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# Inequity aversion in rats, *Rattus norvegicus*

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Disadvantageous inequity aversion (IA) is a behavioural response to an inequitable outcome distribution yielding a smaller reward to oneself than to a conspecific, given comparable efforts to obtain the reward. This behavioural response aims to minimize unfair reward distributions. It has been proposed to be essential for the emergence of cooperation. Humans show choice patterns compatible with IA and, as recently suggested, cooperative nonhuman species such as primates, corvids and dogs also respond negatively to disadvantageous inequitable outcomes. Here, we asked whether rats are sensitive to such inequitable outcomes. In a double T-maze apparatus, actor rats could choose to enter one of two different compartments after which a conspecific (partner rat) entered the adjoining partner compartment. One side of the paired compartments was associated with an equitable reward distribution (identical amount for the actor and the partner) whereas entry into the other paired compartment led to an inequitable reward distribution (in which the partner received a larger reward). Both compartments yielded an identical reward for the actor. Using a within-subjects design, we compared the actor rats' choices in the social condition with a nonsocial baseline control condition in which a toy rat replaced the partner rat. Actor rats exhibited disadvantageous IA: they preferred equitable outcomes in the social, but not the toy condition. Moreover, there was large variability in IA between rats. This heterogeneity in social preference could be partly explained by a social-hierarchy-dependent sensitivity to IA, as dominant animals showed higher IA than subordinate animals. Our study provides evidence for social-hierarchy-dependent disadvantageous IA in social vertebrates. Our findings are consistent with the notion that a sense of fairness may have evolved long before humans emerged. IA may therefore be a basic organizational principle, shared by many social species, that shapes the intricate social dynamics of individuals interrelating in larger groups.

Beyond maximizing one's own material gains, fairness plays an important role in human behaviour and economic decision making (Fehr & Schmidt, 1999). The tendency to base decisions not solely on selfish motives but considering others' outcomes as well has often been studied with economic games (Margittai et al., 2015; Strombach et al., 2015; Yamagishi et al., 2009). For instance, some people voluntarily share money in the dictator game (Bolton, Katok, & Zwick, 1998), and give up their own gains to punish unfair offers in the ultimatum game (Güth, Schmittberger, & Schwarze, 1982). These examples are often considered the consequence of so-called inequity aversion (IA), an affective, cognitive and behavioural response to inequitable outcomes. Generally, two forms of IA can be distinguished: the aversion towards outcomes (1) that yield a higher payoff for a partner relative to one's own payoff (disadvantageous IA) given matched efforts to obtain the payoff and (2) that produce a lower payoff for a partner relative to one's own payoff (advantageous IA). Here, we focus on disadvantageous IA (in the following simply referred to as IA for brevity, unless specified otherwise).

In their prominent model of IA, Fehr and Schmidt (1999, p. 822) noted that ‘in addition to purely selfish subjects, there are subjects who dislike inequitable outcomes‘. Although costly responses to unfair offers result in material disadvantage in economic games, IA is thought to be essential for the evolution of successful cooperation with nonkin (Brosnan, 2006, 2011; but see Chen & Santos, 2006). According to this idea, costly help provided to others might be based on expecting a return of investment in the form of a similar helping hand from others in the future (Trivers, 1971). Such reciprocity is prone to cheating and, thus, inequitable outcomes

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(Brosnan, 2006, 2011). The detection of unfairness, and an appropriate response to it, may therefore be necessary for the emergence of stable cooperation through reciprocity. Hence, IA's functional principle can be described as a 'fairness detector' driven by the aversion against exploitation.

Comparative research has begun to understand the evolutionary origins and underlying mechanisms of human responses to inequity (Brosnan, 2006). There is an ongoing debate whether IA can be found in nonhuman animals. In their pioneering experiment, Brosnan and de Waal (2003) investigated IA in the brown capuchin monkey, *Cebus apella*, using a token exchange paradigm. Animals were tested in pairs to allow social comparison of inequity. An experimenter distributed rewards such that one animal received a less valuable reward (cucumber) than that received by a second animal (grape) for performing the same token exchange task. The results showed that animals rejected a substantial proportion of unfair offers (refusing the food reward and/or abandonment of continuing task performance), a finding that the authors interpreted as IA in the brown capuchin monkey (Brosnan & de Waal, 2003). Using variants of this paradigm, IA has also been found in chimpanzees, *Pan troglodytes* (Brosnan, Schiff, & de Waal, 2005; Brosnan, Talbot, Ahlgren, Lambeth, & Schapiro, 2010) and long-tailed macaques, *Macaca fascicularis* (Massen, van den Berg, Spruijt, & Sterck, 2012). IA was not found in two rather uncooperative species, namely orang-utans, *Pongo pygmaeus* (Brosnan, Flemming, Talbot, Mayo, & Stoinski, 2010) and squirrel monkeys, *Saimiri sciureus* (Talbot, Freeman, Williams, & Brosnan, 2011), raising the possibility that IA and cooperation may have coevolved (Brosnan, 2006, 2011). Besides primates, evidence for IA has also been found in other social species: domestic dogs, *Canis familiaris* (Range, Horn, Virányi, & Huber, 2009; Range, Leitner, & Virányi, 2012) and corvids (Wascher & Bugnyar, 2013). These results indicate that IA is not universal; specifically IA could depend on the social structure of the species.

However, other studies using similar paradigms have failed to demonstrate IA in social species, including brown capuchin monkeys (Dubreuil, Gentile, & Visalberghi, 2006; Fontenot, Watson, Roberts, & Miller, 2007; Roma, Silberberg Ruggiero & Suomi, 2006; Silberberg, Crescimbene, Addessi, Anderson, & Visalberghi, 2009) or any great ape species (Bräuer, Call, & Tomasello, 2006, 2009; see also Raihani, McAuliffe, Brosnan, & Bshary, 2012 for evidence against IA in food-cooperative cleaner fish) and therefore argue for nonsocial motives of costly rejections of unfair offers in previous tasks, such as reward expectation (e.g. Bräuer et al., 2006) or frustration (e.g. Roma et al., 2006).

Another possibility for the heterogeneity in evidence for IA in animals may be that preferences are also affected by the cost associated with a refusal of an unequal outcome distribution. That is, individuals may be more sensitive to their own payoff than to inequality, and consequently accept unfair offers if rejecting them would imply missing out on a reward; in other words, behavioural responses to inequality may be masked by the animals' natural egocentricities. In support of this view, IA was recently demonstrated in capuchin monkeys in a newly developed choice-based task (Fletcher, 2008) in which the costs for equitable (identical reward for both animals) and inequitable outcomes (higher reward to conspecific than actor) were kept constant.

