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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).