Inequity aversion in social species

Inaugural Dissertation

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Abstract (English)

The current dissertation project deals with the topic of inequity aversion (IA). IA is defined as a negative response to inequitable outcomes, and might thus be important for successful long-term cooperation (Brosnan, 2006, 2011). Considering man´s social nature, it appears relevant to gain insight into the mechanisms of cooperation. Only a deep understanding of the factors which facilitate or hinder cooperation may in the long run generate practical advice to foster cooperation on an individual as well as a societal level.

To thoroughly address the topic of IA, I approached it from a theoretical as well as a practical angle, and from a phylogenetic as well as an ontogenetic perspective. A main focus of the current dissertation project is the discussion and development of alternative choice-based tasks to measure IA in non-human animal species.

A theoretical framework in form of a review enabled us to thoroughly examine different theories of (respectively against) IA and to learn about potential moderators influencing the inequity response. We provided a detailed analysis of social versus non-social theories of IA and focused on the experimental setup as one crucial moderator of IA.

Two studies on social animals (rats and canids) allowed us to learn about the evolutionary roots of IA. By implementing a choice-based task, we could find evidence for disadvantageous IA in rats for the first time. Interestingly, dominant animals showed a stronger preference for an equitable reward distribution than subordinate individuals. In wolves and dogs, we could not find evidence for disadvantageous IA in a newly implemented touchscreen-based choice task. Presumably, the animals got stuck to their preference for the inequitable option which they developed during training and did not understand the altered reward contingencies between individuals in the test. Although the touchscreen-based task is not yet methodologically sound enough to study IA in canids or other non-human animal species, our study unfolded important indications to develop and pursue such paradigms.

A comprehensive study on children of different ages provided the opportunity to learn about the ontogenetic development of IA. We could replicate age effects of IA such that disadvantageous IA develops earlier than advantageous IA. Furthermore, we could show that egalitarian preferences depended on both the sex of the decision-maker and of their dyadic interaction partner. We assume that sex-specific fairness preferences are influenced by same- and cross-sex past interaction experiences, but possibly also by acquired gendered social norms that can come to override those interactive experiences.

Abstract (German)

Die vorliegenden Dissertation beschäftigt sich mit dem Thema Ungerechtigkeitsaversion. Diese wird definiert als eine negative Reaktion auf ungerechte Belohnungsverteilungen und könnte daher für eine erfolgreiche Langzeit-Kooperation von Bedeutung sein (Brosnan, 2006, 2011). In Anbetracht der sozialen Natur des Menschen ist es von hoher Relevanz, Einblicke in die Funktionsweisen von Kooperation zu erhalten. Nur ein tieferes Verständnis der Faktoren, die Kooperation erleichtern oder hemmen, kann auf lange Sicht dabei helfen, Kooperation in der Praxis zu fördern, sowohl auf individueller als auch auf gesellschaftlicher Ebene.

Ich habe das Thema Ungerechtigkeitsaversion sowohl von einem theoretischen als auch von einem praktischen Blickwinkel aus beleuchtet. Zudem habe ich einen phylogenetischen und einen ontogenetischen Ansatz gewählt. Ein Hauptaugenmerk der vorliegenden Dissertation ist die Diskussion und Entwicklung von Paradigmen. Diese ermöglichen es, Ungerechtigkeitsaversion bei Tieren mithilfe von Entscheidungsaufgaben zu messen.

Im Rahmen einer theoretischen Ausarbeitung in Form eines Reviews konnten wir verschiedene Theorien zu (bzw. gegen) Ungerechtigkeitsaversion einer kritischen Prüfung unterziehen. Auch mögliche Faktoren, die die Reaktion auf Ungerechtigkeit beeinflussen, konnten wir herausarbeiten. Das Resultat ist eine detaillierte Analyse von verschiedenen sozial und nicht-sozial begründeten Erklärungsansätzen für Ungerechtigkeitsaversion. Darüber hinaus haben wir uns insbesondere auf die Bedeutung des experimentellen Designs, ein wichtiger Moderator von Ungerechtigkeitsaversion, spezialisiert.

Zwei Studien mit sozialen Tierspezies (Ratten und Caniden) ermöglichten es uns, die evolutionären Wurzeln von Ungerechtigkeitsaversion näher zu ergründen. Mithilfe eines Paradigmas, in dem Ratten zwischen gerechten und ungerechten, sie relativ benachteiligenden Belohnungsverteilungen wählen konnten, fanden wir zum ersten Mal Hinweise auf Ungerechtigkeitsaversion bei Ratten. Dabei zeigten dominantere Ratten eine stärkere Präferenz für eine gerechte Belohnungsverteilung. In einer Studie mit Wölfen und Hunden konnten wir keinen Hinweis für eine derartige Ungerechtigkeitsaversion in einem neu implementierten Touchscreen-basierten Paradigma finden. Vermutlich blieben die Tiere bei ihrer Präferenz für die ungerechte, sie relativ benachteiligende Belohnung, die sie während des vorhegehenden Trainings aufgebaut hatten und waren nicht in der Lage die veränderten Belohnungskontingenzen ausreichend zu verstehen. Obwohl das Touchscreen Paradigma noch nicht ausgereift genug ist, um Aussagen über Ungerechtigkeitsaversion bei Caniden oder anderen Tierarten zu machen, liefert diese Studie dennoch wichtige Informationen zur weiteren Entwicklung und Verfeinerung derartiger Paradigmen.

Eine umfassende Studie an Kindern verschiedener Altersstufen ermöglichte es uns, auch die ontogenetische Entwicklung von Ungerechtigkeitsaversion näher zu untersuchen. Wir konnten Alterseffekte von Vorgängerstudien replizieren. Diese zeigten, dass Kinder bereits in jüngerem Alter negativ auf eine relative Benachteiligung reagieren. Erst mit zunehmendem Alter lehnen sie auch solche Belohnungsverteilungen ab, die sie selbst gegenüber einem anderen Individuum übervorteilen. Darüber hinaus fanden wir Hinweise darauf, dass egalitäre Präferenzen sowohl vom Geschlecht des Entscheiders als auch vom Geschlecht des jeweiligen Interaktionspartners abhingen. Wir nehmen an, dass geschlechtsspezifische Fairnesspräferenzen durch Erfahrungen mit gleich- und gegengeschlechtlichen Partnern moduliert werden. Gleichzeitig lassen unsere Daten vermuten, dass geschlechtsspezifische soziale Normen die auf Basis von interaktiven Erfahrungen gebildeten Präferenzen teilweise außer Kraft setzen.

Publications

Chapter 1:

Oberliessen, L. & Kalenscher, T. (2019). Social and non-social mechanisms of inequity aversion in non-human animals. *Frontiers in Behavioral Neuroscience, 13*, 133.

Chapter 2:

Oberliessen, L., Hernandez-Lallement, J., Schäble, S., van Wingerden, M., Seinstra, M., & Kalenscher, T. (2016). Inequity aversion in rats, Rattus norvegicus. *Animal Behaviour, 115*, 157-166.

Chapter 3:

Oberliessen, L. & Range, F. Wolves and dogs do not prefer equal outcomes in a touchscreen-based paradigm. *In preparation*.

Chapter 4:

Van Wingerden, M.*, Oberliessen, L.*, & Kalenscher, T. Dyad-sex composition affects the development of egalitarianism in young children. Submitted to: *Journal of Experimental Psychology*.

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General Introduction

The current dissertation starts with a general introduction about social behavior and cooperation. Ensuing from that, the concept of inequity aversion (IA) is introduced. The introduction ends with an outlook on the four chapters which are individually presented afterwards. Since the first of the four chapters is a detailed review about IA, the introduction is kept rather short to avoid repetition. The chapters are followed by a comprehensive and critical discussion. Ideas and suggestions for future research are provided.

The advantage of being social

Our planet is covered with social species. Bees dance to indicate food sources to conspecifics (von Frisch & Lindauer, 1956), ants medicate wounded allies (Frank, Wehrhahn, & Linsenmair, 2018), and dolphins have a remarkable social memory and recognize unique signature whistles of former tank mates (Bruck, 2013). Especially we as human beings live together in a complex social environment and interact with a great many people in the course of our lives.

But how is sociality defined? Sociality means to live in a group and, from a biological perspective, all of the individuals involved have to somehow profit from this kind of living (Alexander, 1974). It becomes obvious that the actual way of living together in a group can and does considerably differ amongst species. This is nicely mirrored by various labels of sociality (Costa & Fitzgerald, 2005); terms like “presocial”, “subsocial”, or “eusocial” were developed to capture the differently marked levels of sociality of different species. On a behavioral level, activities can be named social when they involve interactions among members of the same species and influence behavior, immediately or in the future (Robinson, Fernald, & Clayton, 2008).

According to Alexander (1974), the development of social behavior in groups is due to three reasons: (1) Social behavior may enhance benefits of group living by offering a higher level of coordination, e.g. explicit warning calls, strategies of common territorial defense, or cooperative hunting techniques. Cooperation also offers the possibility to exchange favors over time (direct, indirect, and generalized reciprocity; e.g. delousing behavior in monkeys; Brosnan & de Waal, 2014; Stevens & Hauser, 2004). (2) Social behavior reduces the likelihood of disease and parasite transmission due to the development and spread of resistance to various diseases. (3) Social behavior positively effects the reproductive competition of group members.

For the current thesis the focus should be on point 1 as coordination, respectively cooperation, is discussed to be the basis and cause for so-called inequity aversion (IA).

Cooperation

As Nowak (2006) nicely puts it, cooperation is the basis "to construct new levels of organization" (p. 1560). Not only humans, the self-proclaimed champions of cooperation, but also animals, insects, genomes, cells, and multicellular organisms engage in cooperation (Nowak, 2006). Next to kin-selected cooperation (Hamilton, 1964), which provides a direct own genetic benefit, intra-specific cooperation with unrelated individuals and even inter-specific cooperation (see e.g. Range, Marshall-Pescini, Kratz, & Virányi, 2019) seems to be advantageous. There are different explanations for the benefit of cooperation among unrelated individuals. Trivers (1971) proposed direct reciprocity as one mechanism, i.e. two individuals are exchanging favors over time. Axelrod (1984) modelled this in a computer tournament of the so-called Prisoner´s Dilemma and discovered that the winning strategy is indeed tit-for-tat. His work was pursued and refined by many other authors (e.g. Axelrod & Hamilton, 1981; Milinski, 1987; Dugatkin, 1997; Fudenberg & Maskin, 1990; Selten & Hammerstein, 1984; Nowak & Sigmund, 1992, 1993; for an overview see Nowak, 2006). However, direct reciprocity is not sufficient to explain (human) cooperation as it requires repeated encounters of the same individuals who are both able to provide help for the other person (Nowak, 2006). Of course, this is not always the case. When we for example donate money for children in need, we normally do not expect them to pay us back later. But where are the benefits? The reward we get is reputation (Rand & Nowak, 2013; Nowak, 2006). By helping someone we establish a good reputation, which will be rewarded by others. This is not only a nice idea, but empirically proven by theoretical and empirical studies of indirect reciprocity. Subjects who help others are more likely to receive help themselves (Wedekind & Milinski, 2000; Ohtsuki & Iwasa, 2004; Brandt & Sigmund, 2004; Leimar & Hammerstein, 2001; Milinski, Semmann, & Krambeck, 2002; Fishman, 2003; Hauser, Chen, Chen, & Chuang, 2003; Panchanathan & Boyd, 2004; Nowak & Sigmund, 2005). Indirect reciprocity is assumed to also lead to the evolution of social norms (Ohtsuki & Iwasa, 2004; Brandt & Sigmund, 2004) and morality (Alexander, 1987; see Matthews, 2018, for a critical review of human morality and ideologies). Due to the fact that in a real population individuals do not interact equally likely with each other, a mechanism called “network reciprocity” is assumed. This means that cooperators prevail against defectors by forming network clusters where they help each other (Nowak, 2006; Nowak & May, 1992). Finally, it is assumed that selection is not limited to individuals but also involves groups, so-called group selection or multilevel selection (Rand & Nowak, 2013). Analogous to the individual benefit of being cooperative, a group of cooperators might also be more successful than a group of defectors (e.g. Traulsen & Nowak, 2006; Boyd & Richerson, 1990; Wilson, 1975).

But are there mechanisms to promote (successful) cooperation? Especially when focusing on dyadic interactions, i.e. direct reciprocity, Brosnan (2011) rightly points out that cooperative actions are only sustainable if both interaction partners are profiting in the long run. Thus, the detection of inequitable outcomes as well as a response to them (as a last consequence choosing another cooperation partner) should increase an individual´s payoff from cooperation with others (Brosnan, 2011). This is referred to as so-called inequity aversion (IA).

Inequity aversion

Not only parents can witness that children have an extremely fine sense for inequity. Gummi bears, smarties, and Christmas presents have to be counted precisely so that everybody is satisfied, and fatal drama is avoided. I remember a video clip that my parents once showed to me. It was videotaped in one of our summer holidays and showed me as a five-year-old screaming like hell because my little brother had one piece of tomato more on his plate. Luckily, I found out that I was not an isolated and hopeless case. Quite recently, my boyfriend sent me a picture of three identical little rakes that his brother and him had bought for gardening for his three little nieces. He commented the picture with the words "avoiding trouble".

Scientifically speaking, IA is defined as a negative response to inequitable outcomes for performing the same action (Brosnan, 2006). Inequity can occur in a twofold manner: A subject´s outcome can be lower or higher than that of another individual. Accordingly, a subject shows disadvantageous IA when being relatively disadvantaged or advantageous IA when being relatively advantaged (see Fehr & Schmidt, 1999). Massen, van den Berg, Spruijt and Sterck (2012) rightly emphasize that IA always includes two components. As a first step it is necessary that an individual evaluates its own payoffs. The second step is a comparison of own versus others´ payoffs. Thus, it becomes obvious that IA is the result of a mentally complex procedure. It is necessary to perceive a "relation between relations" (Dubreuil, Gentile, & Visalberghi, 2006, p. 1227), i.e. a comparison of the relation between own effort and reward with the relation between effort and reward of another individual (Dubreuil et al., 2006).

In their prominent model of IA, Fehr and Schmidt (1999) presume that "in addition to purely selfish subjects, there are subjects who dislike inequitable outcomes" (p. 822) and as a result show IA. For simplicity, a linear utility function is supposed. Furthermore, the authors assume that people are more displeased by disadvantageous compared to advantageous inequity, i.e. own material disadvantage is worse than having a material advantage to others (Fehr & Schmidt, 1999). This assumption is supported by the work of Loewenstein, Thompson, and Bazerman (1989). Fehr and Schmidt (1999) provide evidence that their model is in accord

”with the most important facts in ultimatum, market, and cooperation games” (p. 847). They also note that their model predictions comply with empirical findings in various other games (Fehr & Schmidt, 1999). For the sake of completeness, it shall be noted that there are also other models of other-regarding preferences (see e.g. Rabin, 1993; Dufwenberg & Kirchsteiger, 2004; Levine, 1998; Bolton & Ockenfels, 2000).

It becomes obvious that IA is not merely a theoretical idea, but actually occurs in various economic games played by humans. As already mentioned above, the detection of inequitable outcomes as well as a response to them is assumed to increase an individual´s payoff from cooperation with others (Brosnan, 2011). A co-evolution between these two constructs across the animal kingdom is hypothesized (Brosnan, 2011). This would mean that IA is not a uniquely human achievement but also ensures successful cooperation in other social species (Brosnan, 2006). Indeed, there is experimental evidence for non-human IA, however, the results are quite heterogeneous (Brosnan & de Waal, 2003; van Wolkenten, Brosnan, & de Waal, 2007; Fletcher, 2008; Takimoto, Kuroshima, & Fujita, 2010; Takimoto & Fujita, 2011; Hopper, Lambeth, Schapiro, Bernacky, & Brosnan, 2013; Massen et al., 2012; Brosnan, Talbot, Ahlgren, Lambeth, & Schapiro, 2010; Brosnan, Schiff, & de Waal, 2005; Neiworth, Johnson, Whillock, Greenberg, & Brown, 2009; Range, Horn, Virányi, & Huber, 2009; Range, Leitner, & Virányi, 2012; Brucks, Essler, Marshall-Pescini, & Range, 2016; Essler, Marshall-Pescini, & Range, 2017; Wascher & Bugnyar, 2013; Heidary, Mahdavi, Momeni, Minaii, Rogani, Fallah, et al., 2008; Oberliessen, Hernandez-Lallement, Schäble, van Wingerden, Seinstra, & Kalenscher, 2016; but see Dubreuil et al., 2006; Fontenot, Watson, Roberts, & Miller, 2007; Roma, Silberberg, Ruggiero, & Suomi, 2006; Silberberg, Crescimbene, Addessi, Anderson, & Visalberghi, 2009; Bräuer, Call, & Tomasello, 2006, 2009; Raihani, McAuliffe, Brosnan, & Bshary, 2012; Heaney, Gray, & Taylor, 2017; Horowitz, 2012; Brucks, Marshall-Pescini, Essler, McGetrick, Huber, & Range, 2017; Brosnan, Flemming, Talbot, Mayo, & Stoinski, 2011; Talbot, Freeman, Williams, & Brosnan, 2011; Freeman, Sullivan, Hopper, Talbot, Holmes, Schultz-Darken, et al., 2013) and many questions remain open.

Contribution of the current thesis

A detailed overview about the current state of research on non-human IA is provided (Chapter 1). In this context, we examined alternative theories to Brosnan´s cooperation hypothesis that take account of the heterogeneous results. Notably, we also summarized and discussed potential moderators of IA which were identified in various animal studies. We put a special emphasis on the experimental design as it seems to be one eminently important moderator of IA.

We also gathered practical evidence for (respectively against) IA and its moderators in two social animal species (rats and canids) and in children. Importantly, we implemented and piloted different choice-based tasks (Chapters 2-4) to measure IA. Choice-based paradigms are (so far) rarely used, at least in studies on non-human animals. However, they offer a promising alternative to standard IA tasks. Their special feature is that subjects are not confronted with inequity but can actively choose between equal and unequal outcome options (see Chapter 1).

Animal studies

Rats (*Rattus norvegicus*) were the adorable participants of the first experiment. This species was chosen as rats are known to be highly social (Whishaw & Kolb, 2005; Daniel, 1942; Rice & Gainer, 1962; Greene, 1969; Lopuch & Popik, 2011; Schuster, 2002; Rutte & Taborsky, 2007; Bartal, Decety, & Mason, 2011), but had not been tested with respect to IA before. Furthermore, rats are one of the most prominent animal models for various diseases like depression (e.g. Carboni, Becchi, Piubelli, Mallei, Giambelli, Razzoli, et al., 2010; Solberg, Olson, Turek, & Redei, 2001), Alzheimer´s disease (e.g. Nitta, Itoh, Hasegawa, & Nabeshima, 1994), schizophrenia (e.g. Chambers, Moore, McEvoy, & Levin, 1996; Becker, Peters, Schroeder, Mann, Huether, & Grecksch, 2003), etc. Hence, it appears promising to also try them as a basal model for human IA. Rats were tested in a social maze apparatus that was already validated to assess mutual reward preferences (Hernandez-Lallement, van Wingerden, Marx, Srejic, & Kalenscher, 2015; Hernandez-Lallement, van Wingerden, Schäble, & Kalenscher, 2016).

Wolves (*Canis lupus*) and dogs (*Canis lupus familiaris*) were the lovely but challenging participants of the second animal study. Wolves are known for their complex social behavior and cooperativeness (Mech & Boitani, 2003). They might be one of the best models for human social behavior as their social structures are intriguingly similar. Like humans, wolves live together in families and raise their offspring together (Moehlman & Hofer, 1997; Mech & Boitani, 2003). Furthermore, they hunt together (Schmidt & Mech, 1997; Mech & Boitani, 2003), and commonly defend their territory against foreigners (Harrington & Mech, 1979; Mech & Boitani, 2003). It is intriguing to speculate that this remarkable resemblance might be the reason why wolves were the very first species that (got?) domesticated a long time ago (Thalmann, Shapiro, Cui, Schuenemann, Sawyer, Greenfield, et al., 2013; Wang, Zhai, Yang, Wang, Zhong, Liu, et al., 2016; Franz, Mullin, Pionnier-Capitan, Lebrasseur, Ollivier, Perri, et al., 2016). There is already some evidence for IA in wolves and dogs (Range et al., 2009; Brucks et al., 2016; Essler et al., 2017), however, it is still ambiguous (see Horowitz, 2012; Brucks et al., 2017) and seems to depend on the concrete experimental setting (see McGetrick & Range, 2018). Due to that, we confronted wolves and dogs with a new touchscreen-based choice task to assess whether they would avoid quality inequity in this particular non-costly setting.