Using an adaption of this cost-controlled task for rodents, we have recently shown that rats prefer mutual over own-reward outcomes, possibly indicating advantageous IA (Hernandez-Lallement, van Wingerden, Marx, Srejic, & Kalenscher, 2015; Hernandez-Lallement, van Wingerden, Schäble, & Kalenscher, 2016, in press). However, it is unknown whether rats also exhibit disadvantageous IA. To tackle this question, we developed a rodent version of the choice-based, cost-controlled disadvantageous IA experiment originally designed for monkeys (Fletcher, 2008). In this IA choice task, actor rats chose between equitable and inequitable reward outcomes, both in a social (paired with a real partner rat) and a toy control condition (paired with an inanimate rat toy).

Rats are a highly social species (Whishaw & Kolb, 2005) and develop in hierarchically structured, well-organized social groups. We therefore hypothesized that they also exhibit a sense of equity that would become manifest in an (in)equity choice task. There is partial support for this idea in the literature, suggesting that rats may have rudiments of social preferences. As mentioned, rats prefer mutual rewards in a prosocial choice task and show advantageous inequity aversion (Hernandez-Lallement et al., 2015, 2016, in press) and are sensitive to food-seeking behaviour of partners (Marquez, Rennie, Costa, & Moita, 2015). Furthermore, early pioneering studies found evidence for cooperation (Daniel, 1942) and even altruism (Rice & Gainer, 1962; Greene, 1969; but see Daniel, 1943; Mihalick & Bruning, 1967). More recently, coordinated cooperative actions (Lopuch & Popik, 2011; Schuster, 2002), reciprocity (Rutte & Taborsky, 2007) and empathy (Bartal, Decety, & Mason, 2011) have been demonstrated in rats.

Rats are known to develop stable social dominance orders (Baenninger, 1966) and there is some evidence showing that weight (as a potential proxy for hierarchy) influences mutual reward preferences in males (Hernandez-Lallement et al., 2015). To investigate whether social dominance status modulates IA in rats in our task, we performed a social hierarchy assessment with our rats prior to training them in the IA task. We hypothesized a modulating role of social status on IA, but we had no clear prediction regarding the direction of a potential dominance effect. Social status could have influenced IA in both ways. On the one hand it is possible that dominant animals would show lower levels of disadvantageous IA because they can afford to be more generous. On the other hand, it is also possible that dominant animals would show higher levels of disadvantageous IA because they are used to having priority of access to food.

## METHODS

### Subjects

Twenty-three genetically unrelated male Long Evans rats were tested in two consecutive batches (batch 1: $N = 12$, bred by Janvier Labs, St. Berthevin, France; batch 2: $N = 11$, bred by Charles River Labs, Calco, Italy). Three animals of one cage from batch 1 were used as partner animals for both batches. The remaining 20 animals were used as actors. One rat from batch 1 had to be excluded after shaping (see below). All rats were 4–5 months old at the beginning of the experiment and weighed between 400 and 533 g (mean ± SEM: 466 ± 6.56 g). Animals were housed in groups of three animals per cage (59 × 38 cm and 20 cm high). For logistic reasons, one cage contained two animals. Cages were enriched with hiding places (tunnels) and wood. Rats were housed under an inverted 12:12 h light:dark cycle (lights off at 0700 hours) to simulate their active phase during the day. The colony room was temperature (20 ± 2 °C) and humidity controlled (60%). Water was provided ad libitum in the home cage at all times. Daily feeding was adapted to a mild food deprivation schedule on weekdays (20% less than animals consume ad libitum). Rats were weighed daily during the whole experimental phase to monitor their health. All experiments were performed in accordance with the German Welfare Act and were authorized by the local authorities (Landesamt für Natur-, Umwelt- und Verbaucherschutz, LANUV, North Rhine-Westphalia, Germany).

## Apparatus

The IA choice task took place in a similar double T-maze as described in Hernandez-Lallement et al. (2015; see Fig. 1). It consisted of two starting boxes (20 × 20 cm and 30 cm high), two decision boxes (25 × 20 cm and 30 cm high) and 2 × 2 opposing choice compartments (30 × 30 cm and 40 cm high; see Fig. 1a). The choice compartments were separated by transparent multi-perforated walls allowing visual, auditory and olfactory communication between animals. Each starting box was equipped with a sliding door which provided access to the decision box. From the decision box, two independently operated doors led to either of the two choice compartments. To minimize distractive cues, the whole apparatus was covered with red lids, only opened when manually putting the animals back from the choice compartment to the starting box. Rewards (dustless precision pellets, 45 mg, Bio Serv, Germany) were delivered through metallic tubes placed in the centre of the maze (one tube in each inner corner of the four choice compartments).

