were 6.506 and 3.448 respectively

(3) z-transformed to a mean of 0 and a standard deviation of 1; mean and SD of the original variable were 4.412 and 2.275 respectively

Table S6

Model 1A (reduced model lacking the interaction between partner presence and distributor): Testing the effect of distributor, partner presence, trial, session, sex and counterbalance on the probability to refuse low-value food under conditions of inequality (estimates, standard errors, confidence intervals, and test results).

Term	Estimate	SE	CI _{Lower}	CI _{Upper}	LRT	Df	P-value
Intercept	-3.186	0.764	-4.967	-1.733			(1)
Distributor (machine)	-2.571	0.672	-4.210	-1.334	9.066	1	0.003
Partner presence (yes)	-0.795	0.637	-1.992	0.420	1.455	1	0.228
Trial ⁽²⁾	0.239	0.277	-0.321	0.757	0.689	1	0.407
Session ⁽³⁾	0.400	0.363	-0.312	1.104	1.207	1	0.272
Sex (male)	1.246	0.635	0.087	2.610	3.074	1	0.080
Counterbalance (partner)	2.350	0.608	0.954	4.083	10.434	1	0.001

(1) Not indicated as of limited interpretability

(2) z-transformed to a mean of 0 and a standard deviation of 1; mean and SD of the original variable were 6.506 and 3.448 respectively

(3) z-transformed to a mean of 0 and a standard deviation of 1; mean and SD of the original variable were 4.412 and 2.275 respectively

Model 1B

Our motivation in fitting Model 1B was to account for possible partner ID effects. Model 1B used a subset of the data to estimate the effect of distributor and partner presence on monkeys' food refusal behaviour. This model utilised only the data collected with the first partner (using the subset collected with the second partner would have resulted in order effects unaccounted for by the model). The sample size was 597 trials collected in 52 sessions and the data came from 12 subjects with 1 partner. As explained in the previous sub-section, we initially intended that only one monkey (Ilja) would partner all subjects. Ill-health meant Ilja had to be replaced part-way through the study. Ilja's replacement (Linus) was male and similar in age. It is likely that subjects respond to particular partner identities differently, however with only two partner identities it was not possible to include partner ID or dyad as random effects in Model 1A. The structure of Model 1B was identical to that of Model 1A and we followed the same general approach, although for Model 1B we used *bobyqa* rather than the *nlminbwrap* optimizer to achieve convergence.

The output of the full model revealed that the interaction of distributor and partner presence was not significant ($p = 0.316$). We therefore dropped the interaction and proceeded with the reduced model. The output from the full model is reported in Table S7 and the output from the reduced model in Table S8. Note that we do not report p-values for Model 1B given that these change as a function of sample size. The direction of the estimates listed in Table S5 match those listed in S7. Similarly, for Tables S6 and S8, there is consistency in terms of direction of effect. From this we tentatively conclude Partner-ID to have a negligible effect.

Table S7

Model 1B (full): Using a data subset (data collected with partner ID 1) to test the effect of distributor, partner presence, trial, session, sex and counterbalance on the probability to refuse low-value food under conditions of inequality (estimates, standard errors, confidence intervals and minimum and maximum of model estimates obtained after dropping levels of random effects one at a time).

Term	Estimate	SE	CI _{Lower}	CI _{Upper}	min.	max.
Intercept	-4.312	1.019	-7.031	-2.709	-5.089	-2.948
Distributor (machine)	-3.687	1.091	-7.446	-2.007	-4.689	-2.727
Partner presence (yes)	-0.707	1.008	-3.005	1.624	-1.190	-0.215
Trial ⁽¹⁾	0.328	0.393	-0.422	1.165	0.267	0.611
Session ⁽²⁾	0.572	0.731	-1.218	2.535	0.342	0.933
Sex (male)	2.223	0.959	0.848	3.884	-0.657	2.993
Counterbalance (partner)	3.386	0.724	1.841	5.692	2.135	4.456
Distributor : Partner presence	-2.085	2.285	-11.943	1.758	-17.248	-1.217

⁽¹⁾ z-transformed to a mean of 0 and a standard deviation of 1; mean and SD of the original variable were 6.508 and 3.454 respectively

⁽²⁾ z-transformed to a mean of 0 and a standard deviation of 1; mean and SD of the original variable were 3.008 and 1.774 respectively

Table S8

Model 1B (reduced): Using a data subset (data collected with partner ID 1) to test the effect of distributor, partner presence, trial, session, sex and counterbalance on the probability to refuse low-value food under conditions of inequality (estimates, standard errors and confidence intervals).