A study on children

Besides the two animal studies which offer insight into the evolutionary development of IA, we also wanted to gain insight into the ontogenetic development of IA in humans. Correspondingly, children were the charming (but noisy) participants of the third study, a common choice task (see e.g. Fehr, Bernhard, & Rockenbach, 2008) in which they could choose between distributions of highly coveted smiley stickers. In this experiment, we especially focused on the sexes of decision maker and recipient as the gender composition of dyads could be a potentially important moderator of IA and had not been studied before.

Chapter 1: Social and non-social mechanisms of inequity aversion in non-human animals

Photo credit: Lina Oberließen

Abstract

Research over the last decades has shown that humans and other animals reveal behavioral and emotional responses to unequal reward distributions between themselves and other conspecifics. However, cross-species findings about the mechanisms underlying such inequity aversion are heterogeneous, and there is an ongoing discussion if inequity aversion represents a truly social phenomenon or if it is driven by non-social aspects of the task. There is not even general consensus whether inequity aversion exists in non-human animals at all. In this review article, we discuss variables that were found to affect inequity averse behavior in animals and examine mechanistic and evolutionary theories of inequity aversion. We review a range of moderator variables and focus especially on the comparison of social vs. non-social explanations of inequity aversion. Particular emphasis is placed on the importance of considering the experimental design when interpreting behavior in inequity aversion tasks: the tasks used to probe inequity aversion are often based on impunity-game-like designs in which animals are faced with unfair reward distributions, and they can choose to accept the unfair offer, or reject it, leaving them with no reward. We compare inequity-averse behavior in such impunity-game-like designs with behavior in less common choice-based designs in which animals actively choose between fair and unfair rewards distributions. This review concludes with a discussion of the different mechanistic explanations of inequity aversion, especially in light of the particular features of the different task designs, and we give suggestions on experimental requirements to understand the “true nature” of inequity aversion.

The Concept of Inequity Aversion

Other-regarding preferences, i.e., the consideration of the well-being of others when making decisions, are pertinent in human behavior and economic decision making (Fehr and Schmidt, 1999). Such decisions are not solely based on egoistic, materialistic motives, but others' outcomes are considered as well. Other-regarding preferences have often been studied with economic games (e.g., Yamagishi et al., 2009; Margittai et al., 2015; Strombach et al., 2015). For instance, in the dictator game, participants are asked to split an endowment between themselves and a co-player. Decades of research with the dictator game has shown that people across many cultures and socio-economic groups voluntarily share money and other resources with others (Bolton et al., 1998; Engel, 2011). Another game is the ultimatum game (Güth et al., 1982) in which one player, the proposer, splits a sum of money between herself and another player, the responder. The responder can decide whether to accept or reject the share. If she accepts, both players can keep their share. If she rejects, both players receive nothing. Several thousand replications of the ultimatum game (Güth and Schmidt, 2013) have revealed that the vast majority of responders rejects offers that are perceived unfair, i.e., they forego own-payoffs, to punish unfair proposers. Yet another game is the impunity game (Bolton and Zwick, 1995). In this game, one player, the proposer, can share an endowment between herself and a second player, the responder. The responder can either accept or reject the offer. If she accepts the offer, both players keep their share, if she rejects, the responder receives nothing while the proposer keeps her share. Unfair offers are often rejected by responders (Bolton and Zwick, 1995), thus leaving them empty-handed with no economic consequences for the proposer. Rejections are puzzling at first sight, but are likely fueled by an emotional response to unfairness, revealing that responders derive more disutility from small, but unfair gains than from no gains at all.

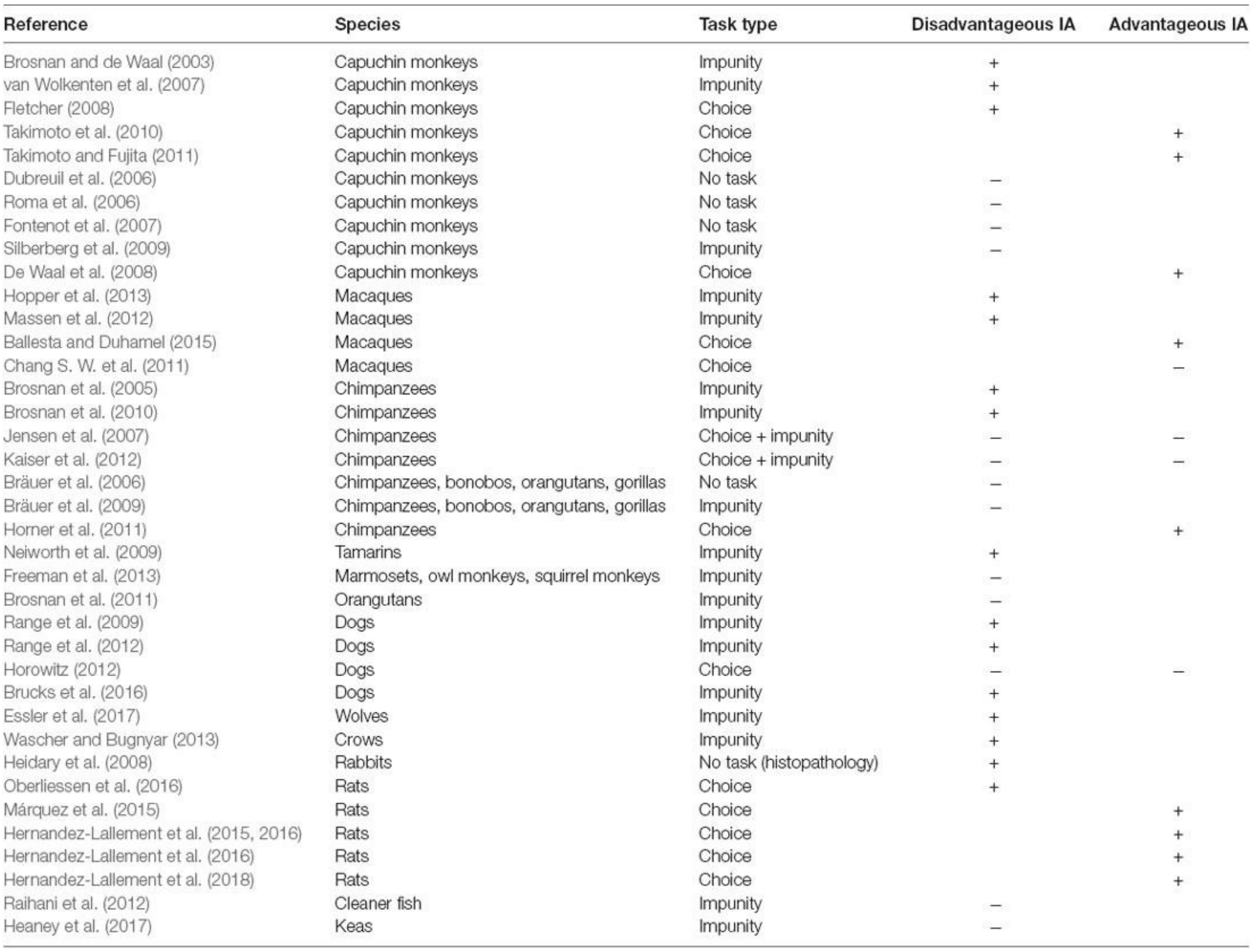
Even though such fairness-driven behaviors appear economically unreasonable on the surface because of their costliness (recipients forego rewards or accept costs to punish fairness violators), they are often considered the consequence of so-called inequity aversion (IA), an affective, cognitive and behavioral response to unequal outcomes (Oberliessen et al., 2016). Generally, two forms of IA can be distinguished: (1) aversion against outcome distributions that yield a higher payoff for a partner relative to one's own payoff, given matched efforts to obtain the payoff (disadvantageous IA); and (2) aversion against outcomes that produce a lower payoff for a partner relative to one's own payoff (advantageous IA; Oberliessen et al., 2016).

But what is the benefit of costly IA if it does not increase, or even lowers, an organism's immediate (economic or Darwinian) fitness? IA has been hypothesized to function as a mechanism to ensure the sharing of payoffs and, thus, to enable and maintain long-term cooperation with non-kin. It is proposed to serve as an unfairness detector, protecting individuals from exploitation (Brosnan, 2006, 2011; Brosnan and de Waal, 2014). Cooperation allows individuals to achieve goals that they could not achieve alone (e.g., teamwork in humans, or cooperative hunting and cooperative breeding in non-human animals) and offers the possibility to exchange favors over time (direct, indirect and generalized reciprocity; e.g., delousing behavior in monkeys; Stevens and Hauser, 2004; Brosnan and de Waal, 2014).

Inequity Aversion in Non-human Animals

This explanation already foreshadows, and the examples imply, that IA might not solely occur in humans, but can also be expected in social non-human animal species that engage in cooperative behaviors. Indeed, evidence has accumulated over the last years suggesting that disadvantageous IA exists in various social species. In 2003, Brosnan and de Waal (2003) published a pioneering study testing the response of brown capuchin monkeys to unequal rewards. In this study, two monkeys in adjacent cages could both exchange a token for a food reward with a human experimenter. In the equity condition, both individuals received a piece of cucumber reward for successfully exchanging the token. In the inequity condition, one of the monkeys received a more valuable grape while the other monkey continued to receive the lower valued piece of cucumber for performing the same token exchange task. As a consequence, the disadvantaged monkey refused to exchange the token, or rejected the cucumber reward entirely, tentatively reminiscent of the behavior of human responders in the impunity game (see below for critical discussion). Since this early study, IA was replicated in capuchin monkeys (van Wolkenten et al., 2007; Fletcher, 2008; Takimoto et al., 2010; Takimoto and Fujita, 2011), and reported in macaques (Massen et al., 2012; Hopper et al., 2013), chimpanzees (Brosnan et al., 2005, 2010), cotton top tamarins (Neiworth et al., 2009), dogs (Range et al., 2009, 2012; Brucks et al., 2016; see McGetrick and Range, 2018 for an overview), wolves (Essler et al., 2017), crows (Wascher and Bugnyar, 2013), rabbits (Heidary, Mahdavi, Momeni, Minaii, Rogani, Fallah, et al., 2008) and rats (Oberliessen et al., 2016).

However, some studies failed to demonstrate disadvantageous IA in non-human animals, for example in capuchin monkeys (Dubreuil et al., 2006; Roma et al., 2006; Fontenot et al., 2007; Silberberg et al., 2009), chimpanzees, bonobos, orangutans, and gorillas (Bräuer et al., 2006, 2009), cleaner fish (Raihani et al., 2012), keas (Heaney et al., 2017), and dogs (Horowitz, 2012). While the lack of IA in less cooperative species like orangutans (Bräuer et al., 2009; Brosnan et al., 2011) or squirrel monkeys (Talbot et al., 2011; Freeman et al., 2013) might not come unexpected, given the hypothesis that IA is primarily a mechanism for maintaining cooperation, it is hard to explain its absence in cooperative species like capuchin monkeys, dogs, chimpanzees and cleaner fish (see Table 1 for an overview of all studies). Consequently, there is an ongoing, relatively heated debate about the true nature of IA, whether it truly serves to maintain cooperation, and whether it even exists at all in non-human animals.



Reference	Species	Task type	Disadvantageous IA	Advantageous IA
Brosnan and de Waal (2003)	Capuchin monkeys	Impunity	+	
van Wolkenten et al. (2007)	Capuchin monkeys	Impunity	+	
Fletcher (2008)	Capuchin monkeys	Choice	+	
Takimoto et al. (2010)	Capuchin monkeys	Choice		+
Takimoto and Fujita (2011)	Capuchin monkeys	Choice		+
Dubreuil et al. (2006)	Capuchin monkeys	No task	–	
Roma et al. (2006)	Capuchin monkeys	No task	–	
Fontenot et al. (2007)	Capuchin monkeys	No task	–	
Silberberg et al. (2009)	Capuchin monkeys	Impunity	–	
De Waal et al. (2008)	Capuchin monkeys	Choice		+
Hopper et al. (2013)	Macaques	Impunity	+	
Massen et al. (2012)	Macaques	Impunity	+	
Ballesta and Duhamel (2015)	Macaques	Choice		+
Chang S. W. et al. (2011)	Macaques	Choice		–
Brosnan et al. (2005)	Chimpanzees	Impunity	+	
Brosnan et al. (2010)	Chimpanzees	Impunity	+	
Jensen et al. (2007)	Chimpanzees	Choice + impunity	–	–
Kaiser et al. (2012)	Chimpanzees	Choice + impunity	–	–
Bräuer et al. (2006)	Chimpanzees, bonobos, orangutans, gorillas	No task	–	
Bräuer et al. (2009)	Chimpanzees, bonobos, orangutans, gorillas	Impunity	–	
Horner et al. (2011)	Chimpanzees	Choice		+
Neiworth et al. (2009)	Tamarins	Impunity	+	
Freeman et al. (2013)	Marmosets, owl monkeys, squirrel monkeys	Impunity	–	
Brosnan et al. (2011)	Orangutans	Impunity	–	
Range et al. (2009)	Dogs	Impunity	+	
Range et al. (2012)	Dogs	Impunity	+	
Horowitz (2012)	Dogs	Choice	–	–
Brucks et al. (2016)	Dogs	Impunity	+	
Essler et al. (2017)	Wolves	Impunity	+	
Wascher and Bugnyar (2013)	Crows	Impunity	+	
Heidary et al. (2008)	Rabbits	No task (histopathology)	+	
Oberliessen et al. (2016)	Rats	Choice	+	
Márquez et al. (2015)	Rats	Choice		+
Hernandez-Lallement et al. (2015, 2016)	Rats	Choice		+
Hernandez-Lallement et al. (2016)	Rats	Choice		+
Hernandez-Lallement et al. (2018)	Rats	Choice		+
Raihani et al. (2012)	Cleaner fish	Impunity	–	
Heaney et al. (2017)	Keas	Impunity	–	

Table 1. For each species tested on IA, the particular task type is specified. “Impunity” refers to impunity-like tasks (e.g., token exchange tasks) in which pairs of animals are confronted with equal or unequal outcomes, and they can choose to reject rewards and/or refuse further task performance. “Choice” refers to tasks in which an actor animal can actively choose between an equal and an unequal reward distribution. “No task” implies that equal, respectively unequal rewards are offered by an experimenter for free, and the animals can decide to accept or reject these food rewards. A “+” means that the particular authors found evidence for the respective kind of IA, a “–“ means that there was no such evidence.

One Concept - Many Theories

In this section, we will more closely consider different theories of IA that have been proposed to account for the heterogeneous results. Some of these theories refer to social motives, but others explain previous alleged IA-like behaviors with non-social cognitive mechanisms.

Social Hypotheses: Maintaining Cooperation vs. Social Disappointment

Brosnan (2006, 2011) posits that fairness preferences, ultimately leading to IA, are advantageous for an organism because, as mentioned above, they serve as a mechanism to ensure the sharing of payoffs and thus, to enable and maintain long-term cooperation with non-kin. However, other authors offer different, more mechanistic interpretations of the animals' behavior in the above-mentioned tasks. The social disappointment hypothesis (Engelmann et al., 2017) suggests that, rather than being sensitive to the relative advantage of the conspecific, animals actually respond to reward expectations triggered by the human experimenter. According to this hypothesis, the actor animal would simply be disappointed by the experimenter because she is not rewarding it as well as well as he could obviously have. Engelmann et al. (2017) tested their hypothesis in an experiment with chimpanzees. They used a two-by-two design in which food was either distributed by an experimenter or a machine and with a partner present or absent. In accordance with their hypothesis, they found that chimpanzees were more likely to reject food when it was distributed by an experimenter compared to a machine. Rejection rates were unaffected by the presence or absence of a partner chimpanzee. Hence, the authors concluded that the refusal of the less preferred food item stemmed from the social disappointment in the experimenter and not from the violation of the animals' sense of fairness.

However, this conclusion can be debated, too. First, Engelmann et al.'s (2017) result might be species- and context-specific; for instance, while chimpanzees might emotionally respond to violations of reward expectations associated with their human experimenter, other animals, like rodents and birds, might be less sensitive to their experimenter's behavior. In addition, this hypothesis is, at closer inspection, not very parsimonious, but makes relatively strong assumptions about the animals' computational capabilities: disappointment by the experimenter's bad rewarding performance requires the ability to actually realize that the experimenter could have performed better in providing higher quality of rewards. Finally, the social disappointment hypothesis seems more about the source of unfairness sentiments than about the existence of such sentiments per se: the hypothesis is perfectly consistent with the idea that the chimpanzees actually felt treated unfairly, it just predicts that they attributed this negative state to the experimenter, and not to the conspecific; hence, the animals would still show a form of IA.

One way to resolve these ambiguities would be to design tasks without experimenter interference, e.g., tasks in which two individuals have to negotiate the distribution of rewards over successive trials (e.g., Brosnan et al., 2006; Melis et al., 2009). Promising approaches on rule observance and conflict resolution have recently been developed for mice (e.g., Choe et al., 2017), but the implications for IA are still elusive. Future research should focus on the development of inter-conspecific negotiation tasks.

Frustration Hypothesis

Other authors proposed that non-social motives might also explain the animals' behavior in IA tasks. For example, Roma et al. (2006) suggested that frustration rather than IA might account for some of the findings. They investigated pairs of capuchin monkeys and offered the "model" monkey grape or cucumber while the "witness" monkey always received cucumber. The authors found that the witnesses' rejections of cucumber were not dependent on whether the model received grape or cucumber, i.e., they found no evidence of behaviorally measurable sensitivity to inequity. However, they also observed that, when cucumber was offered to the model monkeys who were used to grapes, they showed higher rejection rates of cucumber than the witnesses. This finding suggests that previous experience with a more valuable reward (grape) results in a relative devaluation of the less valuable reward, and, hence, its rejection. Thus, rejections might reflect frustration about the poor reward rather than feelings of unfairness. Nevertheless, it should be noted that the experimental setup differed to the one of Brosnan and de Waal (2003) as the animals received the rewards for free, i.e., without an effort requirement or token exchange. This lack of a cost requirement might be crucial because other research has shown that effort seems to be an important moderator of the magnitude of the IA response (van Wolkenten et al., 2007; Wascher and Bugnyar, 2013). This raises the question of whether the lack of any effort requirement in Roma et al.'s (2006) experiment might explain the absence of IA. Nevertheless, this consideration does not entirely disqualify frustration as a potential, non-social moderator of the animals' rejection behavior in IA tasks.

Reward Expectation Hypothesis

A related non-social explanation of the rejection of unequal rewards in IA tasks is the reward expectation hypothesis (Bräuer et al., 2006; see also Dubreuil et al., 2006; Neiworth et al., 2009). The hypothesis states that seeing another individual receiving a more valuable reward raises the expectation of receiving the same valuable reward. Deliveries of less valuable rewards thus violate the animal's reward expectation. By consequence, reward rejections or refusals of task performance could also be caused by failed expectations and negative reward prediction errors, and, hence, cannot with certainty be attributed to IA. A recent human study provided further evidence for the importance of expectations (Vavra et al., 2018). Participants in an ultimatum game were provided with explicit information on what kind of offers to expect by a certain proposer. The authors showed four different distributions, manipulating both the mean and the variance of these expected sets of offers. They found that 50% of the participants systematically changed their behavior as a function of their reward expectations (Vavra et al., 2018). As only the offer expectations differed between conditions, social processes alone cannot explain the changes in behavior corresponding to these offer expectations.

However, this line of reasoning still leaves room for social processes underlying rejection behavior in IA tasks. In standard reinforcement learning, non-human animals derive reward expectations purely from own-experience with past rewards. But in Brosnan and de Waal's original experiment as well as in follow-up studies, subjects never received the more valuable reward, so any elevated reward expectations based on own-reward history is unlikely. The reward-expectation hypothesis therefore specifically states that own-reward expectations would be influenced by the perception of rewards delivered to others. But the assumption that perceiving rewards delivered to others vicariously elevates own-reward expectations actually require the existence of social comparison processes, and, hence, implies social cognition; this hypothesis, therefore, cannot qualify as a non-social explanation of the variance in rejection behavior in IA tasks.