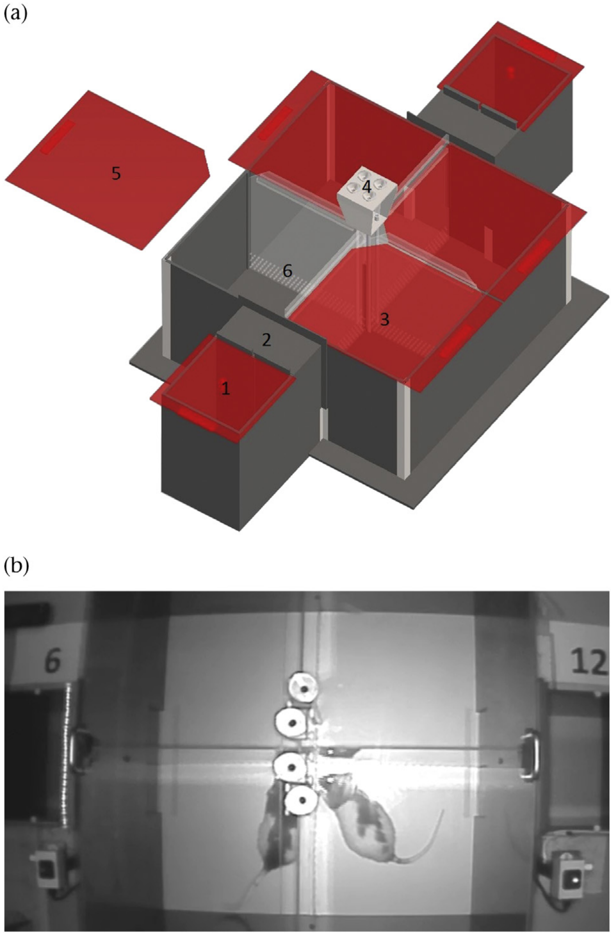

**Figure 1.** Apparatus. (a) Illustration of the social maze. Each T-maze of the social maze consisted of one starting box (1), one decision box (2) and two choice compartments (3). From the starting box, a sliding door led to the decision box. There, two independent sliding doors allowed entrance to each choice compartment. A reward delivery system consisting of metallic tubes was placed at the intersection between the four inner walls (4). The whole apparatus was covered with red semitransparent lids (nontransparent for rats' eyes) to minimize distraction from outside cues (5). The walls between all four test compartments were perforated and transparent (6) to allow visual, auditory and olfactory communication between animals. (b) Photo of the apparatus depicting the actor and the partner near the reward delivery area.

## Experimental Outline

Prior to the actual IA choice task, a hierarchy assessment was conducted separately for each cage in an open field arena. Next, all animals went through 2 consecutive days of habituation on the social maze and at least 2 × 5 consecutive days of shaping. Finally, rats were trained and tested in the IA choice task. Every actor performed 2 × 12 sessions in a social and a toy condition (one session per test day). Testing took place on weekdays in the daytime during the rats' active phase.

## Hierarchy Test

To estimate hierarchy rank among cage mates, pairs of rats were placed in an open field arena (50 × 50 cm) for 30 min, under red light conditions. A black food cup with six sucrose pellets was placed in the open field. Rats were allowed to explore and (inter)act freely during the whole time. Their behaviour was recorded on DVD using a black-and-white CCD Camera. Behaviours of interest were duration and frequency of partner exploration and genital exploration. These behaviours are easily detectable and, due to their offensive nature, are assumed to be indicative of higher levels of social dominance (Blanchard & Blanchard, 1990). The rats occasionally engaged in other types of offensive and defensive behaviour, such as mounting or showing submissive postures, too. However, these behaviours were infrequent, presumably because stable social hierarchies were already established among cage mates. Thus, because only partner and genital exploration were shown reliably and consistently, we restricted our analysis to these behaviours. The behavioural data were analysed with Ethovision XT (Noldus, Wageningen, The Netherlands) by an expert coder. Each animal had two open field interactions, one with each of the two other cage mates. For rats housed in cages of three, the rat that had a consistently higher proportion of genital and partner exploration in each of the dyadic interactions with the two other cage mates was classified as being dominant. The two remaining rats were classified as submissive. In one cage there was no consistent order, so none of these rats was classified as dominant. For the one cage with only two animals only one interaction session took place. We obtained hierarchy estimates for cage mates only, not for rats between cages. Note that actor and partner rats in the IA choice task never came from the same cage, but had an opportunity to interact briefly before the choice task started (see below). We decided to measure hierarchy among cage mates for several reasons. First, relationships are relatively stable among cage mates, but not necessarily among pairs of rats that experience only sporadic and transient encounters (i.e. actor and partner). Thus, any dominance relation estimate between actor and partner is just a (presumably unreliable) snapshot in time. Second, by analysing cage mates, we had the opportunity to perform two hierarchy assessments per animal (see above). This allowed us to be more conservative in classifying animals: only rats that were dominant in both encounters were eventually classified as dominant. Third, by assessing social dominance status in relation to animals that were not subsequently encountered in the social T-maze, dominance could be interpreted as a general trait variable of the actor rat above and beyond any situational behavioural interaction pattern between actor and partner in the experimental set-up.

## Habituation and Shaping

All animals underwent a habituation procedure to become acquainted with the apparatus. On 2 consecutive days, each animal was individually put in the starting box for 2 min. The entrances to both compartments were opened and one sucrose pellet was placed underneath the food dispenser in each compartment. At the end of the 2 min interval the animal was put back in its home cage.

Upon completion of the habituation phase, all animals underwent shaping procedures. The purpose of the shaping stage was for the rat to learn the functional principles of the social maze and get used to the presence of another animal/toy within the apparatus. Actor rats were paired either with another rat or with a toy. Sessions alternated between social and toy condition during shaping. The procedure of shaping itself was identical to the IA choice task (see below) except for the reward distribution. A reward was delivered to only one of the two compartments (one sucrose pellet for each rat or toy). Over social and toy sessions, the reward was pseudorandomly distributed between left and right compartment. After eight forced choice trials, actor rats performed 20 free choice trials in which they could choose which compartment to enter. Rats were trained in the shaping procedure until they met the following criteria: (1) enter the compartments autonomously within 10 s on each trial; (2) consume all delivered rewards; (3) choose the rewarded compartment in at least 75% of the trials. All rats except one reached criteria in 10–12 sessions. One rat had to be excluded from the experiment because it never reached criterion 3.

## *IA Choice Task*

### *General task design*

Similar to Hernandez-Lallement et al. (2015), pairs of rats, an actor and a partner rat, were tested in two main conditions. In the social condition ($N = 12$ sessions), both actor and partner rats were placed in the social maze in their respective starting boxes; in the toy condition ($N = 12$ session), a toy rat was used as a partner (see below). The experimenter indicated the beginning of a trial by opening the doors to both compartments. The actor was always the first to move and could decide to enter either compartment. When the actor had entered one compartment, the partner was directed to the compartment facing the actor. After entering a compartment, actors received an identical amount of reward (one sucrose pellet) in either compartment, delivered after the same delay. Importantly, entering one compartment resulted in a reward delivery of the same magnitude and delay in both the actors' and partners' compartments (one sucrose pellet), whereas choosing the alternative compartment yielded a larger reward to the partner (three sucrose pellets), leaving the partner better off than the actor. Thus, the alternatives did not differ with respect to the actor's own payoff; the only difference was the reward magnitude (triple versus equal) to the partner.