Term	Estimate	SE	CI _{Lower}	CI _{Upper}
Intercept	-4.218	1.013	-6.909	-2.540
Distributor (machine)	-4.182	1.024	-7.585	-2.443
Partner presence (yes)	-1.036	1.019	-3.437	1.072
Trial ⁽¹⁾	0.333	0.382	-0.457	1.066
Session ⁽²⁾	0.474	0.722	-1.137	2.011
Sex (male)	2.261	0.932	0.983	4.038
Counterbalance (partner)	3.403	0.718	1.857	5.647

⁽¹⁾ z-transformed to a mean of 0 and a standard deviation of 1; mean and SD of the original variable were 6.508 and 3.454 respectively

⁽²⁾ z-transformed to a mean of 0 and a standard deviation of 1; mean and SD of the original variable were 3.008 and 1.774 respectively

Model 2

We ran the control conditions after the original experimental conditions to match the study design of Engelmann et al. (2017) as closely as possible. Naturally, this approach confounds condition differences with presentation order. As a consequence, we didn't compare test and control conditions directly but rather analysed the data separately (test conditions: Model 1A; control conditions: Model 2).

Model 2 tested whether there was an effect of distributor when the partner was offered the same value of food as the subject. The response (food refusal) was binary (refusal = 1) and so the model was fitted with a binomial error structure and logit link function (McCullagh & Nelder, 1989). The model consisted of the fixed effects of distributor, trial number, session number and sex. Both trial number and session number entered the model as z-transformed variables, each with a mean of zero and a standard deviation of one. As repeated measures were taken of a small pool of individuals, subject identity was included in the model as a random effect. As we ran repeated test sessions using the same individuals, subject-session ID was also included in the model as a random effect.

The random slopes of partner presence, trial and session within subject and trial within subject-session ID were included in the model. We dummy-coded and centred partner presence before including it as a random slope. Originally we included estimates of the correlations between the random intercept and slopes in the model, however as all correlations were high, we went on to remove these from the model. This led to a slight decrease in model fit (log-likelihoods: full model with correlations: - 64.234; full model lacking the correlations: - 67.056).

We estimated model stability by dropping the levels of the random effects (one at a time) and comparing the estimates derived from each reduced dataset with those obtained from the full dataset. This check revealed that model stability was fine (see columns *min.* and *max.* in Table S9).

To check whether we should be concerned about collinearity we looked at the Variance Inflation Factors (VIFs; Field, 2005). The largest VIF was 1.00 and as such collinearity was not an issue.

To establish the overall effect of our factors of interest, we used a likelihood ratio test to compare the full model as described above with a null model lacking distributor, our factor of interest (Dobson, 2002). Here we found that the full model did not differ significantly from

the null (likelihood ratio test: $\chi^2_3 = 0.000$, $p = 0.984$). The output of Model 2 is shown in Table S9.

Model 2 utilised 437 control condition trials collected in 40 sessions and the data came from 10 subjects with 1 partner.

We fitted the model in R (version 4.1.1; R Core Team, 2021), using the *glmer* function from the *lme4* package the package (version 1.1-27.1; Bates et al., 2015). To aid convergence we used the *bobyqa* optimizer. To obtain the VIFs we used the *vif* function from the *car* package; this function was applied to a linear model lacking the random effects. Confidence intervals were derived using the *bootMer* function of the *lme4* package.

Table S9

Model 2 (full): Testing the effect of distributor, trial, session, sex and counterbalance on the probability to refuse low-value food in equality conditions (estimates, standard errors, confidence intervals, test results and minimum and maximum of model estimates obtained after dropping levels of random effects one at a time).

Term	Estimate	SE	CI _{Lower}	CI _{Upper}	LRT	Df	P-value	min.	max.
Intercept	-4.152	1.059	-8.598	-2.806			(1)	-5.036	-3.288
Distributor (machine)	-0.020	0.960	-1.955	2.084	0.000	1	0.984	-1.403	0.659
Trial ⁽²⁾	0.102	0.419	-0.661	0.990	0.059	1	0.809	-0.171	0.310
Session ⁽³⁾	0.633	0.570	-0.593	1.967	1.043	1	0.307	0.265	0.893
Sex (male)	-2.871	1.336	-16.533	-0.802	5.454	1	0.020	-19.494	-2.268

(1) Not indicated as of limited interpretability

(2) z-transformed to a mean of 0 and a standard deviation of 1; mean and SD of the original variable were 6.531 and 3.466 respectively

(3) z-transformed to a mean of 0 and a standard deviation of 1; mean and SD of the original variable were 2.469 and 1.122 respectively

7.2. Exploratory analysis

Model 3

We explored via a survival analysis (GLMM Model 3), whether distributor and partner presence had a systematic effect upon the timing of monkeys' lever pulls - for instance whether monkeys in the human group would wait longer before pulling the lever compared to those in the machine group. The survival analysis approach is appropriate for latency data such as ours, where no-pull events have to be accounted for.