Yet, it is still possible that the mere presentation of more valuable rewards raised reward expectations beyond vicarious reward tracking. However, van Wolkenten et al. (2007) pointed out that the more valuable reward in the original task by Brosnan and de Waal (2003) and others was equally visible in both the inequity and equity conditions (the experimenter visibly stored the rewards in front of the experimental cages; van Wolkenten et al., 2007). This symmetry in reward presentation means that a putative presentation-effect on reward expectation is insufficient to explain the higher rejection rates in the inequity compared to the equity condition as the animals could see (and thus expect) the more valuable reward in both conditions. Nonetheless, admittedly, it is still possible that the accessibility of the more valuable reward to the conspecific (inequity condition; the reward is merely visible in the equity condition) might affect the level of expectation (see e.g., Brosnan et al., 2010). Consequently, the fact remains that reward expectation, like frustration, might be another plausible, non-social, moderator of IA.

Reference-Dependent Reward Valuation and Loss Aversion

Chen and Santos (2006) offer yet another non-social mechanism to account for the rejection behavior in all types of IA tasks. They suggest that reference-dependent reward valuation and loss-aversion can account for the evolution of IA. Reference-dependent reward valuation refers to the subjective evaluation of reward magnitude, or reward quality, relative to a benchmark criterion, such as a standard reward; i.e., a given reward magnitude might be valued differently, depending on whether it is higher or lower than the reference reward magnitude (Marsh and Kacelnik, 2002; Chen et al., 2006). Loss-aversion describes the overweighting of negative reward magnitudes during reward evaluation, i.e., reward magnitudes that are lower than expected, or the overweighting of actual losses, respectively (note that losses are difficult to implement in animal research; most research on loss aversion in animals operationalizes losses as negative deviations from a reference point; Chen et al., 2006).

Chen and Santos (2006) maintain that the monkeys' behavior in the original IA task (e.g., Brosnan and de Waal, 2003) could be explained by translating reference-dependency and loss aversion concepts to the social domain; that is, they assume a socially generated reference point. According to this idea, the payoff to the other individual in Brosnan and de Waal's (2003) task might become the reference point against which own-rewards are evaluated. Own-rewards below this reference-point, i.e., cucumber instead of grape, would then be perceived as a loss, generating frustration and loss avoidance, and hence rejection (Chen and Santos, 2006).

Summary

Thus, in summary, there are a number of social explanations for the animals' rejection patterns in IA tasks, including genuine fairness preferences and social disappointment, but a range of non-social motives have also been proposed to account for the animals' behavior, including frustration, reward expectation, reference-point dependency and loss aversion. Note that the different social and non-social motives are not necessarily mutually exclusive, but might work in concert to influence behavior in IA tasks. Furthermore, it is worthwhile pointing out that particularly the non-social explanations are conceptually similar. Reward expectation might be considered a direct result of reference-dependent reward valuation, and hence frustration might occur as a result of loss aversion. The two social explanations mainly differ in the causal attribution of IA, as both assume a form of social disappointment: Either in the human experimenter who rewards below his best or in the relative unfairness between subject and partner. Interestingly, the explanation by Brosnan (2006, 2011) can also be seen as a (social) subcategory of reference-dependent reward valuation (the reference point is the outcome of the partner) and, in addition to that, any form of disappointment might eventually result in frustration.

In the next section, we will consider further moderators of IA. We especially highlight the importance of considering the particular characteristics of the different experimental designs used to elicit inequity aversion. We attempt to link these moderator variables, especially the task design, to the abovementioned theories on IA and provide suggestions for future research.

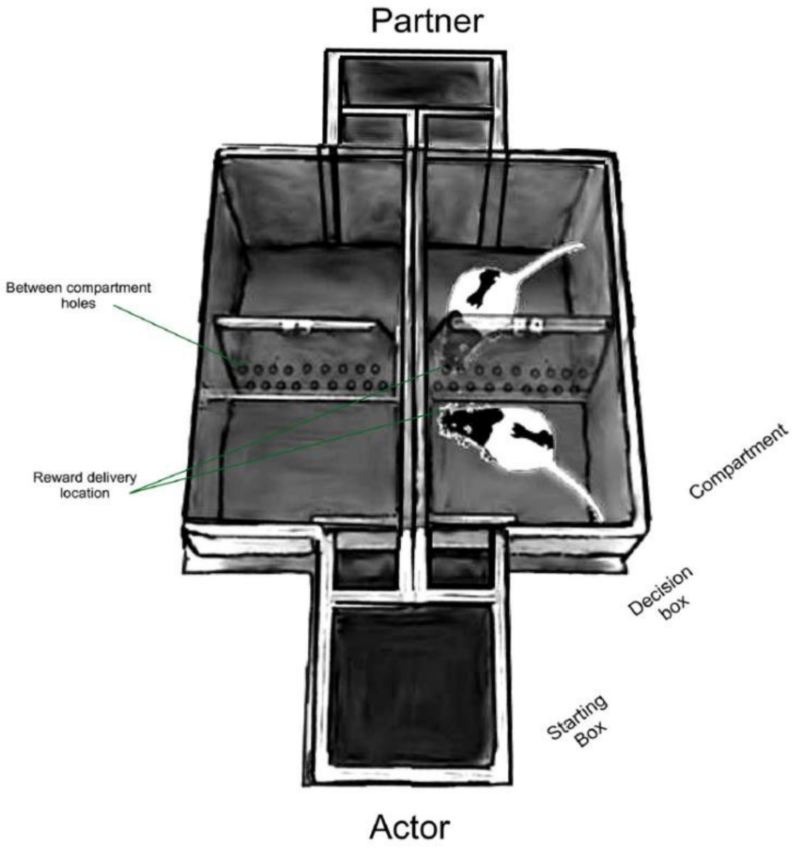
The Experimental Design and Other Moderators of Inequity Aversion

There are a number of variables that moderate the extent, or even existence, of IA. As already mentioned, effort seems to be an important moderator of the magnitude of the IA response (van Wolkenten et al., 2007; Wascher and Bugnyar, 2013). Furthermore, the quality of the relationship between the pairs of animals tested in an IA task has been shown to influence the level of IA (Brosnan et al., 2005; De Waal et al., 2008; but see Massen et al., 2012; Brosnan, Hopper, Richey, Freeman, Talbot, Gosling, et al., 2015). Social hierarchy position also seems to moderate the level of IA, such that higher rank is associated with more pronounced IA (Brosnan et al., 2010; Oberliessen et al., 2016; but see Massen et al., 2012). Further social moderators are sex (Brosnan et al., 2010) and personality (Brosnan et al., 2015): male chimpanzees, more than females, responded to violations of inequity, refusing to complete the interaction with the experimenter when the partner received a better reward (Brosnan et al., 2010). Chimpanzees that were rated higher in the extraversion dimension and lower in the agreeableness dimension were more likely to respond to inequity (Brosnan et al., 2015). In a recent human study, the sensitivity to pain was also identified as a factor to predict the experience of unfairness (the more pain-sensitive, the more experienced unfairness; Wang et al., 2019).

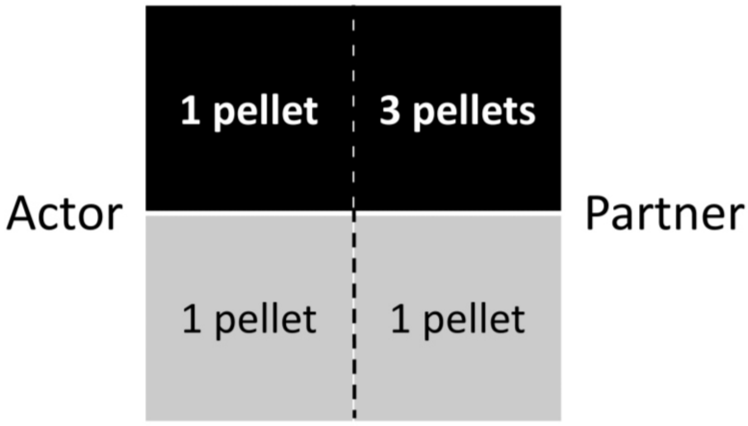
Perhaps the most important influencing factor of IA is the experimental setting in which IA is probed. Almost all of the above-mentioned studies on IA in animals are variants of the original experiment by Brosnan and de Waal (2003) in which pairs of animals are confronted with equal or unequal outcomes, and they can choose to reject rewards and/or refuse further task performance. These tasks strongly resemble the design structure of the impunity game (Bolton and Zwick, 1995) developed for humans (see above) because, in both the animal and human tasks, individuals engage in costly refusals of their own reward with no economic consequence to the conspecific/proposer. Due to their prevalence in the non-human animal literature, the different theories about the cognitive mechanisms underlying non-human IA mostly explain the behavioral particularities in impunity-like tasks. Here, we propose that the use of a different task design might enrich the discussion, and shed light on some of the open questions regarding the true (social or non-social) nature of IA. In particular, we suggest that a different IA paradigm—choice-based IA task designs—might be a promising complement to the existing IA literature as they offer the potential to avoid some of the interpretational caveats mentioned in the preceding section.

Design of Choice-Based Tasks

In a choice-based task (see Figure 1), an actor animal can actively choose between an equal and an unequal reward distribution, either leaving a conspecific better off (unequal distribution), or equally well off, than the actor animal (equal distribution; see e.g., Fletcher, 2008; Oberliessen et al., 2016). Importantly, the actor animal's choice is non-costly, i.e., its reward is equal in both reward distributions and thus, independent of the animal's decision. Preferences for equality are compared between two conditions: a social condition with a conspecific present, and a non-social control condition in which the outcome distributions are identical to the social condition, but the conspecific is absent; e.g., rewards are dropped in an empty, adjacent chamber or compartment. Using such choice-based tasks, it has been shown that both rats (Oberliessen et al., 2016) and capuchin monkeys (Fletcher, 2008) preferred equal over unequal outcome distributions when paired with a conspecific, and that this preference for equal distributions was weaker, or entirely absent, in a non-social control condition with no conspecific present.

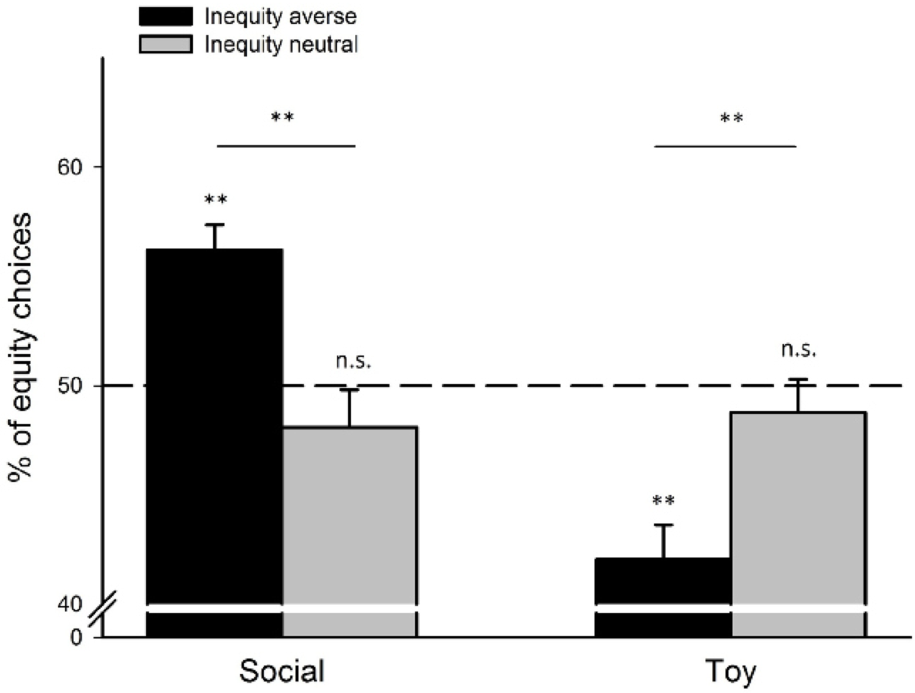


(a)



Actor	Partner
1 pellet	**3 pellets**
1 pellet	1 pellet

(b)



(c)

Figure 1. Choice-based disadvantageous inequity aversion task for rats. (A) Double T-maze apparatus for quantifying disadvantageous IA in rats. Pairs of rats are trained in this task. The actor rat chooses to enter either an equal-reward compartment, or an unequal-reward compartment. The partner is always directed towards the opposite compartment facing the actor. Actor's and partner's compartments are separated by a transparent, perforated wall, allowing rats to see, hear and smell each other, but neither rat can access the other rat's compartment. The actor rat selects the reward distribution for both rats by entering one of the two compartments in each trial: entering the equal reward compartment produces one food pellet for each rat, entering the unequal-reward compartment yields one food pellet for the actor rat, and three food pellets for the partner rat. Thus, the actor's decisions are non-costly because its own-payoff is always identical and independent of its choice, but it can choose between a fair outcome (both rats receive the same reward magnitude), or an unfair outcome (the partner rat receives a higher reward than the actor rat). In a non-social control condition (the toy condition), reward contingencies, payoff matrix and all other features of the task are identical, but the partner rat is replaced by an inanimate toy rat. Adapted from Hernandez-Lallement et al. (2015, 2016) with friendly permission by Frontiers in Neuroscience, (B) illustration of the payoff matrix, (C) rats were classified as inequity averse, or inequity neutral, depending on their individual sensitivity to unequal reward distributions (see Oberliessen et al., 2016 for details). Unlike inequity-neutral rats, inequity-averse rats preferred equal over unequal outcomes in the social, but not in the non-social control condition, the toy condition (**p < 0.01; n.s., not significant). Adapted from Oberliessen et al. (2016) with friendly permission by Elsevier.

In this type of designs, the subject can reveal its fairness preference by its choice, and thus control if inequity occurs at all. The clear advantage of such choice-based IA designs is that the animals do not need to forego own rewards to express their aversion to inequity; thus, they differ from the impunity-like flavor of previous IA tasks that involved costly refusals of own-rewards. This is an important design feature as egoistic desires to maximize food intake in standard impunity-like IA tasks might override any faint, but non-zero IA motives; by consequence, an existent IA preference in an impunity-like task might be masked by an overly strong dislike of sacrificing own-rewards, and it might thus remain undetected.

The Added Value of Choice-Based Tasks

Choice-based tasks allow to control for some of the alternative factors discussed above that are supposed to influence IA. First of all, because the reward distributions and, hence, rewards to the actor animal, are identical between the social and the non-social condition, frustration effects and violations of reward expectation are unlikely to account for the higher preference for equal-reward outcomes in the social compared to the non-social control condition (but see below for more in-depth discussion of possible further frustration and reward expectation effects in choice-based tasks). Hence, differences in behavior between conditions can more plausibly be attributed to the social component of the task (however, note that many impunity-like IA tasks also had a non-social control condition).

Another reason why fairness-preferences in choice-based tasks cannot easily be explained by frustration effects or violations of reward expectations is the invariance in own-reward value; that is, frustration and reward expectations should only occur if the animal had previous experience with more valuable rewards. However, because own-reward quality and magnitude, as well as delay-to-reward and other reward parameters, are always identical in all trials, irrespective of the actor animal’s choice, the subjects in choice-based tasks have no previous experience with better rewards, making frustration and expectation effects unlikely.

For the same reason, reference-point-dependence and loss-aversion (Chen and Santos, 2006) are also unlikely explanations of equity preferences in choice-based tasks. Because of the invariance in own-reward outcomes, choice-based tasks entail no reference-dependent reward evaluation or negative deviations from a standard reward (i.e., losses).

A counterargument holds that, at closer inspection, some design features of choice-based tasks might actually prompt frustration, reward expectancy and/or reference-dependency effects, albeit in more subtle ways: the total reward magnitude, i.e., the sum of rewards to the actor animal and the conspecific (or empty compartment, respectively), is higher after unfair than fair choices. This difference in total reward magnitude might affect the level of expectation, it might set a reward magnitude standard, and the actor animal might be frustrated because of the inaccessibility of the reward in the other compartment. These reward expectation, reference and frustration motives might bias choice away from the unfair alternative.

However, if these non-social mechanisms indeed favored equity preferences in choice-based IA task, their influence on choice should be stronger in the non-social control than the social condition, for the following reason: in the social condition, the conspecific has access to the reward and consumes it swiftly, but in the non-social condition, the reward is just dropped in an adjacent compartment without being consumed by an (absent) conspecific. Because of the lack of reward consumption in the control condition, the inaccessible reward in the other compartment is displayed longer than in the social condition. This means that the difference in reward magnitude, and, in particular, the inaccessibility of reward, is more salient in the control than the social condition. By consequence, frustration effects and other non-social drivers of preferences should favor equity choices in the control condition more than in the social condition. Yet, this is inconsistent with the choice data, revealing clear preferences for equity choices in the social, but not the non-social condition. Thus, we consider it implausible that non-social aspects of the task explain the condition-effects on equity preferences.

Finally, disappointment in the human experimenter (Engelmann et al., 2017) can be ruled out in choice-based tasks since the experimenter is not responsible for the choice of reward distributions and is present in both the social and the non-social control condition, or he is even entirely absent if tasks are fully automated.

Of course, there might be additional factors that could bias choices towards one or the other alternative in choice-based IA tasks. For example, the actor animal's perception of the conspecific's reward consumption might incite reward expectancy or might shift reference points, and the fact that the conspecific consumes a reward that the actor animal cannot access might be perceived as frustrating by the actor. It remains to be determined whether these factors are of social nature (e.g., frustration as a consequence of envy-like emotions about the conspecific's reward consumption), or non-social nature (e.g., the conspecific's reward consumption might simply cue the availability of higher rewards that are, however, inaccessible to the actor rat), and it should be investigated if these factors indeed play a role in influencing choice behavior in choice-based IA tasks at all.

Do Choice-Based Tasks Measure Inequity Aversion?

One crucial question is, whether choice-based tasks actually measure the same thing as impunity-like tasks. That is, is a rejection of an unfair offer in an impunity-like task driven by the same mental and affective mechanisms as preference for equity outcomes in a choice-based task, or are the animals' decisions in the respective tasks qualitatively different? Rejections of unfair offers in impunity-like tasks clearly have an affective flavor, while preferences for equal outcomes in choice-based tasks do not necessarily reveal strong emotions. However, empirical evidence that impunity-like tasks involve stronger negative emotions than choice-based tasks is elusive; hence, putative differences in the affective domain between task designs are somewhat speculative.

The answer to the question whether impunity-like or choice-based tasks measure the same form of IA also depends on the particular definition of IA used. Fehr and Schmidt (1999), who developed a theory of IA for human decision-makers, defined inequity aversion as the resistance against inequitable outcomes. They stressed that the aversion against inequity can, but does not have to, go along with the willingness to forego material payoffs for the sake of fairness.

It is also conceivable that IA is a special form of temporal discounting (Stevens and Hauser, 2004; for an overview of temporal discounting see Kalenscher and Pennartz, 2008): IA might be the rejection of a sooner smaller reward (an unequal small payoff) compared to a more valuable reward in the future (fair, high rewards in a successful long-term cooperation).

Both definitions of IA entail the willingness of the decision-maker to incur costs for the sake of equity. Since decisions in the impunity-like designs of IA are costly, but decisions in choice-based tasks are not necessarily costly, the construct measured in the former class of tasks comes closer to the definition of IA as put forward by Fehr and Schmidt (1999) or the idea of temporal discounting. Future research should manipulate the costs of the fair option in choice-based designs, and investigate whether animals are also willing to forego own-payoff for the sake of equitable outcomes in these tasks.

In conclusion, we argue that the use of choice-based IA tasks may shed light on some of the remaining open questions raised by experiments using impunity-like IA tasks. We want to stress that we do not consider choice-based IA tasks superior to impunity-like tasks; they merely complement the existing research. We maintain that the combination of both tasks should be the way forward in future research.