The toy condition was identical to the social condition in terms of task structure, reward delivery, reward distribution and timing, except that the partner was an inanimate toy rat of similar size, shape and colour. Similar to Hernandez-Lallement et al. (2015, 2016, in press), we placed a toy rat in the adjacent compartment in the nonsocial control condition instead of leaving the compartment empty. We opted for this toy manipulation to control for the presence of an entity in the apparatus, as exploration behaviour may have affected the rats' preferences. The toy condition furthermore served to determine individual baseline IA levels; it controlled for pellet delivery sounds and potential secondary reinforcement effects of food delivery. It is important to stress again that the choice–reward payoff structure did not differ between social and toy conditions. Magnitude and delay of reward delivery were identical for payoffs to the toy rat and the animate partner rat. Thus, any difference in choice allocation between the social and the toy condition could be attributed to the influence of social context on the actor's decisions.

The two conditions were presented in blocks of 12 sessions. Half of the animals started the experiment in the social condition and half in the toy condition. The order of the starting condition was pseudorandomized across rats. In the social condition, actor rats were always paired with the same partner.

### *Session structure*

A session started with 1 min of interaction in a neutral cage so that the animals could explore each other (same in rat and toy conditions) before the actual test started. The goal of this interaction opportunity was to minimize putatively distractive (social) exploration behaviour during task performance. After the interaction phase, partner and actor were placed in the social maze in their respective starting boxes. For each session one compartment was associated with an equitable reward distribution (one sucrose pellet for each animal) and the other with a disadvantageous inequitable reward distribution (one sucrose pellet for the actor, three for the partner). The allocation of choice compartment to equitable/inequitable outcomes was pseudorandomized across sessions. Hence, the design involved very frequent reversals of the inequity-compartment assignments.

Each session consisted of 28 trials (eight forced-choice and 20 free choice trials). A session began with the eight forced choice trials (four on each side in a pseudorandom order) in which the actor was directed into one of the two choice compartments by just opening one of the two sliding doors. These forced choice trials allowed rats to sample the outcome contingencies in each session. In the following free choice trials ($N = 20$), both sliding doors were opened so that the actor could choose to enter either compartment. All sessions were videotaped. After the last trial both animals were put back into their home cages.

### *Trial structure*

As mentioned, on each trial, the actor was the first to move, followed by the partner/toy, which was always directed/placed into the compartment facing the actor. Trials followed a strict time schedule to exclude any influence of timing or reward latencies on the decision behaviour (Fig. 2). At time point 0 the experimenter opened the sliding doors to allow access to the choice compartments (one compartment in the forced choice trials, both compartments in the free choice trials). The actor had 10 s to enter the choice compartment. Sliding doors were closed again immediately after the actor had fully entered the choice compartment. At 10 s from trial start, the partner's doors opened to lead the partner into the compartment facing the actor. The partner also had 10 s to enter. In the toy condition the toy rat was manually placed into the choice compartment. In, on average, 1.70 ± 0.48% (mean ± SEM) of free choice trials per session, the actor rats did not enter the choice compartment autonomously. Here, the experimenter gently pushed the animals forwards, paying attention not to influence the actor's decision. At 25 s from trial start, rewards were delivered through the metallic tubes (Fig. 1). Actor and partner received the first pellet simultaneously. For inequitable rewards, the partner's second and third pellets were given successively, guaranteeing that the actor could hear the sound of the single pellets falling in the partner's compartment. At 30 s from trial start, after reward consumption, first the actor and then the partner were manually transferred to their respective starting box (finished at 45 s from trial start). At 60 s from trial start, the next trial started. Importantly, the duration of the intertrial interval was independent of the actor's choice.

### *Analysis*

We first compared the levels of hierarchy markers obtained in our hierarchy assessment (social and genital exploration times, see

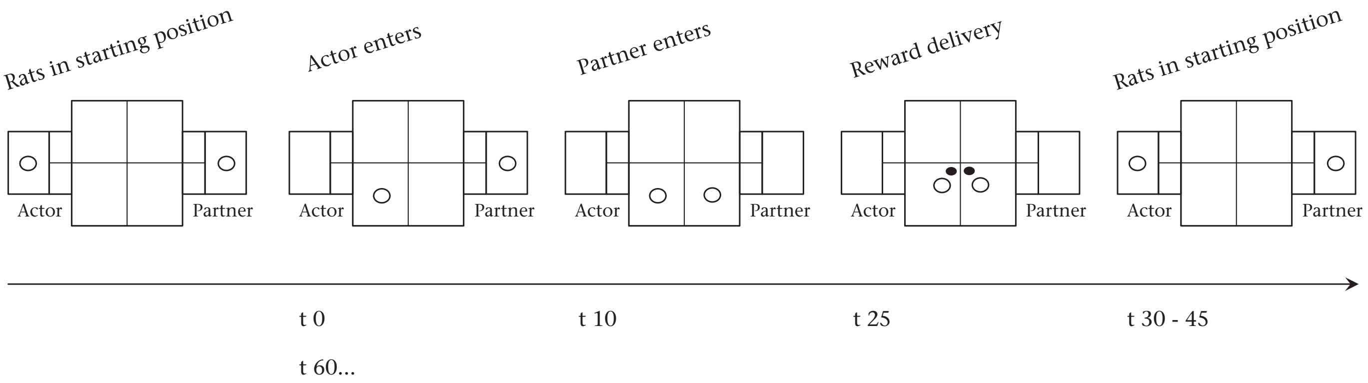

**Figure 2.** Time schedule of the trials in the IA choice task. Actors were always the first animal to move. The actor's doors were opened first (one of them in the forced choice trials, both of them in the free choice trials) and he moved into one of the two choice compartments; t0, trial onset. After 10 s (t10), the partner rat was directed to the choice compartment facing the actor. In the toy condition the toy rat was manually placed in the respective choice compartment. A reward was delivered 25 s after trial onset (t25). Actor and partner received the same reward after equity choices (one sucrose pellet) and the partner received a larger reward (three sucrose pellets) after inequity choices. After reward consumption, between 30 s and 45 s after trial onset (t30–45), rats were manually put back in their starting boxes (actor first) and a new trial started 60 s after trial onset (t60).

above) of dominant versus subordinate animals against chance level with one-tailed *t* tests to verify classification success.