The response variable was pull-latency, this was the time in seconds between the table light coming on and the monkey pulling the lever. The two-way interaction between distributor and partner presence was included, in addition to their fixed effects and the fixed effects of trial number, session number, sex and counterbalance. Both trial number and session number entered the model as z-transformed variables, each with a mean of zero and a standard deviation of one. Sex was included as a fixed effect and counterbalance was included to control for potential effects associated with monkeys having experienced the first two sessions either in the presence or absence of a partner. Subject ID and subject-session ID were included as random effects.

The random slopes of partner presence, trial number and session number within subject and trial number within subject-session ID were included in the model. We dummy-coded and centred partner presence before including it as a random slope. We also included estimates of the correlations between the random intercept and slopes in the model.

To establish the overall effect of our factors of interest, we used a likelihood ratio test to compare the full model as described above with a null model lacking the interaction term and their main effects (Dobson, 2002). This test revealed the two models were borderline in terms of differing from one another (likelihood ratio test: $\chi^2_3 = 6.871$, $p = 0.076$) and as the output from the full model revealed the distributor and partner presence interaction term was not significant ($p = 0.392$), we created a reduced model, dropping the interaction and looking at the fixed effects of distributor and partner presence. The output from the full model is reported in Table S10 and the output from the reduced model in Table S11. In the paper we discuss the output of the reduced model.

We estimated model stability by dropping the levels of the random effects (one at a time) and comparing the estimates derived from each reduced dataset with those obtained from the full dataset. This check revealed model stability was fine (see columns *min.* and *max.* in Table S10).

We fitted the model in R (version 4.1.1; R Core Team, 2021), using the *coxme* function from the *coxme* package (Therneau, 2020; version 2.2-16).

Model 3 utilised the full dataset of 1066 trials. Of these trials 119 were *refusal-to-participate* (i.e. “timeout”) events.

Table S10

Model 3 (full model): Exploring the effect of distributor, partner presence, trial, session, sex and counterbalance on the time taken to pull the lever under conditions of inequality (estimates, standard errors, confidence intervals, test results and minimum and maximum of model estimates obtained after dropping levels of random effects one at a time).

Term	Estimate	SE	LRT	Df	P-value	min.	max.
Distributor (machine)	0.104	0.618				-0.375	0.593
Partner presence (yes)	0.690	0.287				0.510	0.927
Trial ⁽¹⁾	-0.170	0.063	5.662	1	0.017	-0.214	-0.123
Session ⁽²⁾	-0.279	0.159	2.903	1	0.088	-0.349	-0.151
Sex (male)	-1.467	0.579	5.223	1	0.022	-1.890	-0.990
Counterbalance (partner)	-0.718	0.580	2.629	1	0.105	-1.249	-0.296
Distributor: partner presence	-0.367	0.435	0.733	1	0.392	-0.614	-0.077

⁽¹⁾ z-transformed to a mean of 0 and a standard deviation of 1; mean and SD of the original variable were 6.506 and 3.448 respectively

⁽²⁾ z-transformed to a mean of 0 and a standard deviation of 1; mean and SD of the original variable were 4.412 and 2.275 respectively

Table S11

Model 3 (reduced model lacking the interaction between distributor and partner presence): Exploring the effect of distributor, partner presence, trial, session, sex and counterbalance on the time taken to pull the lever under conditions of inequality (estimates, standard errors, confidence intervals and test results).

Term	Estimate	SE	LRT	Df	P-value
Distributor (machine)	-0.081	0.577	0.017	1	0.896
Partner presence (yes)	0.533	0.217	6.134	1	0.013
Trial ⁽¹⁾	-0.169	0.063	5.651	1	0.017
Session ⁽²⁾	-0.279	0.157	2.990	1	0.084
Sex (male)	-1.462	0.578	5.409	1	0.020
Counterbalance (partner)	-0.714	0.578	2.657	1	0.103

⁽¹⁾ z-transformed to a mean of 0 and a standard deviation of 1; mean and SD of the original variable were 6.506 and 3.448 respectively

⁽²⁾ z-transformed to a mean of 0 and a standard deviation of 1; mean and SD of the original variable were 4.412 and 2.275 respectively

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