Advantageous Inequity Aversion

This review focused primarily on moderators and mechanisms of disadvantageous IA, and its putative ultimate reasons. The motivation for prioritizing the coverage of disadvantageous over advantageous IA, the aversion against outcomes that produce a lower payoff for a partner relative to one's own payoff, is that advantageous IA is rarely found (and tested) in impunity-like tasks (Jensen et al., 2007; Horowitz, 2012; Kaiser et al., 2012). However, there are several choice-based IA tasks prompting advantageous IA (also labeled as prosociality or mutual-reward preferences) in different non-human animals, e.g., rats (Hernandez-Lallement et al., 2015, 2016, 2018; Márquez et al., 2015), capuchin monkeys (De Waal et al., 2008; Takimoto et al., 2010; Takimoto and Fujita, 2011), chimpanzees (Horner et al., 2011), and rhesus macaques (Ballesta and Duhamel, 2015; but see Chang S. W. et al., 2011). Similar to disadvantageous IA, the expression of the animals' aversion against advantageous inequity in choice-based tasks is not costly: the own-reward to the deciding animal is always identical and independent of the choice of a fair or unfair alternative. To date, it is unclear if a principle mental component underlies preferences for equal reward distributions in disadvantageous and advantageous IA settings in non-human animals.

This review mainly focuses on IA in non-human animals. It is important to note that IA has been extensively studied in humans, too, with a vast, partly diverging literature in several different disciplines, including economics and psychology. The terminology and experimental methodology used and covered in this review are largely consistent with the literature in economics, where advantageous IA is defined as preference for fair vs. unfair outcomes, and where IA is mainly investigated by means of economic games (e.g., Fehr and Schmidt, 1999). By contrast, psychologists often label advantageous IA guilt and frequently focus on self-reports which can be linked to behavioral intentions underlying other-regarding preferences (e.g., Schmitt et al., 2000), and related concepts, like, e.g., morality, justice, or ethics. We argue that studying IA in animals is not only interesting by itself, but paves the way for harmonizing semantic differences between disciplines as well as highlighting conceptual similarities.

Neural Substrates of IA

Parallel to behavioral studies on IA, another field of research evolved with the technical progress of cognitive neurosciences. Modern neuroimaging methods offer more and more possibilities to directly study brain processes during social decision making (mainly in humans), and thus to learn more about the underlying mechanisms and brain structures. Although this should not be the focus of this review, we consider it worthwhile to shortly touch on this topic and present some interesting results (note that we do not claim to provide a comprehensive overview; for more details, see Ruff and Fehr, 2014). Several studies which investigated neural responses to disadvantageous and advantageous IA in humans suggest that the dorsolateral prefrontal cortex seems to be particularly involved in encoding and interpreting payoff inequalities and implementing inequality averse behaviors (Sanfey et al., 2003; Hsu et al., 2005; Haruno and Frith, 2010; Tricomi et al., 2010; Chang L. J. et al., 2011; Fliessbach et al., 2012; Cappelen et al., 2014; Güroğlu et al., 2014; Haruno et al., 2014; Yu et al., 2014; Nihonsugi et al., 2015; Holper et al., 2018). Tricomi et al. (2010) found that inequality averse preferences were also correlated with activity in the valuation network (Bartra et al., 2013), mainly ventral striatum and ventromedial prefrontal cortex in humans, suggesting that own-reward activity in the valuation system was modulated by the degree of inequality relative to a better or worse reward received by another participant. A recent study by Gao et al. (2018) even distinguished between neural correlates of advantageous vs. disadvantageous IA. They found that the processing of advantageous inequity involved the left anterior insula, the right dorsolateral prefrontal cortex, and the dorsomedial prefrontal cortex. Disadvantageous inequity correlated with activity in the left posterior insula, the right amygdala, and the dorsal anterior cingulate cortex.

In the animal domain, a study on rhesus monkeys provided evidence that striatal neurons play a role in identifying the social actor and own reward in a social setting (Báez-Mendoza et al., 2013), consistent with the human evidence presented by Tricomi et al. (2010). As mentioned above, the amygdala also seems to play an important role in social decision making (Gao et al., 2018). In line with amygdala's hypothesized role in social cognition, Chang et al. (2015) could show that basolateral amygdala neurons signaled social preferences in rhesus macaques and mirrored the value of rewards delivered to self and others when monkeys were free to choose. In line with this finding, Hernandez-Lallement et al. (2016) found that basolateral amygdala lesions abolished mutual reward preferences in rats.

Thus, in summary, evidence from cognitive neuroscience suggests that the brain's valuation system, including ventromedial prefrontal cortex and ventral striatum, as well as a range of structures involved in planning and cognition (dorsolateral prefrontal cortex), emotional processing (amygdala) and the appraisal of negative events (insula) are involved in processing IA in humans as well as non-human animals.

Conclusions

The main purpose of this review is to highlight some of the open questions and, especially, locate potentially essential differences in the various task designs used to probe IA in non-human animals. Future studies should investigate how animals perform in both impunity-like and choice-based variants of disadvantageous IA tasks to learn about the effect of design-specific differences on IA expression, and to test whether the level of IA in the choice-based task can predict the probability to reject rewards in the impunity-like task, or vice versa. Thus, identifying the commonalities and differences in behavior between both types of tasks will help to better differentiate between theories of IA, and to better understand the actual mental mechanisms underlying IA. Furthermore, future research should compare preferences for fair outcomes in disadvantageous IA tasks with preferences for fairness in advantageous IA tasks with the same individuals. This would help to untangle whether both forms of IA are positively or negatively correlated (respectively correlated at all). It is possible that highly disadvantageously inequity averse individuals do also show higher scores of advantageous IA. On the other hand, it is also conceivable that a high sensitivity of being disadvantaged goes along with a reduced sensitivity towards others being disadvantaged. The clarification of this issue might be further supported by additional neuroscientific studies. Isolating the differences, commonalities, moderators and predictors of each type of IA will yield important insights into the mechanistic underpinnings of IA.

Author contributions

Lina Oberliessen developed the first concept of the article, wrote the article, and revised the article. Tobias Kalenscher revised the concept of the article, wrote the article, and revised the article.

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Conflict of Interest Statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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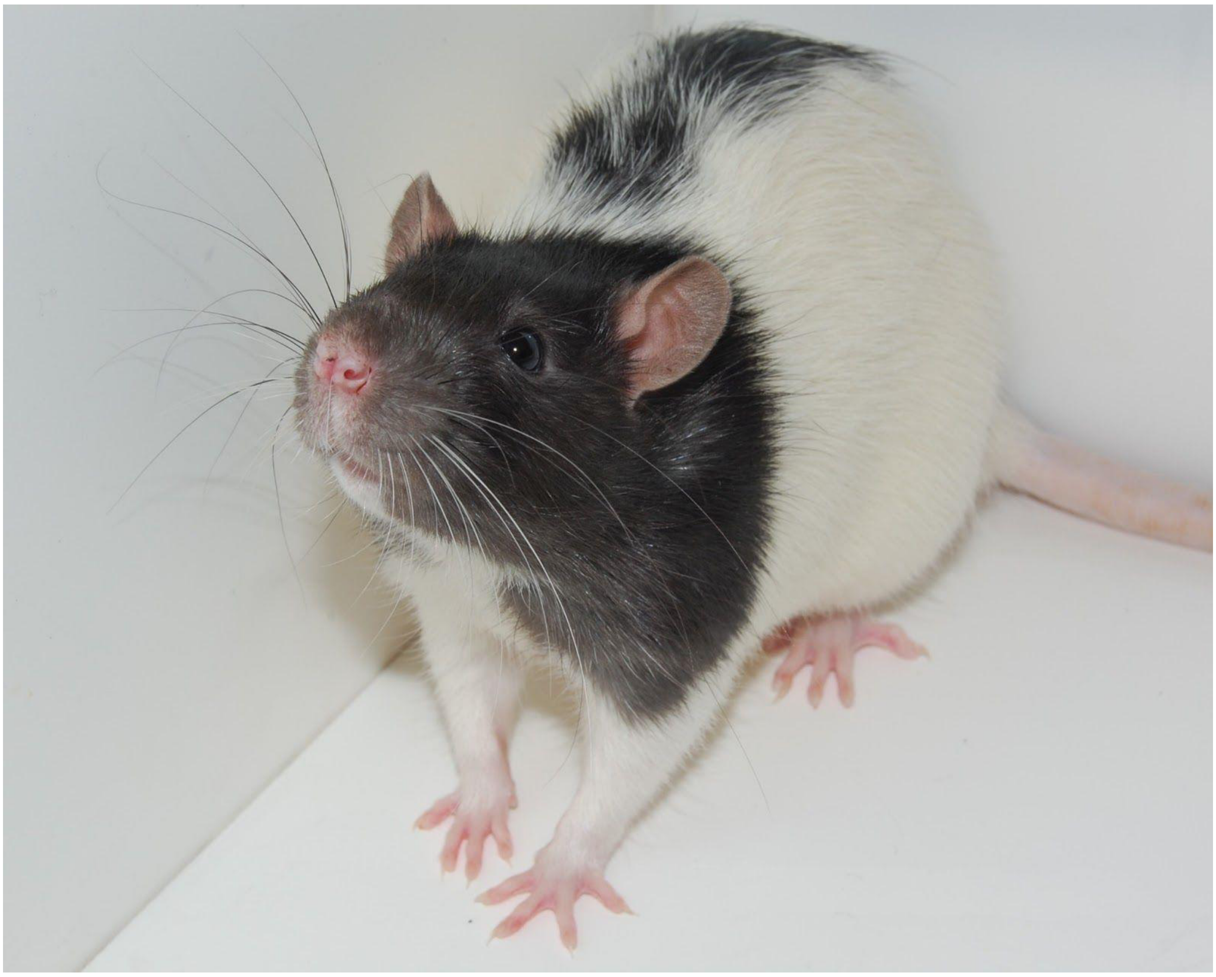
Chapter 2: Inequity aversion in rats (Rattus norvegicus)



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Abstract

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 minimise 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 non-human 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 paired compartments was associated with an equitable reward distribution (identical amount for the actor and the partner) whereas entry into the other paired compartments 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 non-social 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 organisational principle, shared by many social species, that shapes the intricate social dynamics of individuals interrelating in larger groups.

Keywords: decision making, fairness, inequity aversion, rat, social behaviour

Introduction

Beyond maximising 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 other´s outcomes as well has often been studied with economic games (Yamagishi, Horita, Takagishi, Shinada, Tanida & Cook, 2009; Margittai, Strombach, van Wingerden, Joels, Schwabe & Kalenscher, 2015; Strombach, Weber, Hangebrauk, Kenning, Karipidis, Tobler & Kalenscher, 2015). For instance, some people voluntarily share money in the dictator game (Bolton, Katok & Zwick, 1998), and give up 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 pay-off for a partner relative to own pay-off (disadvantageous IA) given matched efforts to obtain the pay-off and (2) that produce a lower pay-off for a partner relative to own pay-off (advantageous IA). Here, we focus on disadvantageous IA (in the following simply referred to as IA for brevity reasons, unless specified otherwise).

In their prominent model of IA, Fehr and Schmidt (1999) note that "*in addition to purely selfish subjects, there are subjects who dislike inequitable outcomes*" (p. 822). 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 non-kin (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 (Triver, 1971). Such reciprocity is prone to cheating and, thus, inequitable outcomes (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 non-human 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) compared to the reward received by a second animal (grape) for performing the same token exchange task. 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 was also found in chimpanzees (Brosnan, Schiff & de Waal, 2005; Brosnan, Talbot, Ahlgren, Lambeth & Schapiro, 2010a) and long-tailed macaques (Massen, van den Berg, Spruijt & Sterck, 2012). IA was not found in two rather uncooperative species, namely orangutans (Brosnan, Flemming, Talbot, Mayo & Stoinski, 2010b) and squirrel monkeys (Talbot, Freeman, Williams & Brosnan, 2011), raising the possibility that IA and cooperation may have co-evolved (Brosnan, 2006, 2011). Besides primates, evidence for IA was also found in other social species; domestic dogs (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 failed to demonstrate IA in social species, including brown capuchin monkeys (Dubreuil, Gentile & Visalberghi, 2006; Roma, Silberberg Ruggiero & Suomi, 2006; Fontenot, Watson, Roberts & Miller, 2007; Silberberg, Crescimbene, Addessi, Anderson & Visalberghi, 2009) or any great ape species (Bräuer, Call & Tomasello, 2006; Bräuer, Call, Tomasello, 2009; see also Raihani, McAuliffe, Brosnan & Bshary, 2012 for evidence against IA in food-cooperative cleaner fish) and therefore argue for non-social 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 would imply missing out on 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; Hernandez-Lallement, van Wingerden, Schäble & Kalenscher, in press). However, it is unknown if 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 (Wishaw & Kolb, 2005) and develop in hierarchically structured, well-organised social groups. We therefore hypothesise 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; Hernandez-Lallement et al., 2016; Hernandez-Lallement et al., 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 (Łopuch & Popik, 2011; Schuster, 2002), reciprocity (Rutte & Taborsky 2007) and empathy (Bartal, Decety & Mason, 2011) were 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 male individuals (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 hypothesised 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 have prioritised access to food.

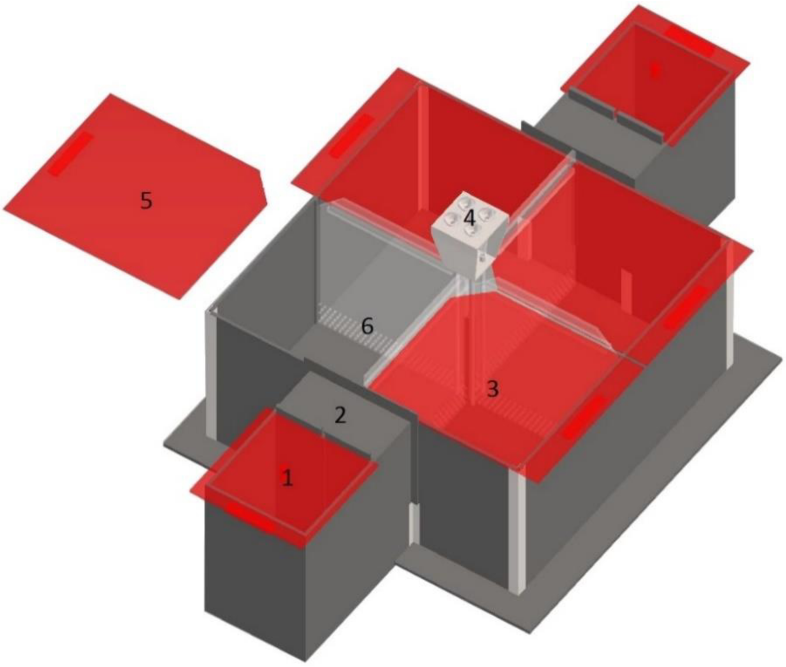
Methods

Subjects

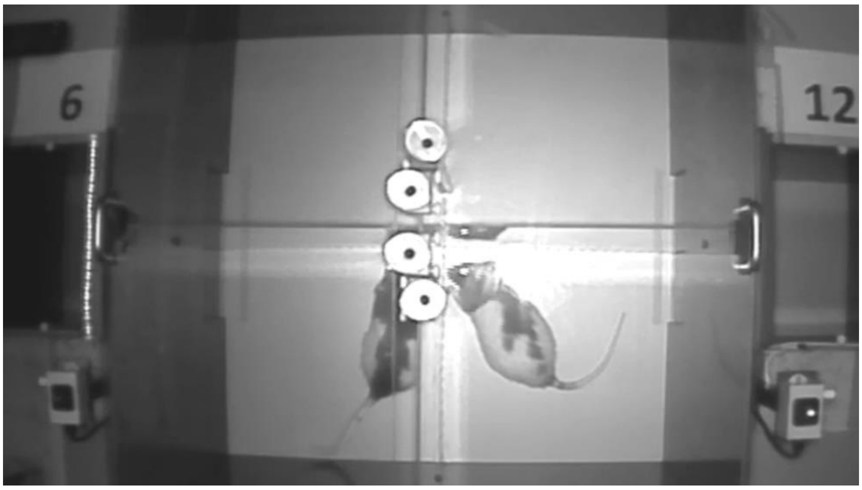
Twenty-three genetically unrelated male Long Evans rats were tested in two consecutive batches (batch1: n = 12, bred by *Janvier Labs, St. Berthevin, France*, batch2: n = 11, bred by *Charles River Labs, Calco, Italy*). N = 3 animals of one cage from batch 1 were used as partner animals for both batches. The remaining twenty 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 ± standard error of the mean (SEM): 466 ± 6.56 g). Animals were housed in groups of three animals per cage (59 x 38 x 20 cm). 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 hours light - dark cycle (lights off at 07:00 AM) 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 status. All experiments were performed in accordance with German Welfare Act and were authorised 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 x 20 x 30 cm), two decision boxes (25 x 20 x 30 cm) and 2 x 2 opposing choice compartments (30 x 30 x 40 cm; 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 lead to either of the two choice compartments. To minimise 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).



(a)



(b)

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 semi-transparent lids (non-transparent for rats´ eyes) to minimise 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 two consecutive days of habituation on the social maze and at least 2 x 5 consecutive days of shaping. Finally, rats were trained and tested in the IA choice task. Every actor performed 2 x 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 x 50 cm) for 30 minutes, under red light conditions. A black food cup with six sucrose pellets was placed into 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 sparse, 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) 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 those 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, no hierarchy ratings were obtained 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 who 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 setup.

Habituation and shaping

All animals underwent a habituation procedure to become acquainted with the apparatus. On two consecutive days, each animal was individually put in the starting box for two minutes. 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 two minutes 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 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 either paired with another rat, or with a toy. Sessions alternated between social and toy condition during the process of shaping. The procedure of shaping itself is identical to the IA choice task (see below) except for the reward distribution. 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 pseudo-randomly distributed between left and right compartment. After 8 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: A) enter the compartments autonomously within 10 s on each trial, B) consume all delivered rewards, C) 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 C.

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 mover 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 same magnitude and delay in both the actors´ and partners´ compartments (one sucrose pellet), whereas deciding for 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 own-payoff to the actor, 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 non-social 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 modulated 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, the remaining half started in the toy condition. The order of the starting condition was pseudorandomised across rats. In the social condition, actor rats were always paired with the same partner.

Session structure: a session started with one minute 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 minimise 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 compartment with a disadvantageous inequitable reward distribution (one sucrose pellet for the actor, three sucrose pellets for the partner). The allocation of choice compartment to equitable-/ inequitable outcomes was pseudorandomised across sessions. Hence, the design involved very frequent reversals of the inequity-compartment assignments.

Each session consisted of 28 trials (8 forced-choice and 20 free choice trials). A session began with the 8 forced choice trials (4 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 mover, followed by the partner / toy, who 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 seconds 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 seconds 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) free choice trials per session, the actor rats did not enter the choice compartment autonomously. Here, the experimenter gently pushed the animals forward, 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 pellet was 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 in 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 inter trial interval was independent of the actor´s choice.

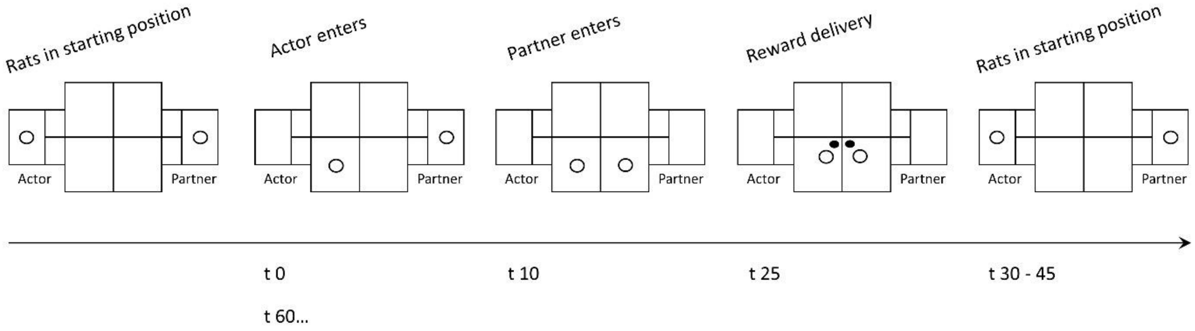


Figure 2. Time schedule of the trials in the IA choice task. Actors were always first movers. The actor´s doors were opened first (one of them in the forced choice trials, both of them in the free choice trials) and he moved into one of the two choice compartments; t0, trial onset. After 10 s (t10), 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. Reward was delivered 25 s after trial onset (t25). Actor and partner received the same reward after equity choices (one sucrose pellet), 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).