To test whether rats are inequity averse in the IA choice task, we compared the percentage equity choices in the social condition with their equity choices in the toy condition using a paired *t* test across all animals, and we also compared the percentage equity choices in both conditions against the 50% chance level. To quantify the premium that rats place on equitable outcomes, we calculated an equity bias score for each animal (see Hernandez-Lallement et al., 2015). The equity bias score for rat *i* is the percentage difference in equity choices between the social and toy conditions relative to the equity choices in the toy condition:

$$\text{Equity bias score}_{\,i} = \left[\frac{\%\ \text{equity choices (social)}_i - \%\ \text{equity choices (toy)}_i}{\%\ \text{equity choices (toy)}_i}\right] \times 100$$

Because the payoff to the actor rat was identical for all choices and conditions, the difference in percentage equity choices between the social and the toy condition reflected the differential valuation of equitable outcomes, depending on the social context. Hence, a positive equity bias score, i.e. more equity choices in the social than the toy condition, can be interpreted as added positive social value placed on equitable outcomes; a negative social bias score can be construed as the disutility of equitable outcomes. Thus, positive equity bias score values can be understood as a measure of IA in rats. We tested the averaged equity bias score of all rats against chance level.

To generate a normative criterion to classify single animals as inequity averse, we ran a bootstrapped permutation analysis to obtain a benchmark equity bias score distribution (see Hernandez-Lallement et al., 2015). This permutation distribution of equity bias scores consisted of $N = 5000$ draws of $12 \times 2$ sessions, with the percentage of equity choices of these sessions randomly assigned to social and toy labels. For each of these draws, the resulting equity bias score was calculated, generating a distribution of 5000 permuted equity bias scores that followed a normal distribution. The upper limit of the 95% confidence interval of this distribution was selected as a benchmark equity bias score, and subsequently the equity bias score of each animal was compared against this condition-randomized equity bias benchmark value.

Rats with equity bias scores exceeding the upper limit of the 95% confidence interval of the benchmark distribution were categorized as inequity averse. Animals within the 95% interval of this reference distribution were categorized as inequity neutral.

Next, we tested whether the percentage equity choices of animals classified as inequity averse versus inequity neutral differed in the social and/or toy condition with a mixed-model ANOVA and post hoc comparisons. Furthermore, we tested the percentage equity choices of both subgroups against chance level in both conditions. Finally, we compared mean equity bias scores of animals classified as socially dominant with mean equity bias scores of animals classified as subordinate and compared mean equity bias scores of both hierarchy groups against zero.

We additionally ran a number of control tests. We controlled for an order effect of starting condition (rats starting the experiment in the social or toy condition) and an effect of batch by calculating independent sample *t* tests on percentage equity choices in either condition. A one-way ANOVA with partner identity as independent and percentage equity choices in the social condition as dependent variable was used to control for an effect of partner rats' identities. Using a repeated measures ANOVA we checked for an effect of session number on percentage equity choices and a putative interaction between condition and session number.

Data were analysed using IBM SPSS Statistics 22 (IBM, New York, U.S.A.) and Matlab R2013a (The MathWorks, Natick, MS, U.S.A.). Graphs were built with SigmaPlot 11.0 (Systat, Erkrath, Germany). For all statistical tests the level of significance was predefined as $P < 0.05$.

## RESULTS

### *Hierarchy Assessment*

Rats classified as dominant spent 75.6 ± 5.5% (mean ± SEM) of the total exploration time exploring subordinate cage mates and their genitals. By contrast, subordinate rats spent only 39 ± 4.7%

(mean ± SEM) of the total exploration time exploring their cage mates (note that these percentage values do not add up to 100% because they are not complementary in triad interactions). For dominant rats, percentages of exploration times were significantly above 50% (one-tailed *t* test: $t_5 = 4.62$, $P < 0.01$), and for subordinate rats they were significantly below 50% (one-tailed *t* test: $t_{13} = -2.34$, $P < 0.05$).

### *Rats are More Inequity Averse in the Social than in the Toy Condition*

Using the toy condition as a baseline for equity preferences, we computed equity bias scores to quantify the equity premium associated with the social context. Equity bias scores ranged from −20.60 to 52.38 (see dots in Fig. 3). At the group level, we found average equity bias scores to be significantly higher than 0 (mean ± SEM: 14.41 ± 4.85; $t_{18} = 2.97$, $P < 0.01$), indicating that rats were more inequity averse in the social than in the toy condition. Unpacking this result, we found that rats selected the equitable option in 51.93 ± 1.41% (mean ± SEM) of free choice trials in the social condition and in 45.58 ± 1.33% (mean ± SEM) in the toy condition. Inequity aversion was significantly higher in the social than in the toy condition ($t_{18} = 3.00$, $P < 0.01$). Even so, the choices for equitable outcomes were significantly different from chance only in the toy condition ($t_{18} = -3.33$, $P < 0.01$), but not in the social condition ($t_{18} = 1.37$, $P = 0.19$).

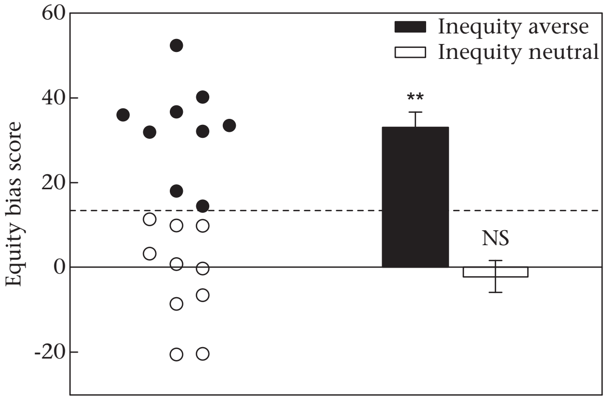

**Figure 3.** Equity bias scores. Dots represent individual equity bias scores. The horizontal dashed line represents the upper limit of the 95% confidence interval of the bootstrapped permutation distribution. Animals with equity bias scores exceeding the upper limit were classified as inequity averse ($N = 9$; black dots); animals with scores within the confidence interval were classified as inequity neutral ($N = 10$; white dots). Bars represent the mean equity bias scores of inequity averse and inequity neutral rats. Error bars represent the SEM. $^{**}P < 0.01$.