Analysis

We first compared the levels of hierarchy markers obtained in our hierarchy assessment (social and genital exploration times, see above) of dominant versus subordinate animals against chance level with one sided *t*-tests to verify classification success.

In order to test if rats are inequity averse in the IA choice task, we compared the percent 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 percent 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 (cf. Hernandez-Lallement et al., 2015). The equity bias score for rat *i* is the percent difference in equity choices between the social and toy conditions relative to the equity choices in the toy condition:

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

Because the payoff to the actor rat was identical for all choices and conditions, the difference in % 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 compared to 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 (cf. Hernandez-Lallement et al., 2015). This permutation distribution of equity bias scores consisted of N = 5 000 draws of 12 x 2 sessions, with the percentage of equity choices of these sessions randomly assigned to social and toy labels. For each of such draws, the resulting equity bias score was calculated, generating a distribution of 5 000 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-randomised equity bias benchmark value.

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

Next, we tested if the percent 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 percent 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 percent equity choices in either condition. A one-way ANOVA with partner identity as independent and percent 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 percent equity choices and a putative interaction between condition and session number.

Data were analysed using IBM SPSS Statistics 22 and Matlab R2013a. Graphs were built with SigmaPlot 11.0. For all statistic 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 percent values do not add up to 100 % because they are not complementary in triad interactions). The dominant rats' proportions of exploration times were significantly above 50 % (one-sided *t*-test, $t_5 = 4.62$, $P < 0.01$), and the subordinate rats proportions of exploration times were significantly below 50 % (one-sided *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 ($t_{18} = 1.37$, $P = 0.19$).

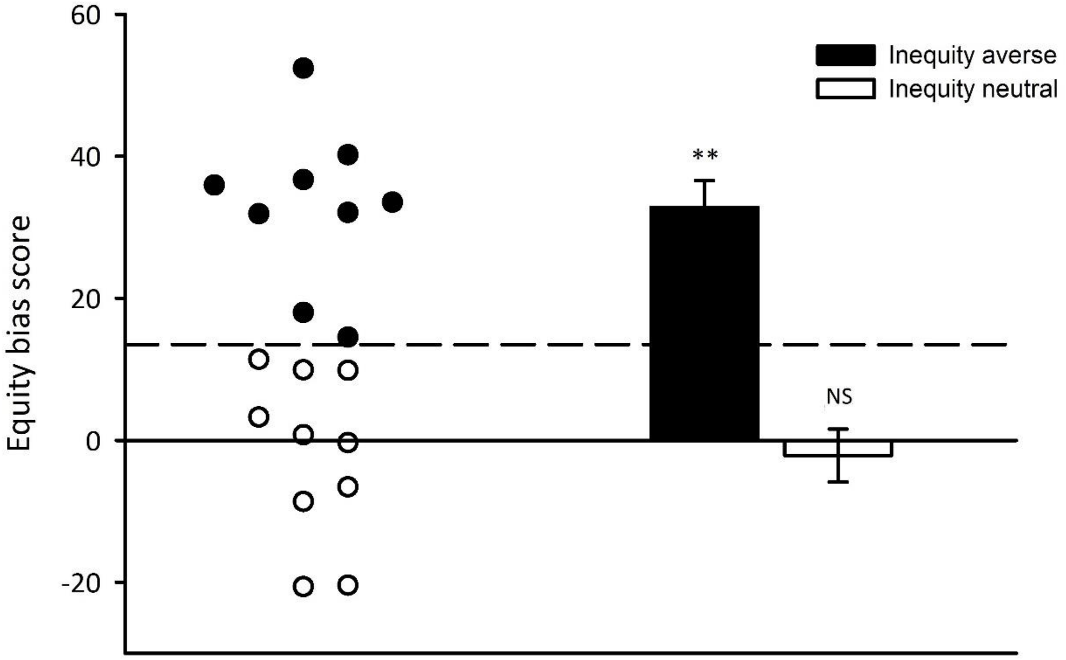


Figure 3. Equity bias scores. Individual equity bias scores (dots) are illustrated on the left side. The horizontal dashed line represents the upper limit of the 95 % confidence interval of the bootstrapped permutation distribution. Animals with equity bias scores exceeding the upper limit were classified as inequity averse (N = 9; black dots), animals with scores within the confidence interval were classified as inequity neutral (N = 10; white dots). Mean equity bias scores of inequity averse and inequity neutral rats are illustrated on the right side. Error bars represent the standard error of mean.

Although mean equity choices were significantly different between social- and toy-condition, the effect was relatively small. However, we found substantial individual differences in percent choice data (Fig. 4) and thus also in equity bias scores. We 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; also, cf. 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-subject, 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 (cut-off 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 9 out of 19 rats as inequity averse showing a mean equity bias score of 32.80 ± 3.76 (mean ± SEM), and 10 as inequity neutral showing 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 ($t_9 = -0.57$, $P = 0.58$).

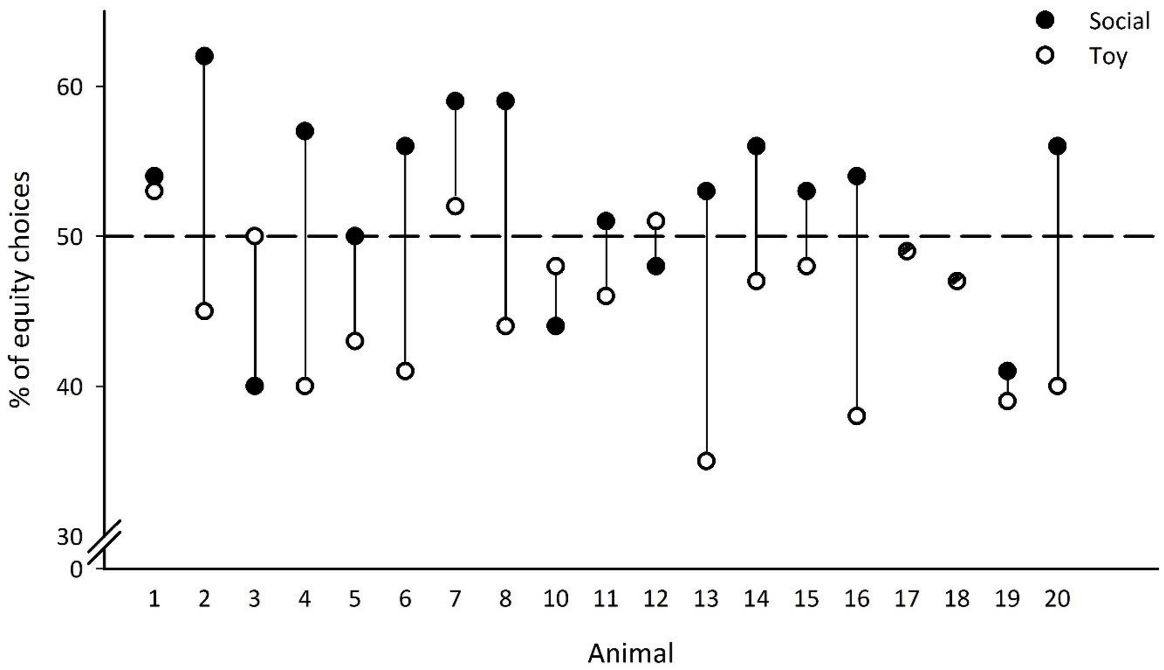


Figure 4. Individual choice data. Percent equity choices of all animals (N = 19) for social (black dots) and toy condition (white dots). Animals 17 and 18 have the same percentage of equity choices in both conditions. Animal 9 was excluded from analysis (see methods). The horizontal dashed line represents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

Next, we compared percent-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 the trials. In the toy condition, inequity averse rats selected the equitable option in 42.04 ± 1.58 % (mean ± SEM) of the trials, and inequity neutral rats in 48.77 ± 1.52 % (mean ± SEM) of the trials. A mixed-model ANOVA revealed a significant main effect of condition on percent-choices of equitable outcomes (social versus toy, $F_{1,17}$ = 29.70, $P < 0.01$), confirming the abovementioned mean comparison of percent equity-choices between social and toy condition, 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 percent 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.

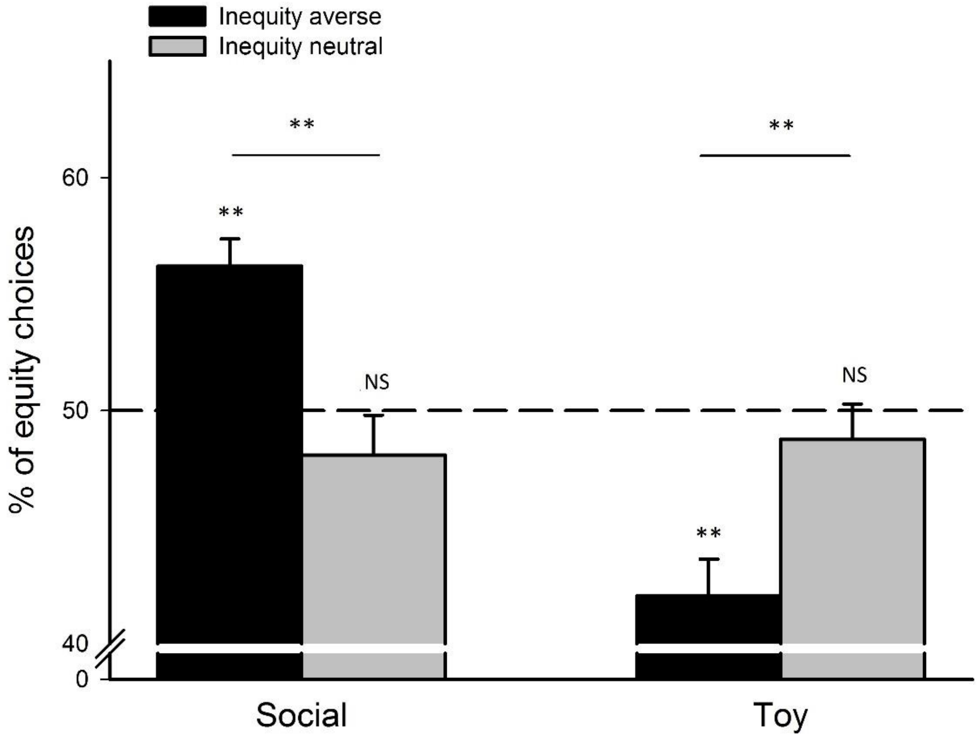


Figure 5. Equity choices in the social and toy condition for inequity averse and inequity neutral animals. Inequity averse animals prefer equity choices more in the social condition and less in the toy condition. Error bars represent the standard error of mean.

There was no order effect of starting condition (rats starting the experiment in the social or toy condition) on percent 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 percent 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 percent 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 percent 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 percent 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 percent 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: $rs = 0.27$, $N = 19$, $P = 0.27$; toy condition: $rs = -0.14$, $N = 19$, $P = 0.58$), 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 significantly differ from zero ($t_{13} = 1.57$, $P = 0.14$). This suggests that dominant rats had a higher propensity for IA than subordinate rats.

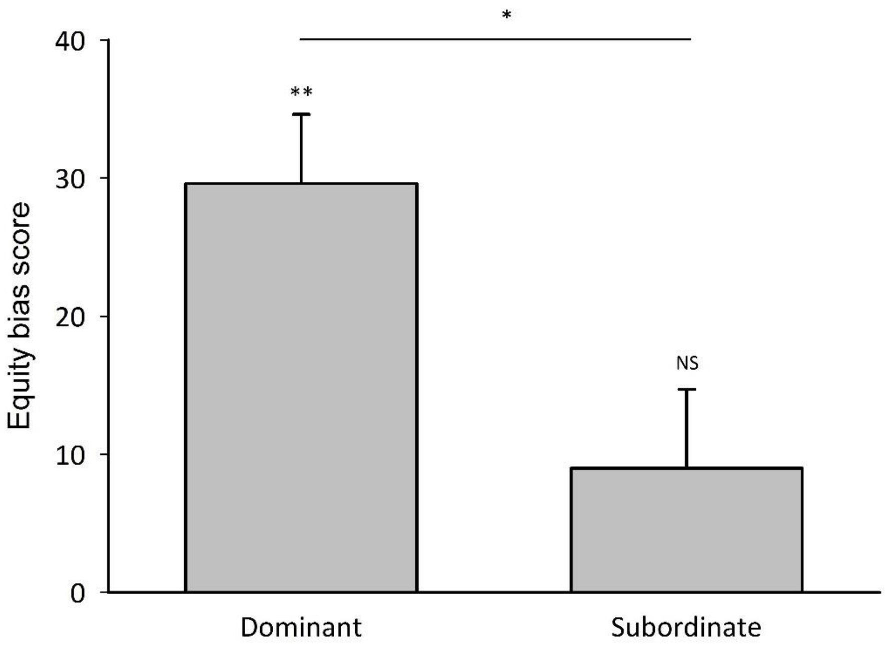


Figure 6. Dominant animals are more inequity averse. Mean equity bias scores of dominant animals and subordinate animals are illustrated. Error bars represent the standard error of mean.

Discussion

Over the last decades, evidence has been accumulated that human and non-human 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 if social species that evolved long before primates show similar aversion against such disadvantageous inequality. Here, we report that rats, a highly social species (Wishaw & Kolb, 2005) that live in well-structured, hierarchically organised 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 maximise own-payoff (compare Silk, Brosnan, Vonk, Henrich, Povinelli, Richardson et al. 2005; Horner, Carter, Suchak & de Waal, 2011; Hernandez-Lallement et al., 2015), the actors´ rewards were always identical between the two choice compartments, so that equity choices were non-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 percent difference in equity choices between the social and toy conditions, served as estimates of the rats' individual levels of IA.

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 a great inter-individual variability in IA, with some rats choosing equal outcomes 50 % more often in the social than the toy condition, yet other rats 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 (9 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, great inter-individual 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 was more important for inequity averse than inequity neutral animals, inequity averse animals may be also more prone to secondary reinforcement effects of food-related cues. During reinforcement learning, non-hedonic sensory features of rewards, such as their smell or sound, often gain incentive value so that animals will work to produce those features even in the absence of primary rewards (e.g. Egger & Miller, 1962; Armus, Carlson, Guinan & Crowell, 1964). 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 compared to 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 semi-natural settings, dominant rats claim prioritised 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, by consequence, 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 rats and laboratory rats, social hierarchies are relatively stable and organised in a near-linear way (Blanchard, Flanelly & Blanchard, 1987; Berdoy et al., 1995). 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 if these strategies are even necessary to enforce stable hierarchies. Future studies need to address the role of IA in stabilising social hierarchies.

It has been argued that costly refusals of unfair offers, as demonstrated in several primate studies, may merely reflect non-social motives, such as frustration effects and/ or violated expectations (Wynne, 2004; Roma et al., 2006; Dubreuil et al., 2006; Bräuer et al., 2006, 2009; Silberberg et al., 2009). However, frustration, expectation violations or other non-social 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 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 compared to 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 non-social 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 if our results apply to populations of wild rats, too. The generalisability from laboratory rats to wild rats has to be addressed in future studies. Furthermore, it would be worthwhile to examine if 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, respectively (Viana, Gordo, Sucena & Moita, 2010; Schneeberger, Dietz & Taborsky, 2012). However, it is unknown in 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, e.g., a negative emotional response to a conspecific´s reward consumption beyond 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 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 (cf. 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 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, amongst 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 evolutionary distant relatives to humans, suggesting both conserved origins and widespread manifestations of social behaviour across species.

Author contributions

Lina Oberliessen designed the study, conducted the experiments, analyzed the data, developed the first concept of the article, wrote the article, and revised the article. Julen Hernandez-Lallement analyzed the data, and revised the article. Sandra Schäble designed the study, and revised the article. Marijn van Wingerden revised the data analysis, wrote the article, and revised the article. Maayke Seinstra revised the article. Tobias Kalenscher designed the study, revised the data analysis, wrote the article, and revised the article.

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Chapter 3: Wolves and dogs do not prefer equal outcomes in a touchscreen-based paradigm

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Abstract

Research over the last decades has shown that not only humans but also other animals respond to unequal reward distributions. This so-called inequity aversion (IA) is discussed to promote successful long-term cooperation. However, cross-species findings are heterogeneous and some studies failed to provide evidence for disadvantageous IA. As wolves and dogs are cooperative species, it would make sense that they are equipped with a cooperation-maintaining mechanism like IA. Indeed, studies on pet dogs, pack-living dogs, and wolves could often find evidence for reward inequity, i.e. animals stopped earlier to perform a task when they received no reward in the presence of a rewarded partner, compared to several control conditions. However, a response to quality inequity, i.e. receiving a reward of lesser value compared to a partner, was not found in pet dogs, and less pronounced in pack-living dogs and wolves. This could be because IA is associated with omitting own rewards in such paradigms. That is why we implemented a new touchscreen-based choice paradigm to disentangle IA from food-maximizing motives. In the test, two symbols associated with different reward distributions (an equal versus an unequal distribution) were presented to the animals. Importantly, the subject´s reward was independent of its choice, only the reward of the partner animal varied between distributions and was either equal or of higher value. Previous training should ensure that the animals learned the different rewards associated with each symbol. We used a within-subjects design to compare choices in the social test condition with a non-social and a social control condition. Against our expectations, wolves and dogs did not prefer the equal reward distribution in neither condition. We assume that they got stuck with their preference for the inequity symbol which they developed during training. Understanding the particular reward contingencies between individuals in the test condition might have been too complex. Although the current design is not yet methodologically sound enough to study IA in canids or other non-human animal species, our study unfolds important aspects to develop and pursue touchscreen-based social choice paradigms. We consider them highly promising as they offer the possibility of automation in the long run.

Introduction

In economic games, humans tend to reject offers that are perceived to be unfair, even though such rejections are economically unreasonable for themselves (Güth & Kocher, 2014). Why is that? One possible reason for that apparently uneconomic decision behavior could be inequity aversion (IA). IA means that people tend to avoid inequitable outcomes, and even forgo some material payoff to move in the direction of equitable outcomes (Fehr & Schmidt, 1999). IA has been hypothesized to function as a mechanism to ensure sharing of payoffs in the long run. By serving as an unfairness detector, it is assumed to enable and maintain long-term cooperation also with non-kin, i.e. protecting individuals from exploitation (Brosnan, 2006, 2011; Brosnan & de Waal, 2014).

Since not just humans cooperate with each other, IA might also benefit cooperative non-human animal species. Brosnan and de Waal (2003) published a pioneering study on IA in capuchin monkeys. Methodologically, the study was a modification of the human impunity game (Bolton & Zwick, 1995). In the original (human) version, a proposer splits a sum of money between himself and a responder. The responder can then decide if he accepts or rejects the proposer´s offer. However, in contrast to the ultimatum game (Güth, Schmittberger, & Schwarze, 1982), the responder´s decision does not affect the proposer in the impunity game. If the responder accepts, both players can keep their share. If the responder rejects, the proposer can keep his share, and the responder receives nothing. In the animal version of the task, the human experimenter takes the role of the proposer, and offers equal or unequal rewards for performing a task (e.g. exchanging a token).

Since that first study, IA has been studied in various non-human animal species. However, the results are quite heterogeneous. IA was demonstrated in capuchin monkeys (Brosnan & de Waal, 2003; van Wolkenten, Brosnan, & de Waal, 2007; Fletcher, 2008; Takimoto, Kuroshima, & Fujita, 2010; Takimoto & Fujita, 2011), macaques (Hopper, Lambeth, Schapiro, Bernacky, & Brosnan, 2013; Massen, van den Berg, Spruijt, & Sterck, 2012), chimpanzees (Brosnan, Talbot, Ahlgren, Lambeth, & Schapiro, 2010; Brosnan, Schiff, & de Waal, 2005), cotton top tamarins (Neiworth, Johnson, Whillock, Greenberg, & Brown, 2009), dogs (Range, Horn, Virányi, & Huber, 2009; Range, Leitner, & Virányi, 2012; Brucks, Essler, Marshall-Pescini, & Range, 2016; see McGetrick & Range, 2018 for an overview), wolves (Essler, Marshall-Pescini, & Range, 2017), crows (Wascher & Bugnyar, 2013), rabbits (Heidary, Mahdavi, Momeni, Minaii, Rogani, Fallah, et al., 2008), and rats (Oberliessen, Hernandez-Lallement, Schäble, van Wingerden, Seinstra, & Kalenscher, 2016). However, other studies could not find evidence for IA in some of the same species such as capuchin monkeys (Dubreuil, Gentile, & Visalberghi, 2006; Fontenot, Watson, Roberts, & Miller, 2007; Roma, Silberberg, Ruggiero, & Suomi, 2006; Silberberg, Crescimbene, Addessi, Anderson, & Visalberghi, 2009), chimpanzees, bonobos, orangutans, and gorillas (Bräuer, Call, & Tomasello, 2006, 2009), cleaner fish (Raihani, McAuliffe, Brosnan, & Bshary, 2012), keas (Heaney, Gray, & Taylor, 2017), and dogs (Brucks, Marshall-Pescini, Essler, McGetrick, Huber, & Range, 2017; Horowitz, 2012). The lack of IA in less cooperative species like orangutans (Brosnan, Flemming, Talbot, Mayo, & Stoinski, 2011; Bräuer et al., 2009) or squirrel monkeys (Talbot, Freeman, Williams, & Brosnan, 2011; Freeman, Sullivan, Hopper, Talbot, Holmes, Schultz-Darken, et al., 2013) conforms with the hypothesis of IA as a cooperation-maintaining mechanism. However, some studies failed to find evidence for IA in cooperative species like capuchin monkeys, dogs, chimpanzees, or cleaner fish.

The heterogeneity in animal studies stimulated alternative theories about (respectively against) IA and its functional mechanisms. Next to the social cooperation hypothesis (Brosnan, 2006, 2011), there is another social hypothesis that assumes that social disappointment in the experimenter is the reason for negative responses, i.e. refusals of rewards and/ or rejections of further task performance (Engelmann, Clift, Herrmann, & Tomasello, 2017). According to this hypothesis, individuals are not disappointed because a partner is relatively advantaged, but they are disappointed because the experimenter does not reward them as well as he obviously could. Furthermore, several non-social hypotheses try to explain the animals´ behavior. These hypotheses assume that IA does not really exist (at least in animals), and present different, non-social explanations. The frustration hypothesis (Roma et al., 2006) predicts that previous experience with a reward of higher value results in a relative devaluation of a reward of lesser value, which is then rejected. The reward expectation hypothesis (Bräuer et al., 2006; see also Dubreuil et al., 2006; Neiworth et al., 2009) states that seeing another individual receiving a reward of higher value raises the expectation of also receiving such a reward. Accordingly, failed expectations and negative reward prediction errors (and not IA) could be the reasons for refusals. Chen and Santos (2006) suggest that reference-dependent reward valuation and loss-aversion could account for the evolution of IA. This would imply that IA is not a genuinely social mechanism, but merely a translation of reference-dependency and loss aversion concepts to the social domain. For a detailed overview see Oberliessen and Kalenscher (2019).

Next to postulating different theories to explain the behavior in such 'IA' experiments, several moderators of IA were identified. There is experimental evidence that effort (van Wolkenten et al., 2007; Wascher & Bugnyar, 2013), relationship quality (Brosnan et al., 2005; de Waal, Leimgruber, & Greenberg, 2008; but see Massen et al., 2012; Brosnan, Hopper, Richey, Freeman, Talbot, Gosling, et al., 2015), social hierarchy position (Oberliessen et al., 2016; Essler et al., 2017; Brosnan et al., 2010; but see Massen et al., 2012), sex (Brosnan et al., 2010), personality (Brosnan et al., 2015), and even pain sensitivity (Wang, Li, & Xie, 2019) modulate the IA response.

Another important and human-made factor is the experimental setup in which IA is tested (Oberliessen & Kalenscher, 2019). Most animal studies on IA used an impunity-like paradigm similar to the first study of Brosnan and de Waal (2003), i.e. subjects were confronted with equal and unequal reward distributions. In such a paradigm, IA is reflected by refusals of relatively disadvantaging rewards, or a rejection of further task performance. However, few studies used a choice-based paradigm in which subjects could actively choose between equal and unequal reward distributions between themselves and a partner animal (rats: Oberliessen et al., 2016; capuchin monkeys: Fletcher, 2008). What is important is that the subject´s choice is non-costly in this paradigm. Independent of its decision, the own reward is identical in both reward distributions. Only the reward of the partner animal varies between the two options (equal reward versus better reward). The advantage of this task design is obvious: Animals do not need to forego own rewards to express IA, i.e. faint IA motives are less likely to be masked by egoistic desires to maximize own food intake, as possible in standard impunity-like tasks (Oberliessen & Kalenscher, 2019). It is very likely that such methodological differences in measuring IA might lead to diverging results, and thus could explain why some studies found evidence for IA while others failed to do so.

Considering that the design seems to play an important role, it appears highly promising to compare a species´ IA response in different experimental settings to finally detangle IA from the specific influence of certain paradigms. That is why we implemented a choice-based IA task in the current study, testing two sub-species, wolves and dogs, that had previously been tested in impunity-like IA tasks. Notably, wolves and dogs did not show a strong response to quality inequity in that paradigm (Essler et al., 2017). That means that their refusals of further task performance were less frequent in a condition in which they received a less valuable reward compared to a partner, than in a reward inequity condition in which they received no reward compared to a partner that got rewarded. Using another paradigm might therefore be fruitful to validate if a reduced sensitivity to quality inequity was due to the experimental setup, or might also occur in a non-costly paradigm.

Wolves are a highly cooperative species. Therefore, it appears plausible that they are equipped with a cooperation-maintaining mechanism like IA. They hunt together, defend their territory together (Harrington & Mech, 1978; Mech & Boitani, 2003), and raise their offspring together (Moehlman & Hofer, 1997; Mech & Boitani, 2003). It could be found that captive wolves can also cooperate with humans (Range, Marshall-Pescini, Kratz, & Virányi, 2019). Dogs descended from grey wolves probably around 32 000 years ago (Thalmann, Shapiro, Cui, Schuenemann, Sawyer, Greenfield, et al., 2013; Wang, Zhai, Yang, Wang, Zhong, Liu, et al., 2016; Franz, Mullin, Pionnier-Capitan, Lebrasseur, Ollivier, Perri, et al., 2016). Although dogs show a reduced cooperativeness among each other compared to wolves (Marshall-Pescini, Schwarz, Kostelnik, Virányi, & Range, 2017; Feddersen-Petersen, 2007), they do cooperate with humans (Range et al., 2019; Ostojic & Clayton, 2014).

As mentioned above, previous studies found evidence for IA in dogs and wolves. Range et al. (2009), using an impunity-like task, found evidence for a primitive form of IA in pet dogs. Pairs of dogs from the same household were seated next to each other and alternately asked to give their paw. Depending on the condition, the dogs were rewarded or not. Dogs did not react to inequity regarding food quality or effort. However, compared to a control condition with no partner present, they stopped earlier to give the paw when they received no reward while the partner was present and still received a reward. These findings were replicated by Brucks et al. (2016).

Essler et al. (2017) found further evidence for IA in pack-living domestic dogs and wolves. They used a similar impunity-like task comparable to Range et al. (2009) and Brucks et al. (2016). However, the task itself differed, as animals were trained to press a buzzer on command instead of giving the paw. Nonetheless, the results were similar to the two previous studies, i.e. both wolves and dogs stopped earlier to perform the task when they received no reward in the presence of a rewarded partner, compared to a control condition without a partner or with a partner who received no rewards either. Essler et al. (2017) also found that wolves and dogs responded to both reward inequity and quality inequity, i.e. they also stopped earlier to perform the task when they received a lower valuable reward compared to their partner. However, as already mentioned above, this effect was weaker compared to a condition in which the subject received no reward. Interestingly, wolves responded stronger to quality inequity than dogs.

However, there are studies that do not support the claim of IA in dogs. Horowitz (2012) could not find evidence for IA in a different choice-of-trainer paradigm. In this study, two trainers rewarded two dogs. One trainer rewarded the dogs equally while the other trainer rewarded them unequally (in one combination of trainers the “unfair” trainer advantaged the partner dog, and in the other combination he disadvantaged the partner dog). After a familiarization period, dogs could choose between the fair and unfair trainer. Dogs showed no preference when they could choose between the fair trainer and the trainer who had previously advantaged them. Interestingly, when they could choose between the fair trainer and the trainer who had previously disadvantaged them, they preferred the unfair trainer. However, some confounding variables could have influenced the results, e.g. there was a difference between the total number of food rewards given by the different trainers during the training phase.

Brucks et al. (2017) also failed to demonstrate IA in pet dogs using a buzzer task comparable to Essler et al. (2017). Dogs did not stop to press the buzzer earlier when a conspecific was still rewarded for its performance. McGetrick and Range (2018) assumed that several factors might have influenced the dogs´ motivation explaining the difference in performance in this new task compared to the previous tasks, for example the visibility of rewards during the sessions. In summary, there is some evidence for IA in wolves and dogs but also evidence against such a response in pet dogs (see McGetrick & Range, 2018, for a detailed review about IA in dogs).

In the current study we wanted to investigate if pack-living wolves and dogs are sensitive to inequity in food quality in a new choice-based touchscreen paradigm. We expected that animals would show a preference for an equal reward distribution as it would not be associated with forgoing own rewards in the current experimental setting. This contrasts with lower-value food rejections in impunity-like tasks which could not be demonstrated in pet dogs (Range et al., 2009; Brucks et al., 2016), and occurred less frequently in pack living dogs and wolves compared to reward inequity responses (Essler et al., 2017). We did not expect any differences between dogs and wolves, as both are highly cooperative species. Wolves are more cooperative among each other (Mech & Boitani, 2003), while dogs show cooperativeness towards human partners (Range et al., 2019; Ostojic & Clayton, 2014; Kaminski & Marshall-Pescini, 2014; for an overview of canine cooperation see Range & Virányi, 2015). Although wolves responded stronger to quality inequity than dogs in the study of Essler et al. (2017), we do not necessarily assume this in the current experiment, as the setup is considerably different.

In our touchscreen-based task, animals could choose between two symbols. The “equity” symbol was associated with one piece of dry food (reward of low value) for the subject and one for the partner. The “inequity” symbol was associated with one piece of dry food for the subject and one piece of meat (reward of high value) for the partner. The number of inequity choices in the social test condition was compared to two control conditions. In the social control condition, the partner animals were present, but a grid prevented them from accessing the rewards. In the non-social control condition, no partner animal was present. Before the test, animals learned the different reward associations by having access to the partner´s compartment, i.e. during two training phases subjects received all rewards for themselves.

Methods

Subjects

Wolves (N=6) and dogs (N = 8) were equally hand-raised at the Wolf Science Center (WSC) in Ernstbrunn, Austria. They had been separated from their mothers at a maximum age of ten days and were bottle-fed and later hand-fed in peer groups by humans. All subjects had 24/7 contact to humans in the first five months of their life. After five months, they were introduced into the adult packs and currently live in large 2000-10000m2 enclosures. All animals still have human contact on a daily basis and receive training or partake in tests several times a week.

For the current experiment, subjects were tested together with a pack member, and in a non-social control condition. They had been living with the pack member partners for at least one year. In order to avoid reciprocity effects, we tried not to test dyads in reverse roles (except for Maisha and Binti who had no further pack mates and both reached criterion).

This study was discussed and approved by the institutional ethics and animal welfare committee at the University of Veterinary Medicine Vienna in accordance with Good Scientific Practice guidelines and national legislation.

Experimental setup

The same mechanical touchscreen as used by Dale, Palma-Jacinto, Marshall-Pescini, and Range (2019) was implemented for the current experiment (length x width = 42.00 cm x 54.70 cm; length x width of the two choice fields = 26.00 cm x 20.00 cm). It was built and programmed at the Comparative Cognition Unit, Messerli Research Institute of the University of Veterinary Medicine, Vienna. In the test, two symbols associated with different reward distributions (an equal versus an unequal distribution) were presented to the animals. Subjects could make their choice by pressing their nose against one stimulus or the other. All subjects were already familiar with using the touchscreen, and had made discriminations on the touchscreen before (e.g. Dale et al., 2019). The semi-automated setup facilitated to reduce potential human handling biases.

As the touchscreen was permanently fixed, the subjects were placed in the touchscreen room plus outside compartment (E1 + O1), while the partner was in an adjacent room plus outside compartment (E2 + O2; Figure 1). As especially wolves do not appreciate to be locked in a room, the outside compartments promoted a more relaxed testing atmosphere. The animals were separated by metal bars inside and by a wire mesh fence outside. That allowed visual, olfactory, and auditory contact, but only minor direct physical contact.

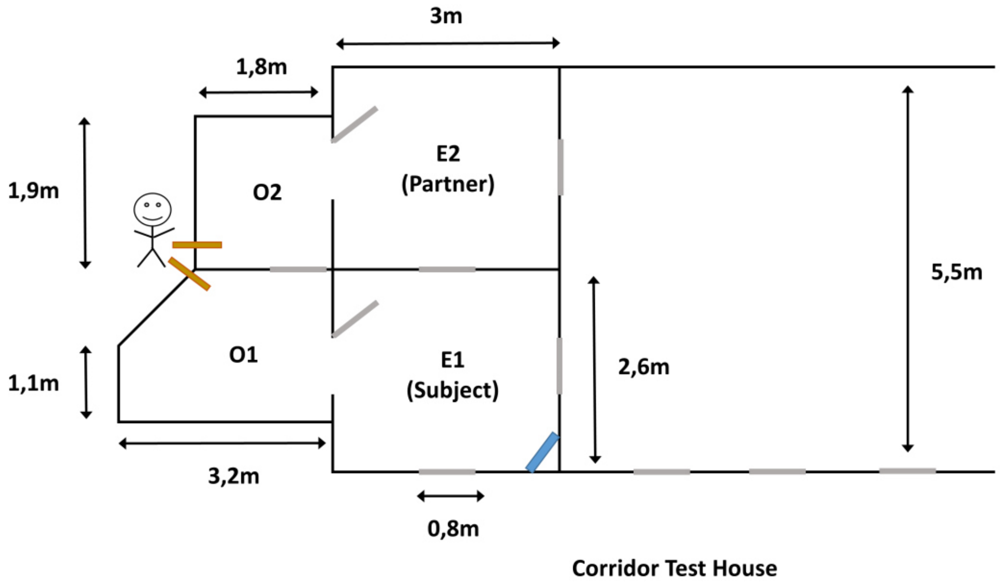

Figure 1. Experimental setup of the touchscreen task. The subject is in E1 (inside) and O1 (outside). The partner animal is in E2 (inside) and O2 (outside). The experimenter is sitting in front of and rewarding in O1 and O2. Rewards are delivered on wooden sticks (red bars). The touchscreen is permanently fixed in E1 (blue bar).

Similar to Dale et al. (2019) each subject was randomly assigned two stimuli (an “equity” and an “inequity” symbol) from a pool of three stimuli in the current experiment (heart, explosion, and hourglass). Figure 2 shows a wolf (Aragorn) choosing the explosion symbol on the touchscreen. Due to unexpectedly high dropout rates and necessary symbol re-assignments (see below), the three symbols were not equally distributed among subjects. The stimuli were presented together on semi-randomized sides, so that one stimulus did not appear on the same side more than twice in a row. For each session, the touchscreen program automatically recorded the number of trials for which the subject chose either symbol. All animals were naïve in relation to the posed questions and symbols.

Figure 2. Wolf Aragorn chooses the explosion symbol on the touchscreen (photo credit: Rooobert Bayer).

Training

Training was separated in two phases.

Training phase 1: Subjects were trained to learn the rewards associated with each symbol. Therefore, each symbol was presented against an empty white screen and semi-randomly appeared ten times, five times on the left side of the touchscreen, and five times on the right side of the touchscreen. We used a clicker to signal a correct choice, i.e. pressing the symbol side and not the empty side with the nose, and rewarded the subject accordingly. The reward depended on the symbol presented. For the “inequity” symbol the subject received a piece of meat in O2, followed by a piece of dry food in O1 (see Figure 1). For the “equity” symbol the subject received a piece of dry food in O2, followed by a piece of dry food in O1. The rewards were delivered on two wooden sticks, one for O1 and one for O2 (except for Amarok who was the partner of Kenai and would have destroyed the sticks; the food was manually thrown into the compartment for him). During this phase, the door between the subject and partner rooms (O1 and O2) was open, giving the subject access to both rewards after a correct choice. When they made an incorrect choice, i.e. chose the empty side of the touchscreen, there was no reward. Following either choice, after 6-8 seconds of a white screen, the next trial was presented. To pass training phase 1, subjects had to choose the side with the symbol in 90% of the trials, i.e. 18/20, in two consecutive sessions without using the clicker as secondary reinforcement. It was important to fade out the clicker for the following training and test phases, as animals could then choose between symbols, i.e. there was no wrong choice anymore. Furthermore, they had to readily move to the O1 and O2 compartments and consume their rewards. Animals that did not reach training phase 1 criterion within 10 sessions were excluded from testing.

Training phase 2: The sessions started with four “reminder trials” identical to training phase 1, i.e. one of the symbols was presented against an empty side (each symbol appeared twice, once on the left side of the touchscreen and once on the right side). After these initial reminder trials, both symbols were presented at the same time, so that the subjects could choose between the “inequity” and the “equity” symbol. By doing so we wanted to make sure that the animals understood the different rewards associated with the two symbols. Each symbol was presented ten times on each side of the touchscreen in a semi-randomized order. To pass training phase 2, the subjects had to show a preference for the “inequity” symbol, i.e. choosing it in 75% (15/20) of the free choice trials in three consecutive sessions. As subjects still had access to the rewards in O1 and O2 in training phase 2, the inequity symbol was associated with a better reward, i.e. a piece of meat and a piece of dry food instead of two pieces of dry food (previous food preference tests showed that wolves and dogs prefer a piece of meat over a piece of dry food, see Rao, Range, Kadletz, Kotrschal, & Marshall-Pescini, 2018). However, several animals did not reach criterion in training phase 2, and sometimes even showed a marked preference for the less valuable “equity” symbol (even though they sometimes omitted the dry food reward but never the meat reward). If there was no tendency to shift preferences in favor of the more valuable “inequity” symbol after five sessions, we assigned a new “equity” symbol to the particular animals. By doing so we tried to overcome potential symbol preferences that were independent of the associated rewards (see e.g. Langbein, Siebert, Nürnberg, & Manteuffel, 2007). For this new symbol, animals received a reduced dry food reward, i.e. a smaller piece of dry food, to make the different rewards between symbols even more obvious. As a consequence of the new symbol assignment, the particular subjects were downgraded to training phase 1 and had to reach criterion again. Animals that did not reach criterion with a new “equity” symbol were excluded from testing. Although this new symbol assignment can be criticized, we preferred it over immediately excluding the particular animals and further reducing our sample.

We started the training with 13 wolves and 13 dogs. One wolf died during the period of testing (Ela). From the 12 remaining wolves, three animals did not reach the criterion of training phase 1 within 10 sessions (Amarok, Geronimo, and Yukon). From the nine wolves that reached the criterion of training phase 1, we excluded one animal from the training/ testing as she did not feel comfortable in the test room and thus was not working reliably (Una). Four animals (Kaspar, Aragorn, Tala, and Shima) showed a strong preference for the less valuable food in training phase 2, so we decided to change their equity (low value) symbol and associate it with a smaller piece of dry food. With the new symbol assignment, two wolves (Kaspar and Aragorn) reached criterion, while the other two wolves (Shima and Tala) did not. These two were excluded from testing. Another wolf (Nanuk) had to be excluded although he reached criterion in training phase 2, as there was no suitable partner animal for him. Thus, only six out of 13 wolves could be tested in the end. From the 13 dogs, two individuals had to be excluded as they left the Wolf Science Center due to medical reasons during training (Nia and Nuru). Another dog (Panya) was excluded during training phase 1 as she was not food motivated enough and refused to eat the rewards. In training phase 2, two individuals (Meru and Sahibu) showed a strong preference for the less valuable food. Like with the wolves, we changed their equity (low value) symbol and associated it with a smaller piece of dry food. One dog (Meru) still did not change his preference and was excluded from testing. The other dog (Sahibu) did change his preference but refused to eat the new dry food pieces, so he was excluded as well. Thus, eight out of 13 dogs participated in the test.