Although mean equity choices were significantly different between social and toy conditions, the effect was relatively small. However, we found substantial individual differences in percentage choice data (Fig. 4) and thus also in equity bias scores. We have previously discussed (Hernandez-Lallement et al., 2015, in press) that averaged preference scores at the group level might be insufficiently informative of the choice allocation dynamics and levels because of large heterogeneity in social preferences across rats. Thus, to get a better understanding of the distribution of equity preferences in the current experiment, we classified animals as inequity averse when their equity bias score exceeded the 95% confidence interval on a reference bootstrapped permutation distribution (see Methods and Hernandez-Lallement et al., 2015). Briefly, this distribution is made up of surrogate equity bias score values, generated by randomly permuting condition (social, toy) labels within subjects, and using these random labels to compute permuted equity bias score values using empirical values. Thus, the upper 95% confidence interval limit of this normally distributed reference distribution (cutoff equity bias score: 13.48; dashed line in Fig. 3) acts as the threshold for detecting significant levels of inequity aversion. Based on this analysis, we classified nine out of 19 rats as inequity averse with a mean equity bias score of 32.80 ± 3.76 (mean ± SEM), and 10 as inequity neutral with a mean equity bias score of −2.14 ± 3.73 (mean ± SEM; see bars in Fig. 3). As expected, rats classified as inequity averse showed equity bias scores significantly higher than zero ($t_8 = 8.72$, $P < 0.01$), whereas equity bias scores of rats classified as inequity neutral did not differ significantly from zero ($t_9 = -0.57$, $P = 0.58$).

Next, we compared percentage choices of equitable outcomes between animals classified as inequity averse and inequity neutral. In the social condition, inequity averse rats chose the equitable option in 56.20 ± 1.17% (mean ± SEM) of trials, while inequity neutral rats chose the equitable option in 48.09 ± 1.72% (mean ± SEM) of trials. In the toy condition, inequity averse rats selected the equitable option in 42.04 ± 1.58% (mean ± SEM) of trials, and inequity neutral rats in 48.77 ± 1.52% (mean ± SEM) of trials. A mixed-model ANOVA

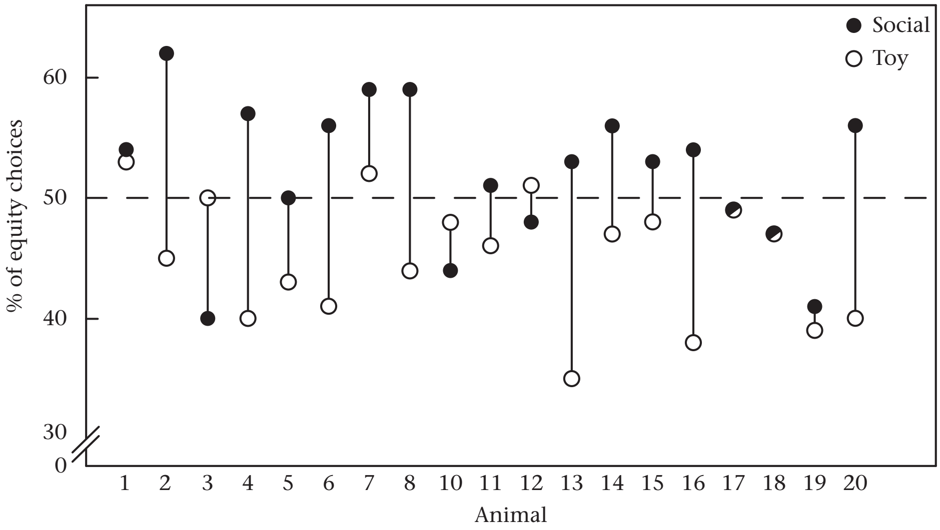

**Figure 4.** Individual choice data. Percentage equity choices of all animals ($N = 19$) for social (black dots) and toy condition (white dots). Animals 17 and 18 have the same percentage of equity choices in both conditions. Animal 9 was excluded from analysis (see Methods). The horizontal dashed line represents 50% chance level.

revealed a significant main effect of condition on percentage choices of equitable outcomes (social versus toy: $F_{1,17} = 29.70$, $P < 0.01$), confirming the abovementioned mean comparison of percentage equity choices between social and toy conditions, and a significant interaction between condition (social, toy) and classification (inequity averse, neutral: $F_{1,17} = 35.98$, $P < 0.01$). Using post hoc $t$ tests, we found that the percentage equity choices differed significantly between inequity averse and inequity neutral rats in both conditions (social condition: $t_{17} = 3.81$, $P < 0.01$; toy condition: $t_{17} = -3.06$, $P < 0.01$; Fig 5). The equity choices in the social condition were significantly above chance level in inequity averse rats ($t_8 = 5.32$, $P < 0.01$) but not inequity neutral rats ($t_9 = -1.11$, $P = 0.30$). In the toy condition, equity choices were significantly below chance level in inequity averse rats ($t_8 = -5.03$, $P < 0.01$), but not inequity neutral rats ($t_9 = -0.81$, $P = 0.44$). This pattern of results suggests that, compared to inequity neutral animals, inequity averse rats showed more inequity aversion when paired with a partner, and less inequity aversion when paired with a toy.

There was no order effect of starting condition (rats starting the experiment in the social or toy condition) on percentage equity choices in either condition (social condition: $t_{17} = -0.02$, $P = 0.99$; toy condition: $t_{17} = 1.57$, $P = 0.14$). Likewise, there was no significant difference between batches of rats on percentage equity choices in either condition (social condition: $t_{17} = 1.64$, $P = 0.12$; toy condition: $t_{17} = 0.27$, $P = 0.79$). The same partner was used with different actors (see Methods). A one-way ANOVA revealed that the partners' identities did not significantly influence the actors' choices in the social condition (between-subject factor: partner identity: $F_{2,16} = 2.24$, $P = 0.14$). A repeated measures ANOVA revealed no significant effect of session number on percentage equity choices ($F_{5.79,18} = 1.29$, $P = 0.27$, Greenhouse-Geisser corrected) and no significant interaction between condition and number of session ($F_{11,18} = 1.14$, $P = 0.33$). The same picture emerges when analysing inequity averse and neutral animals separately (inequity averse rats: no significant effect of session number on percentage equity choices: $F_{11,88} = 0.65$, $P = 0.79$; no significant interaction between condition and number of session: $F_{11,88} = 0.65$, $P = 0.79$; inequity neutral rats: no significant effect of session number on percentage equity choices: $F_{11,99} = 1.75$, $P = 0.07$; no significant interaction between condition and number of session: $F_{11,99} = 1.07$, $P = 0.39$). These analyses indicate that rats made consistent choices over time. Finally, a Pearson product moment correlation between the percentage equity choices in either condition and the percentage of trials in which an actor had to be gently pushed into the choice compartment was not significant (social condition: $r_{17} = 0.27$, $P = 0.27$; toy condition: $r_{17} = -0.14$, $P = 0.58$), suggesting that experimenter intervention is unlikely to have biased actors' choices.