Test

We used a within-subjects design so that each subject participated in one session of all three conditions. Structurally, all test sessions were identical to training phase 2, consisting of four forced-choice reminder trials and 20 free choice trials. Different from training phase 2, the door between O1 and O2 was closed. In the social test condition, a partner animal received the rewards in O2. The two other conditions were control conditions. In the social control condition, a metal grid was attached to the reward delivery area in O2. As in the social test condition, the reward was presented on a wooden stick, however, the partner animal was not able to access it anymore. In the non-social control condition, there was no partner present and the reward delivery stick was slid into O2 and slid out again.

Conditions were presented in a counterbalanced order across dyads. For a better overview, Table 1 shows the subjects' details, their order of conditions, and their symbol assignments. A session ended when a subject refused to choose a symbol within five minutes or showed signs of distress. Each test/ control session was followed by a motivation session. In the two social conditions, the partner animal was brought back to its home enclosure before the motivation session started. Motivation sessions were identical to training phase 2 sessions, i.e. the door between the subject and partner compartments (O1 and O2) was opened and the subject had access to all rewards. However, they only consisted of four forced-choice and six free choice trials to not protract the total test time for the subjects. The purpose of these motivation sessions was to bring the subjects back up to their baseline level of performance and motivation before the next condition. By doing so, any impact of previous test sessions on the following test sessions should be reduced. Note that the experimental design in the current study (in contrast to Dale et al., 2019) was not a classical extinction of a previously rewarded behavior, as the subjects still received their dry food reward in O1. However, they did receive a quantitatively and qualitatively reduced reward compared to training phase 2.

Table 1. The subjects´ details, their order of experimental conditions, and their assigned equity and inequity symbols are listed. Red highlighted names refer to female individuals; blue highlighted names refer to male individuals.

Species	Subject	Partner	1st condition	2nd condition	3rd condition	Equity symbol	Inequity symbol
Wolf	Kaspar	Shima	Social test	Social control	Non-social	✸	♡
Wolf	Aragorn	Shima	Social control	Social test	Non-social	⧗	✸
Wolf	Chitto	Tala	Non-social	Social test	Social control	♡	✸
Wolf	Wamblee	Yukon	Social control	Non-social	Social test	✸	⧗
Wolf	Kenai	Amarok	Non-social	Social control	Social test	⧗	♡
Wolf	Etu	Ela	Social test	Non-social	Social control	✸	⧗
Dog	Enzi	Nuru	Non-social	Social control	Social test	♡	⧗
Dog	Pepeo	Enzi	Social test	Social control	Non-social	✸	♡
Dog	Zuri	Pepeo	Non-social	Social test	Social control	⧗	♡
Dog	Binti	Maisha	Social test	Non-social	Social control	✸	⧗
Dog	Maisha	Binti	Social control	Non-social	Social test	⧗	✸
Dog	Hiari	Meru	Non-social	Social control	Social test	⧗	♡
Dog	Imara	Meru	Social control	Social test	Non-social	⧗	♡
Dog	Gombo	Nia	Social test	Social control	Non-social	⧗	✸

Almost all animals completed the 20 free choice trials per condition. From the wolves, Chitto stopped after four trials in the social test condition and after three trials in the social control condition, and Kenai stopped after eight trials in the social test condition. From the dogs, only Zuri stopped after 15 trials in the non-social control condition. As the total sample size is small anyway, we refrained from removing these incomplete sessions from our analyses. To reasonably access differences in choice behavior between animals who completed all sessions, and animals who stopped performance in particular sessions, a larger sample size would be necessary.

Statistical analysis

We calculated a General Linear Mixed Model (GLMM) to assess main effects and a potential interaction effect of condition (social test, social control, non-social control) and species (wolf, dog). Furthermore, we compared the number of equity choices in the three experimental conditions with the number of equity choices in training phase 2 (i.e. choosing two pieces of dry food instead of one piece of dry food and one higher valuable piece of meat) with pairwise *t*-tests. We expected an increase in equity choices in the social test condition, but not necessarily in the two control conditions. We also tested potential time effects: We ran a GLMM to test potential effects of the order of conditions (e.g. an increase of equity choices over time). We also checked whether equity choices changed in the course of a session by comparing the first and last ten trials of each condition via *t*-tests. Data was analyzed and visualized with IBM SPSS Statistics 25 and Sigmaplot 14.0.

Results

In the social test condition animals chose the equity symbol in 15.18% of the trials (*SD*=8.91%). Wolves chose the equity symbol in 10.42% of the trials (*SD*=5.57%), and dogs chose the equity symbol in 18.75% of the trials (*SD*=9.54%). In the non-social control condition animals chose the equity symbol in 15.00% of the trials (*SD*=13.59%). Wolves chose the equity symbol in 15.83% of the trials (*SD*=17.73%), and dogs chose the equity symbol in 14.38% of the trials (*SD*=10.84%). In the social control condition animals chose the equity symbol in 14.64% of the trials (*SD*=14.47%). Wolves chose the equity symbol in 8.33% of the trials (*SD*=6.06%), and dogs chose the equity symbol in 19.38% of the trials (*SD*=17.41%).

Descriptively, wolves seemed to make more equity choices in the non-social condition compared to both social conditions. With dogs it was the other way around; they seemed to make more equity choices in both social conditions compared to the non-social condition (Figure 3). However, the variance is large and a GLMM revealed no significant interaction between species and condition (*F*(2,24)=1.72, *p*=.20), no significant effect of condition (*F*(2,24)=0.06, *p*=.94), and no significant effect of species (*F*(1,12)=1.29, *p*=.28).

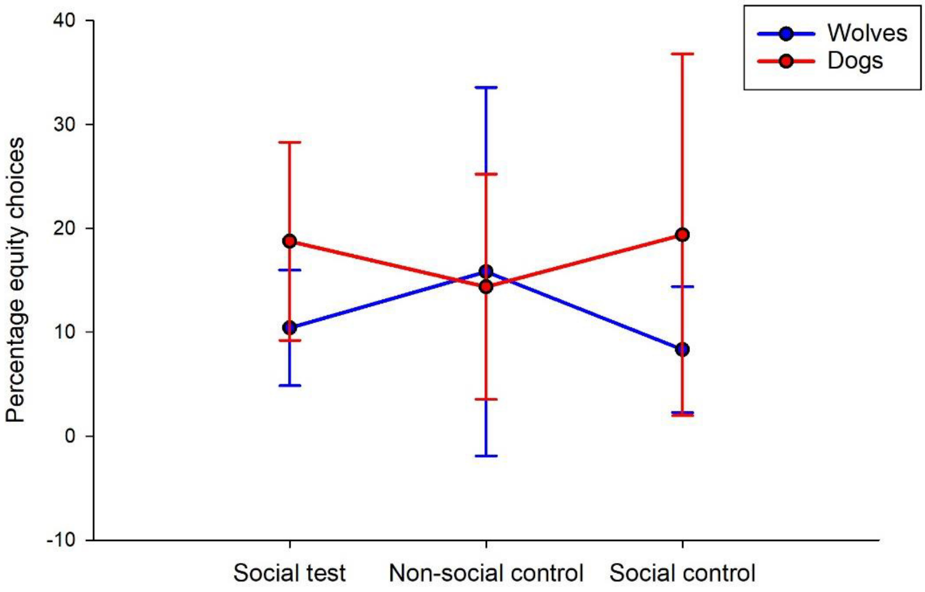

Figure 3. Equity choices over all experimental conditions for wolves and dogs. The three conditions are depicted on the x-axis and the percentages of equity choices are depicted on the y-axis. The blue line shows the equity choices of wolves and the red line the equity choices of dogs. Error bars in the particular colors represent the standard deviation of mean (*SD*).

One sample *t*-tests revealed that equity choices of all three conditions were significantly below 50% chance level for wolves (social test: *t*(5)=-17.40, *p*<.008; non-social control: *t*(5)=-4.72, *p*<.008; social control: *t*(5)=-16.86, *p*<.008) and dogs (social test: *t*(7)=-9,26, *p*<.008; non-social control: *t*(7)=-9.30, *p*<.008; social control: *t*(7)=-4.98, *p*<.008). The alpha level was Bonferroni-corrected according to the six comparisons (0.05/6 = 0.008). Equity choices were normally distributed for all experimental conditions in wolves and dogs (Shapiro Wilk test, *p*>.05).

We calculated repeated measures *t*-tests to assess whether equity choices in the three experimental conditions differed from the average equity choices of the last three training phase 2 sessions (i.e. choosing two pieces of dry food instead of choosing one piece of dry food and one piece of high value meat) for wolves and dogs. In wolves and dogs, the number of equity choices in all experimental conditions did not significantly differ from the number of equity choices in training phase 2 (wolves: social test vs. training: *t*(5)=1.24, *p*=.27; social control vs. training: *t*(5)=0.34, *p*=.75; non-social control vs. training: *t*(5)=1.46, *p*=.21; dogs: social test vs. training: *t*(7)=1.97, *p*=.09; social control vs. training: *t*(7)=1.27, *p*=.24; non-social control vs. training: *t*(7)=0.62, *p* =.55).

We further analyzed whether equity choices changed over time (first, second, and third test session) independently of condition. We found no significant interaction between session and species (*F*(2,24)=0.31, *p*=.74), and no significant effect of session (*F*(2,24)=1.64, *p*=.21). Furthermore, we wanted to analyze if the number of equity choices changed over the course of a session. We calculated a repeated measures *t*-test for each condition and each species to compare equity choices of the first and second ten trials. In wolves and dogs, the number of equity choices in all experimental conditions did not significantly differ between the first ten trials and the last ten trials (wolves: social test: *t*(3)=0.00, *p*=.99; social control: *t*(4)=-1.00, *p*=.37; non-social control: *t*(5)=0.54, *p*=.61); dogs: social test: *t*(7)=0.00, *p*=.99; social control: *t*(7)=-1.93, *p*=.10; non-social control: *t*(7)=-1.69, *p*=.14).

Discussion

It becomes obvious that equity choices over all conditions occurred infrequently (under chance level), which can be interpreted as a floor effect. Against our expectations, there was no difference between the choice behavior in training phase 2 and all test conditions. This might be due to the fact that animals learned to press the inequity symbol in the training procedure as it was associated with the high value (later unequal) reward. It is conceivable that they simply got stuck with their preferred symbol. Either they were not able to adapt their choices according to the different reward allocation during test conditions, or there was no need for them to do so, i.e. they did not really exhibit IA in the current task. Notably, in previous touchscreen-based tasks there was always a right symbol and a wrong symbol associated with no reward (e.g. Dale et al., 2019). Accordingly, the animals were unfamiliar with the current scenario in which there was no wrong choice in terms of discrimination learning (for an overview see Sutherland & Mackintosh, 2016) but different outcomes per choice. This might have influenced choice behavior in a way that our animals were less flexible in their choices compared to naïve animals or animals that had been familiar with choices between different rewards. A certain fixation on the initially more profitable symbol is also supported by the fact that choice behavior did not change over time, neither within a session nor between sessions. However, it is also known from other studies that it is difficult for animals to consider what a partner gets compared to themselves (see e.g. Quervel-Chaumette, Mainix, Range, & Marshall-Pescini, 2016; Drayton & Santos, 2014). This raises the question if the current design was simply too complex for our subjects.

Choice behavior did not significantly differ between species and/ or conditions. It could be possible that wolves and dogs do not show IA in such a choice-based paradigm, i.e. that they do not really care about the reward of another individual. As previous impunity-like tasks on IA and one choice-based study revealed heterogeneous results (Range et al., 2009; Horowitz, 2012; Brucks et al., 2016; Essler et al., 2017; Brucks et al., 2017), this would not be completely astonishing. However, we consider it more plausible that faint IA motives had been masked by various aspects in the current setup.

First, the above-mentioned unfamiliarity and difficulty of tasks with different reward contingencies could have biased the animals in favor of the inequity symbol. Their experience with discrimination learning, i.e. only one correct choice, may have hindered the animals to express potential IA in this choice-based task. This is in line with literature on learning in different species. Animals tend to use previously learned information for subsequent learning in form of a problem-learning strategy (e.g. Langbein et al., 2007 (dwarf goats); Dixon, 1970 (horses)). In the current experiment, the strategy of our wolves and dogs could well be that one option is always correct and the other is always wrong. For future studies this could for example be controlled by an extended training procedure aiming at choice flexibility. This would also be useful for other tasks. Concretely, the animals would learn different symbols associated with different rewards and reward areas. By providing or refusing access to the particular reward areas over sessions, i.e. closed or opened doors, the animals might learn to flexibly adapt their choices to the given circumstances. In a second step, partner animals could be introduced to this setup to test for social preferences.

Secondly, the sample size of the current study was rather small. Equally hand-raised wolves and dogs are rare anyway, and furthermore, many animals did not reach training criterion and had to be excluded from testing in the current experiment. As several animals seemed to show an unexpectedly strong preference for dry food in training phase 2, we had a closer look at the assigned symbols. Interestingly, from the six animals who had to receive new dry food symbols, four avoided the same inequity symbol in the first place, the hourglass. We therefore suspect that there was something about that symbol which stimulated the animals to not choose it. We can only speculate that the shape of the hourglass might have been different compared to the other two symbols in a way that it is narrow in the middle and thus could have appeared two-parted. It is difficult to prevent such symbol related preferences which are obviously independent of reward associations and unfortunately not unusual (Langbein et al., 2007). Again, a more flexible experimental setup as described above, might help to detect and reduce such preferences as animals would learn to flexibly adapt their choices to the given circumstances and not get stuck to one symbol for whatever reason. However, it also remains elusive if training performance and IA might be correlated. This would have led to a selective sample in the current task, and would also lead to a selective sample in a more flexible task if substantial drop out rates occurred. It is known from the human literature that some studies could confirm a link between social preferences and cognitive abilities (e.g. Chen, Chiu, Smith, & Yamada, 2013; Ben-Ner, Kong, & Putterman, 2004; Brandstätter & Güth, 2002; but see Benjamin, Brown, & Shapiro, 2013). This is actually a severe problem, as it would be logically impossible to compare social preferences of animals that reached learning criterion with animals that did not. However, with a greater sample size it would at least be possible to compare fast learners and slow learners regarding their social preferences.

Besides that, we can also not exclude that reward differences between animals might have influenced the results. Two out of six wolves received a smaller dry food reward compared to the rest of the animals, as they had previously shown a strong preference for the "better" dry food reward over meat. Although objectionable, we preferred this approach over entirely excluding them from testing and further reducing our small sample.

Frustration (Roma et al., 2006) and reward expectation (Bräuer et al., 2006) most certainly played a role in the current setup. As animals received a better reward during training when choosing the inequity symbol, they were confronted with a relative reward devaluation in all three test conditions. However, this effect is assumed to be consistent over conditions and thus less crucial. Of course, it would have been possible to directly confront the animals with the test conditions without a previous learning procedure. One could have performed several sessions of a condition following the assumption that at some point the animals would come to understand the outcomes. However, in our opinion this would have been even more problematic, as we would have been completely naïve to any symbol preferences which evidently occurred in the current experiment.

In summary, it can be stated that the current study unfolds important aspects to improve and develop touchscreen-based social choice paradigms. We judge it as highly promising to pursue such paradigms. They offer the possibility of automation (when sufficiently developed), and thus enable to collect substantial data with little effort and with reduced human influence (for examples of automated tasks see Yang, Silverman, & Crawley, 2011; Gazes, Brown, Basile, & Hampton, 2013; Martin, Biro, & Matsuzawa, 2014; Mendonça, Dahl, Carvalho, Matsuzawa, & Adachi, 2018). Admittedly, the current design is not yet methodologically sound enough to tackle the question if wolves and dogs prefer equal over unequal outcomes in a social context. Nevertheless, we consider it highly important to share our findings in order to raise awareness about how important a well-designed setup is and how many factors might actually influence the behavior which subjects show in a certain test situation.

Author contributions

Lina Oberliessen designed the study, conducted the experiments, analyzed the data, developed the first concept of the article, wrote the article, and revised the article. Friederike Range designed the study, wrote the article, and revised the article.

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Chapter 4: Dyad-sex composition affects the development of egalitarianism in young children

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Abstract

In decisions between equal and unequal outcomes, women have been shown to choose more compassionately, and men more competitively, but the developmental origin of such gendered fairness preferences remains unclear. We hypothesized that these preferences are moderated by same- and cross-sex dyadic interaction experiences during childhood. To examine this possibility, we tested 332 three to eight-year-old children in a paired resource allocation task. Using a model-based approach, we found that egalitarian preferences depended on both the sex of the decision-maker and of their dyadic interaction partner, rather than just on the decision-maker's sex per se. Fairness attitudes were often congruent with that of the partner in the dyads, e.g. girls were more envious with boys than with other girls, matching the predominantly envious attitude of boys, and boys were more spiteful with other boys than with girls, matching the more spiteful attitude of boys compared to girls. However, other sex-specific fairness attitudes mismatched across sexes within a dyad, e.g. girls treated boys compassionately, despite the boys' indifferent or even malevolent choices. This pattern of diverging egalitarian choice preferences is congruent with the idea that sex-specific fairness preferences are influenced by same- and cross-sex past interaction experiences, but possibly also by acquired gendered social norms that can come to override those interactive experiences.

Keywords: egalitarianism, inequity aversion, sex differences, sex-dyad effects, development of fairness

Introduction

A mechanism for detecting unfairness is essential for establishing and maintaining long-term cooperation in larger groups (Nowak, 2006). Humans and several other social species reject disadvantageous unequal reward distributions (disadvantageous or 'first-order inequity aversion (IA)': the dislike of being worse off than others, given comparable efforts; Brosnan & de Waal, 2014; Oberliessen, Hernandez-Lallement, Schäble, van Wingerden, Seinstra & Kalenscher, 2016). But only humans and, possibly, very few other species have developed a complete fairness concept, including the rejection of unequal advantageous distributions (advantageous or 'second-order IA': the dislike of others being worse off; Brosnan & de Waal, 2014; Fehr & Schmidt, 1999; Proctor, Williamson, de Waal & Brosnan, 2013; but see Ulber, Hamann & Tomasello, 2017; Bräuer & Hanus, 2012). In humans, IA is usually studied through resource allocation tasks in which predefined fair or unfair resource allocations can be either accepted or rejected (Bolton, Katok & Zwick, 1998; Güth, Schmittberger & Schwarze, 1982). In these studies, adult female decision-makers generally show more compassionate, and males more competitive behavior, such as envy or even spite (Soutschek, Burke, Beharelle, Schreiber, Weber, Karipidis, et al., 2017; Rand, Brescoll, Everett, Capraro & Barcelo, 2016; Croson & Gneezy, 2009; Saad & Gill, 2001a; Saad & Gill, 2001b).

Emergence of sex differences in social preferences

Recent insights suggest that such adult sex-differences in social preferences are acquired during childhood and adolescence (Rand et al. 2016; Eagly, 1987). Children start to act fairly between the ages of 3-8 (Fehr, Bernhard, & Rockenbach, 2008; Blake & McAuliffe, 2011; McAuliffe, Blake, Steinbeis & Warneken, 2017), a period that coincides with differentiation in sex-specific behaviors (Martin, Wood & Little, 1990; O'Brien, Peyton, Mistry, Hruda, Jacobs, Caldera, et al., 2000; Bian, Leslie & Cimpian, 2017), but when and, in particular, how fairness preferences start to diverge between sexes is still an open question. Recent theories posit that social preferences are likely shaped by past social interaction experiences with same- and opposite-sex others during development (Rand, Peysakhovich, Kraft-Todd, Newman, Wurzbacher, Nowak, et al., 2014; Rand, 2016), highlighting the putatively moderating influence of the sex of dyadic interaction partners on molding egalitarian attitudes. Other accounts hold that additional factors, such as acquired social gender norms and social stereotypes, could influence sex-specific fairness preferences beyond direct experience with same- and cross-sex others (Martin et al.,1990; O'Brien et al., 2000; Bian et al., 2017). To better understand the modifiers of egalitarian preferences, we explored the development of these preferences during childhood, focusing explicitly on the dyad-sex composition in same- or cross-sex interactions. We hypothesized that the moderating effect of the sex of dyadic interaction partners on fairness preferences would become evident in the comparison of egalitarian choice patterns for same-sex vs. opposite sex dyads.