### *Dominant Animals Show Stronger IA*

Next, we assessed whether there was a link between the actor's social hierarchy position and his IA. We found that equity bias scores were significantly higher in dominant animals (mean ± SEM: 29.61 ± 5.01) than subordinate animals (mean ± SEM: 8.98 ± 5.73; $t_{13.96} = 2.71$, $P < 0.05$, Fig. 6). Equity bias scores of dominant animals were significantly higher than zero ($t_4 = 5.91$, $P < 0.01$). Equity bias scores of subordinate animals did not differ significantly from zero ($t_{13} = 1.57$, $P = 0.14$). This suggests that dominant rats had a higher propensity for IA than subordinate rats.

## DISCUSSION

Over the last few decades, evidence has accumulated that human and nonhuman primates completing an effortful task are sensitive to unequal reward distributions that leave them worse off than a conspecific (Brosnan & de Waal, 2014). However, it is unclear whether social species that evolved long before primates show similar aversion against such disadvantageous inequality. Here, we report that rats, a highly social species (Whishaw & Kolb, 2005) that live in well-structured, hierarchically organized groups, show IA. Individual levels of IA differed strongly between rats and were higher in socially dominant than submissive animals.

In the IA choice task, pairs of rats, an actor and a partner rat, were trained in a social maze choice paradigm. Actor rats chose between equitable and inequitable outcomes by moving into one of two choice compartments, yielding either a same-sized reward for themselves and a partner rat (equity choice), or a higher reward for a partner rat in an adjacent compartment (inequity choice). To control for competing selfish motives to maximize their own payoff (compare Hernandez-Lallement et al., 2015; Horner, Carter, Suchak, & de Waal, 2011; Silk et al., 2005), the actors' rewards were always identical between the two choice compartments, so that equity choices were not costly to the actor. An identical payoff structure was applied in a toy condition, in which actor rats were paired with a similarly shaped and sized toy rat instead of an actual partner rat. Equity bias scores, i.e. the percentage difference in equity choices between the social and toy conditions, served as estimates of the rats' individual levels of IA.

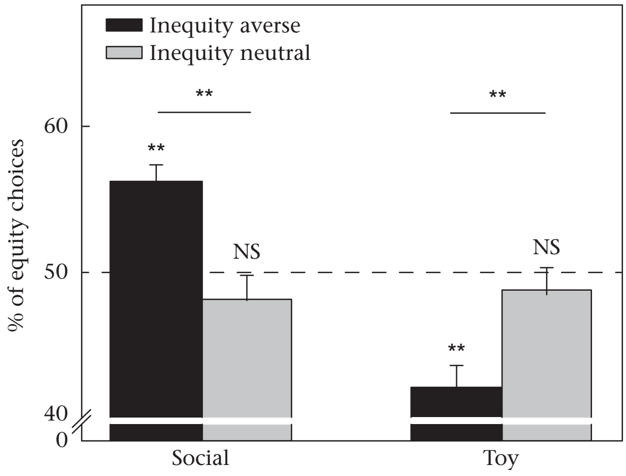

**Figure 5.** Equity choices in the social and toy conditions for inequity averse and inequity neutral animals. Error bars represent the SEM. **$P < 0.01$.

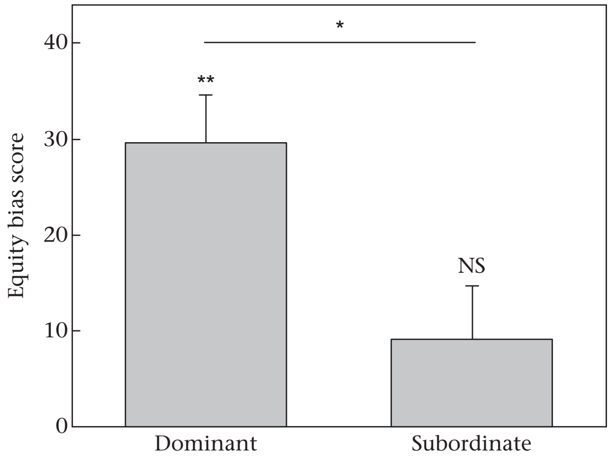

**Figure 6.** Mean equity bias scores of dominant and subordinate animals. Error bars represent the SEM. *$P < 0.05$; **$P < 0.01$.

Our results show that rats, on average, preferred equal outcomes more in the social than in the toy condition. Their equity bias scores were significantly positive, suggesting IA in rats. Although the mean level of IA was relatively small, there was large interindividual variability in IA, with some rats choosing equal outcomes 50% more often in the social than the toy condition and others choosing equal outcomes 20% less often. We compared individual equity bias scores to a normative benchmark score distribution and found that approximately half of the animals (nine out of 19) could be classified as inequity averse, whereas the other half (10 out of 19) were classified as inequity neutral. Thus, our analysis revealed a large degree of heterogeneity in rats' sensitivity to inequity in this task. Note that variation in the extent of IA between individuals was also found in other species, e.g. chimpanzees (Brosnan et al., 2005) and corvids (Wascher & Bugnyar, 2013). Furthermore, large interindividual variability was also found in rats' mutual reward preferences in a related paradigm (Hernandez-Lallement et al., 2015, in press).

Finally, we found higher equity bias scores in socially dominant rats than subordinate rats, suggesting that social hierarchy status may be related to sensitivity to unequal outcomes. It is therefore possible that part of the variance in IA between rats can be explained by their differences in social hierarchy status.

Inequity averse rats, but not inequity neutral rats, chose equitable outcomes significantly above chance level in the social condition, but significantly below chance level in the toy condition. Thus, in the toy condition, inequity averse rats preferred higher over equal rewards to the toy in the other compartment. One possible explanation for this somewhat surprising result could be a diverging importance of food, and food-related stimuli, between the subgroups of rats. If food is more important for inequity averse than inequity neutral animals, inequity averse animals may also be more sensitive to secondary reinforcement effects of food-related cues. During reinforcement learning, nonhedonic sensory features of rewards, such as their smell or sound, often gain incentive value so that animals will work to produce these features even in the absence of primary rewards (e.g. Armus, Carlson, Guinan, & Crowell, 1964; Egger & Miller, 1962). The preference for unequal outcomes in the toy condition may be due to the rewarding secondary reinforcement features of the pellet delivery to the other compartment. In other words, if inequity averse rats were indeed more sensitive to primary and secondary reinforcers, they will prefer impartial outcomes in the social, but partial outcomes in the toy condition.

The possibility that inequity averse rats were more sensitive to primary and secondary rewards than inequity neutral rats fits our finding of social dominance effects on IA. Importantly, social hierarchy dynamics may provide insights into the ultimate reasons for the evolution of IA as well as the underlying proximal mechanisms. In laboratory and seminatural settings, dominant rats claim prioritized access to food when resources are sparse (Blanchard & Blanchard, 1990). It is intriguing to speculate that social-hierarchy-related food claims shape, or are shaped by, the rats' individual responsiveness to food incentives in general, and, consequently, sensitivity to disadvantageous food distributions in particular. In other words, the motivation to prevent a partial advantage to a conspecific may be a proximal behavioural mechanism that ultimately helps in gaining and maintaining high social status so that IA conditions social dominance. According to this view, dominant rats would be unwilling to provide a nutritional advantage to subordinates to fight off, or prevent the subordinates from challenging the dominant's hierarchy position. However, challenges by subordinates and overt aggression by dominants are actually rare (Berdoy, Smith, & Macdonald, 1995). In addition, in wild and laboratory rats, social hierarchies are relatively stable and organized in a near linear way (Berdoy et al., 1995; Blanchard, Flannelly, & Blanchard, 1987). The stability of social hierarchies, as well as the low frequency of status challenges, might be the consequence of the dominant rats' effective strategies, such as strong IA, to maintain their social status, but they may also call into question whether these strategies are even necessary to enforce stable hierarchies. Future studies need to address the role of IA in stabilizing social hierarchies.

It has been argued that costly refusals of unfair offers, as demonstrated in several primate studies, may merely reflect nonsocial motives, such as frustration effects and/or violated expectations (Bräuer et al., 2006, 2009; Dubreuil et al., 2006; Roma et al., 2006; Silberberg et al., 2009; Wynne, 2004). However, frustration, expectation violations or other nonsocial motives are unlikely to explain IA of rats in our current design. Because animals were not confronted with an (unfair) fait accompli, their choices did not represent a response to a biased outcome distribution, but reflected an active decision between equity and inequity. In addition, actor rats always received the same reward after all choices. Thus, the rats' preference for equal outcomes was not confounded by a mismatch between expected and actual rewards. Furthermore, frustration about the inability to access visible food in the neighbouring compartment may have biased the rats to avoid higher rewards to the partners. However, frustration about inaccessibility of reward should be even stronger in the toy condition where pellets were not instantly consumed by the partner, and were therefore on display to the actor even longer than in the social condition. Thus, if frustration about food inaccessibility drove the rats' aversion against partial outcomes, they should have had an even higher preference for equal rewards in the toy condition. But, inconsistent with the frustration hypothesis, inequity averse rats were less prone to seek equal outcomes in the toy than the social condition. Finally, the rats' choices may have been driven by secondary reinforcement mechanisms, as mentioned above. However, although secondary reinforcement learning may explain preferences for larger rewards to toys, it cannot explain preferences for equal reward distributions when paired with a partner because the same secondary reinforcement mechanisms should be at work in the social condition, too. We conclude that nonsocial motives are unlikely to explain our rats' IA.

Our experiment was designed as proof-of-principle that rats show IA. Our findings were obtained in the laboratory with an outbred rat strain. The benefits of a controlled laboratory environment and a rigorous experimental design are obvious. Nevertheless, it is unclear whether our results apply to populations of wild rats, too. The generalizability from laboratory rats to wild rats has to be addressed in future studies. Furthermore, it would be worth examining whether the actor's level of hunger/satiety influences the propensity to show IA. We decided on a mild food deprivation schedule because social preferences in general seem to be affected by stronger hunger or satiety (Schneeberger, Dietz, & Taborsky, 2012; Viana, Gordo, Sucena, & Moita, 2010). However, it is unknown how far IA in particular is modulated by levels of food deprivation. Again, future studies need to manipulate food restriction to determine its role in IA.

A limitation of our study is that it allows only partial insights into the putative cognitive and motivational mechanisms underlying preferences for equality. It is possible that the rats' preference for equitable outcomes is the consequence of an adverse affective response to unequal outcomes, for example a negative emotional response to a conspecific's reward consumption beyond its own reward consumption. This explanation is attractive because the averseness of a higher reward to a partner should be scaled to the level of competitiveness between actor and partner, which, in turn, is known to be modulated by social dominance (Blanchard & Blanchard, 1990). Our finding that socially dominant rats showed higher equity bias scores than subordinate rats is consistent with this assumption. Future studies need to test the hypothesis that rats show a negative affective response to a conspecific's access to higher rewards.

We have recently shown that rats prefer mutual rewards over their own rewards in a rodent prosocial choice task (Hernandez-Lallement et al., 2015). Preferences for mutual rewards can be interpreted as aversion against advantageous inequality (see Hernandez-Lallement et al., 2015, in press for mechanistic explanations). Because the variability in individual mutual reward preferences in our previous study was comparable to the variability of IA in the current study, it is tempting to speculate that IA, advantageous as well as disadvantageous, is a common trait. It would therefore be instructive for future studies to combine the prosocial choice task (Hernandez-Lallement et al., 2015) with the current IA choice task to determine advantageous and disadvantageous inequality aversion in the same rats (see also the model of Fehr & Schmidt, 1999).

Human studies already reveal some explanations of apparently concurring social motives underlying advantageous and disadvantageous inequality aversion, such as the importance of agency (Choshen-Hillel & Yaniv, 2011). Interestingly, imaging studies show that similar brain areas but different neural pathways are involved in processing disadvantageous and advantageous IA (Yu, Calder, & Mobbs, 2014). In addition, in a recent study on rodent mutual reward preferences, we reported that the integrity of the amygdala was necessary for the acquisition and expression of advantageous IA (Hernandez-Lallement et al., 2016). This raises the possibility that the amygdala may also be relevant for disadvantageous IA.

In conclusion, we have found behavioural indications for social-hierarchy-dependent IA in rats. Inequity aversion and fairness sensitivity, among many other social coordinating behaviours, are thought to support the intricate social dynamics of individuals cooperating in larger groups. The current results lend support to the notion that the rudiments for such social motives can be found in evolutionarily distant relatives to humans, suggesting both conserved origins and widespread manifestations of social behaviour across species.

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