Testing the influence of dyad-sex composition on egalitarian preferences

Previous research has highlighted sex differences in adult egalitarian preferences, but so far, very little is known about the role of the sex of dyadic interaction partners (dyad-sex composition) in fairness preferences. This is puzzling, as the sex of the interaction partner is an obvious trait that could contextualize egalitarian preferences, potentially reflecting gendered stereotypes of these interaction partners. The studies we reviewed did not report sex differences in resource allocation tasks, or they used preference elicitation methods that omitted information about the interaction partners' sexes, as for example in hypothetical partner scenarios (Cherneyak & Sobel, 2015; Kenward & Dahl, 2011; Rizzo & Killen, 2016; Elenbaas, Rizzo, Cooley & Killen, 2016; Baumard, Mascaro & Chevallier, 2012; Paulus & Moore, 2014; Shaw & Olson, 2012). Hence, to date, the potential moderating influence of dyad-sex composition on the development of egalitarian preferences remains elusive, even though it is known from other experimental contexts, e.g. bargaining, that dyad-sex composition, more than sex per se, plays an important role in explaining the observed behavior (Sutter, Bosmann, Kocher & van Winden, 2009). To study the effect of dyad-sex composition on egalitarianism, we implemented a typical resource allocation task which is widely used to measure social preferences in children (Fehr et al., 2008; Moore, 2009; House, Henrich, Brosnan & Silk, 2012).

Methods

Participants

We tested 332 children between three and eight years (females = 176, males = 156; mean age = 71.95 months, s.e.m. = 1.05 months, range = 37 – 111 months). Thirty-six children who could not answer all control questions correctly (see below) and 17 children who had a distinctly positive or negative relationship with their assigned partner were excluded from data analysis.

The remaining sample of 279 children (females = 146, males = 133) was separated into three age groups: (1) 3-4 years old (39 – 59 months): females = 32, males = 33, mean age = 51.46, s.e.m. = 0.68; (2) 5-6 years old (60 – 83 months): females = 56, males = 56, mean age = 72.60, s.e.m. = 0.70; (3) 7-8 years old (84 – 111 months): females = 58, males = 44, mean age = 93.11, s.e.m. = 0.62. The relatively lower sample size of the youngest age group results from a higher exclusion rate due to comprehension problems (inability to answer all control questions correctly).

Data were collected in five primary schools and eight daycare facilities for children in urban, middle- to upper-middle class areas (Düsseldorf, Germany). With the consent of the school / daycare facility administration, information letters were sent to the parents of the children requesting permission for their child´s participation in the study. In these, the parents were informed about the experimental procedure, anonymization and data storage policies. Our study was approved by the Ethics Committee for non-invasive human research of Heinrich-Heine-University, Düsseldorf.

Procedure & Apparatus

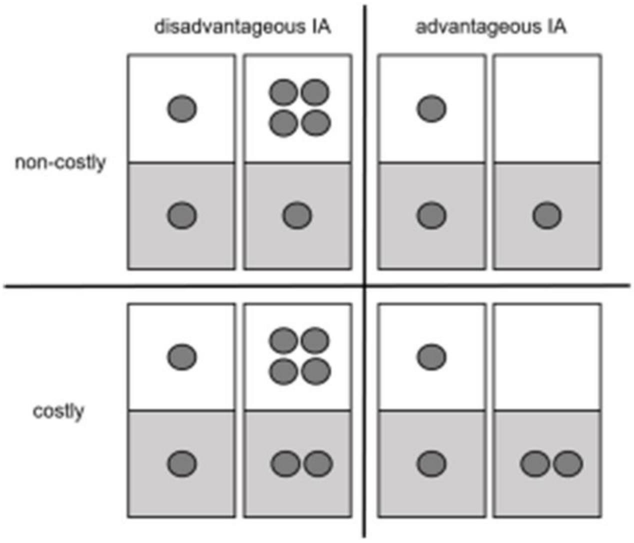
Children participated in the study in same- or cross-sex pairs. To minimize potential reputational concerns, like merit considerations, effort and need which might influence children´s decisions above and beyond IA (Kenward & Dahl, 2011; Rizzo & Killen, 2016;

Elenbaas et al. 2016; Baumard et al. 2012; Kienbaum & Wilkening, 2009), we only considered pairs of children who had little or no previous connection, none of them were friends or felt aversion against each other. We therefore opted for pairs from different groups/ classes so that there was no relationship between children. However, this was not feasible in all facilities. For pairings from one and the same group we asked the responsible caretaker for an evaluation of the relationship of the paired children on a 10 cm-rating-scale from -5 to +5 afterwards (-5 = maximally negative relationship, 0 = neutral relationship, +5 = maximally positive relationship). We excluded children with distinctly positive or negative relationships represented by values above +2.5 or below -2.5.

The inequity aversion (IA) choice task took place on a table in a separate room within the particular facility. It consisted of two choice boxes with two equally sized compartments of different colors (white and green) and two separate collection boxes (Figure 1a). Yellow smiley stickers were used as reinforcers to construct, in total, four reward distributions (Figure 1b). We manipulated the type of inequality (advantageous versus disadvantageous) and cost (costly versus non-costly equal outcomes, relative to the own-outcome in the unequal distribution). Two unequal distributions present disadvantageous or advantageous inequality choices. Similarly, two distributions were non-costly or costly and all choice options were pitted against a fair 1:1 alternative resulting in a 2x2 choice design:

- Disadvantageous IA (envy) non-costly (1:1 vs. 1:4 stickers)
- Advantageous IA (compassion) non-costly (1:1 vs. 1:0 stickers)
- Disadvantageous IA (envy) costly (1:1 vs. 2:4 stickers)
- Advantageous IA (compassion) costly (1:1 vs. 2:0 stickers)

(a)



(b)

Figure 1. Experimental arrangement of the IA choice task. The experimenter (brown chair) sat opposite the subject (actor, green chair) performing the IA choice task while the partner worked on the distraction task at the same time in the same room (1a). Reward distributions differed in type of inequality and cost (1b). In each trial, the actor selected one of two boxes with different reward distributions. The grey part of each box depicts the actor´s outcome, the white part the partner´s outcome. All unfair choice options were pitted against a fair 1:1 alternative. The unfair distributions yielded either disadvantageous IA (left), or advantageous IA (right) outcomes and were either non-costly (top), or costly (bottom).

The whole experimental procedure followed a standardized protocol. The children were welcomed and asked if they wanted to participate. They were informed that the current study was a university project to investigate how children make decisions and distribute rewards (yellow smiley stickers) between themselves and another child by choosing one of two boxes with different distributions of stickers. It was randomly decided which child started with the IA choice task. The experimenter was always the same female person. She sat opposite the subject in the IA choice task and first informed the participants that they could stop the experiment any time. She explained that in each box, one side (white) contains the stickers for the other child (partner´s name is used), whereas the other side (green) contains the stickers for the actor (the child making the decision). The number of trials was not communicated but children were informed that they could keep the stickers subsequent to the experiment. For all four trials, the experimenter verbally informed the participant of the amount of stickers for each child in each box. Before children made their decision by pointing at one of the boxes, they had to repeat the amount of stickers they themselves and the other child would receive in each option. This control question allowed to evaluate task comprehension. After each choice, the experimenter transferred the stickers from the selected decision box to the collection boxes without any feedback and arranged the next distribution in the choice boxes. The order of distributions as well as the presentation side (left or right) of the equal distribution was counterbalanced among children. After the last decision of the fist decider, the stickers from the collection boxes were put in envelopes. Children switched position and the second child likewise performed the decision task. Envelopes were handed over to the subjects after the second child had also finished the decision task and all stickers were collected in the envelopes. Depending on the choices the number of stickers per child varied between 6 and 16. The task-related effort was the same for all tasks and participants.

The picture distraction task (German version of "Where´s Waldo", Martin Handford, 8th edition, 2010) took place in the same room at another table, or on the carpet on the floor. However, tables were arranged in a way that the children were not sitting within their field of view to avoid any interaction and to keep choices private. The partner child worked on the picture distraction task together with a second experimenter, alone or with a local teacher. They were briefed to try to find Waldo on the pictures, highlight him with a marker and then turn over to the next page.

Data analysis

To condense choice data, we used the Fehr-Schmidt-model of inequity aversion (Fehr & Schmidt, 1999) to compare levels of disadvantageous (αi parameter, level of envy of subgroup i) and advantageous inequity aversion (βi parameter, level of compassion of subgroup i) of different subgroups (age, sex, sex recipient):

$$U_i(x) = x_i - \alpha_i \max\{x_j - x_i, 0\} - \beta_i \max\{x_i - x_j, 0\}, \quad i \neq j,$$

where $U_i(x)$ represents the utility of outcome x to player i as a function of the magnitude of x, reduced by the amount of units the decision maker is worse off relative to the payoff to player j (x_j - x_i) weighed by the α-parameter, and reduced by the amount of units the decision maker is better off (x_i - x_j) weighed by the β-parameter. Thus, the weighing parameters α and β capture the individual sensitivity to disadvantageous inequality (α), or advantageous inequality (β), respectively, that is, how much the utility of x is reduced by each type of inequality. Note that we allow β-parameter values to become negative, indicating that individuals might derive utility from being better off than the other player as children have occasionally been reported to derive utility from being better off than others (Sheskin, Bloom & Wynn, 2014). One choice alternative can thus only load on the α OR β-parameter (depending on whether $x_j > x_j$ or $x_i > x_j$), and one needs a set of choices that features both disadvantageous and advantageous unequal options to concurrently estimate both parameters.

In the following, α-parameter values (disadvantageous IA) will be labeled "envy", in line with the nomenclature used by previous studies, and β-parameter values (advantageous IA) will be labeled "compassion", or with negative sign, "spite" (e.g. Fehr & Schmidt, 1999; Fehr et al., 2008; West & Gardner, 2010). Despite the allusion to social affect inherent to this terminology, we strongly emphasize that the Fehr-Schmidt model is agnostic to whether the children's choices were indeed guided by these emotional motives or not; here, we use these terms in a purely descriptive sense to characterize the children's behavioral sensitivity to unfair outcome distributions that are in their favor or to their disadvantage. In line with Fehr and Schmidt (1999), Fehr et al. (2008), and West and Gardner (2010), we prefer these terms over more technical terms, such as advantageous or disadvantageous inequity aversion, for the sake of clarity and accessibility of our report.

Because children made only one choice per outcome distribution, it is not possible to model α and β at the subject level. However, population scores can be constructed by averaging across individual decisions in a certain subgroup, and the population scores can then be modeled to obtain values for α and β. To estimate variability in α and β for a given subgroup, we applied a bootstrap approach with resampling, essentially repeating the modelling step for a randomized subsection of the original group and aggregating the obtained α and β values in a distribution from which we report the mean and variance.

To obtain a distribution of choices within subgroups we sampled N=5000 draws of 150 randomly selected choices (with resampling) within the particular subgroups. For example, the target group of interest could be all choices made by children in the middle age group, all choices made by actors (male or female) paired with female partners or all choices made by male-male dyads in the highest age group. For each bootstrap, the N=150 choices were pooled and averaged. The resulting percentage choices for the equal alternatives were fit using a least-squares regression method optimizing the parameters of a sigmoidal softmax decision function linking the utility differences through the noise parameter μ:

$$P(Equity) = \frac{1}{1+e^{\mu*(U_i-U_e)}},$$

where U_i is the utility of the unequal option (see equation above), U_e is the utility of the equitable option (1/1) and μ is the noise parameter indicating choice inconsistencies (the lower μ the higher the inconsistencies).

Different to Fehr and Schmidt (1999), we did not place a limit on either α or β and, as mentioned above, also allowed β to be < 0 to capture spite (negative compassion) occasionally reported in children (Sheskin et al., 2014). Instead, we rejected and re-drew bootstraps iterations where the fit returned a μ parameter smaller than 0.2, indicating very large differences between U_i and U_e due to extreme and unreasonable values in α and/or β. The resulting α and β parameter distributions followed a normal distribution shape. This allowed us to define a population median and a standard deviation (to be construed as the standard error). For statistical comparisons of the differences between subgroups (for example, male actors partnered with male vs. female partners), we added a permutation step in each bootstrap. Briefly, the binary labels indicating the target variable (partner sex in this example) were shuffled and reassigned in a randomly permuted way to the pairs, keeping the number of equitable and inequitable choices intact. Then, the sample was split according to the target variable and the Fehr-Schmidt model was run. The resulting permuted distributions indexed the range of putative differences for α and β values, respectively, between the subgroups, followed a normal distribution and were centered on zero. The real difference for α and β parameters between the subgroups of the original sample was also calculated and compared to the reference permutation distribution for empirical significance levels, using two-tailed confidence intervals for hypothesis-free comparisons, and one-tailed confidence intervals for directed hypotheses based on previous results. To assess the significance of α and β parameter values per subgroup, we compared these values to a reference bootstrap distribution for α and β, constructed from N=5000 randomly selected samples of N=279 participants taken (with replacement) from the entire population. The choices were again averaged within each sample, and entered into the Fehr-Schmidt model. The resulting reference distributions were then consulted to check if α or β values from specific subgroups fell outside the confidence intervals (95,99,99.9%) of these reference distributions, either above or below.

Data was analyzed and edited using Matlab R2016 (MathWorks, Natick, Massachussets, U.S.A.), IBM SPSS Statistics 22 (IBM, New York, U.S.A.) and Inkscape. For all statistical tests the level of significance was predefined as $p < .05$ if not otherwise specified. For multiple comparisons, *p*-levels were Bonferroni-corrected.

Results

To discriminate between disadvantageous and advantageous IA, we aggregated the choice data across all four reward distributions at the age, actor-, partner-, and dyad-sex level. Descriptively, the percentages of equity choices increased across age in all four reward distributions. The lowest proportion of equity choices was found in 3-4-year-old children in the costly disadvantageous distribution (31.30%), the highest in 7-8-year-old children in the non-costly disadvantageous distribution (87.90%). Regarding dyad-sex, on a descriptive level, boys made more equity choices in both disadvantageous distributions when paired with a male (non-costly: 81.30%; costly: 62.50%) compared to a female partner (non-costly: 72.50%; costly: 59.40%). The reversed pattern was found in the two advantageous distributions, i.e. boys preferred equity choices when paired with a female (non-costly: 58.00%; costly: 39.10%) compared to a male partner (non-costly: 48.40%; costly: 23.40%). Likewise, girls made more equity choices in both disadvantageous distributions when paired with a male (non-costly: 81.40%; costly: 64.30%) compared to a female partner (non-costly: 67.10%; costly: 48.70%). In the two advantageous distributions there was no consistent choice behavior. Girls made more equity choices with female partners in the non-costly distribution (71.10%; with male partners: 51.40%), but more equity choices with male partners in the costly distribution (50.00%; with female partners: 43.40%). In all dyad-sex compositions, there were always more equity choices in the non-costly than the costly distributions. On the whole, these results already preclude a simple efficiency maximizing choice heuristic as both boys and girls preferred the numerically inferior option (2 vs. 5 or 6 tokens) in the disadvantageous distributions. Similarly, an always-choose-equal rule cannot explain these results, because of considerable within-subject divergence in choosing the equal option across choice options. Moreover, in at least the costly advantageous conditions, both boys and girls did not prefer the equal outcome.

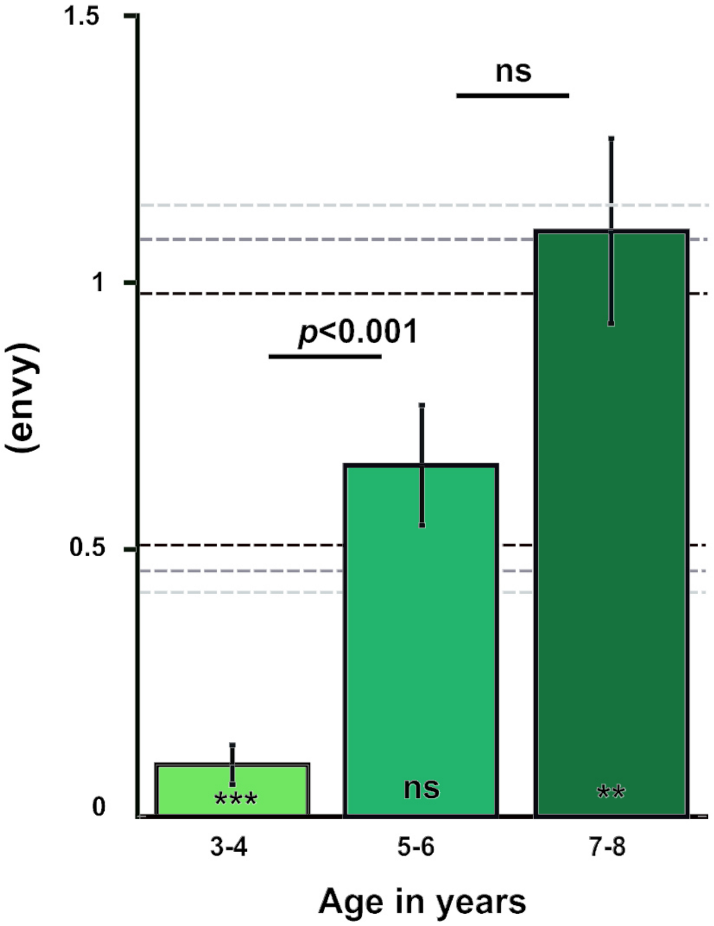
Model-based analysis of sex-dyad dependent inequity aversion

In order to get a better understanding of the social preferences underlying these choice patterns, we fitted the Fehr-Schmidt model of IA (Fehr & Schmidt, 1999) to the raw choice data. The Fehr-Schmidt-model reduces the data and yields quantitative parameter estimates for α (disadvantageous IA, or *envy*) and β (advantageous IA, or *compassion*, or with negative sign, *spite*, see methods).

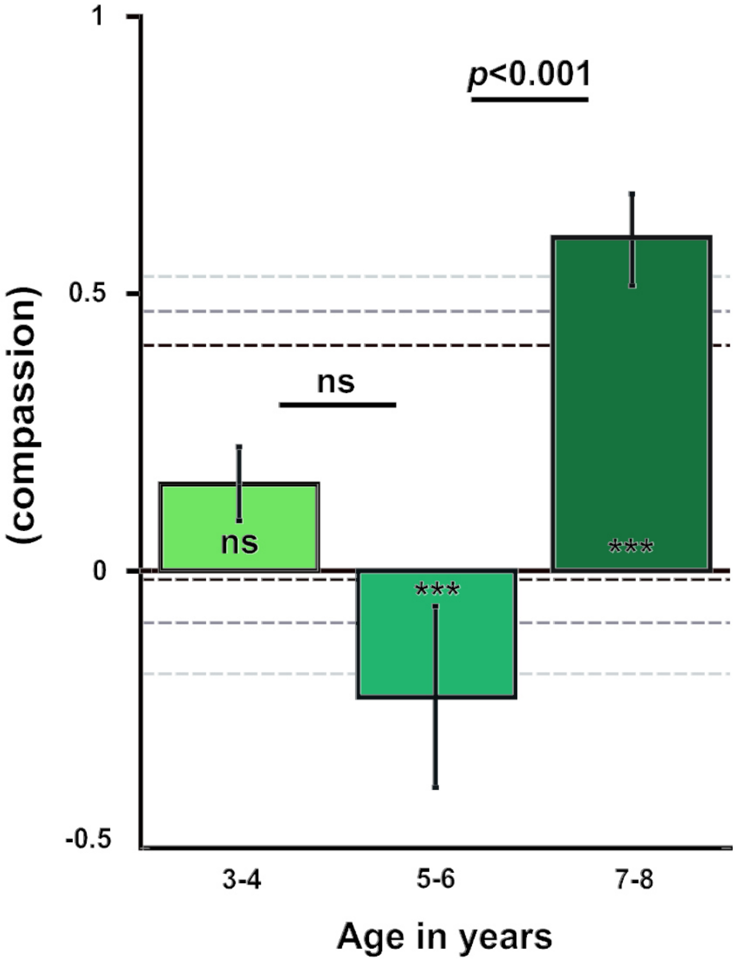
Briefly, to estimate variability in α and β for a given subgroup, we applied a bootstrap approach with resampling, essentially repeating the modelling step for a randomized subsection of the original group and aggregating the obtained α and β values in a distribution from which we report the mean and variance (see methods for details). Subgroup scores were assessed for significance in comparison to confidence intervals on a reference population acquired similarly through bootstrap resampling of the original complete dataset. The 95th, 99th, and 99.9th percentile confidence intervals on these distributions are represented by dashed gray lines in the figure panels below. Comparisons between subgroups were assessed for significance through bootstrap permutation analyses.

Inequity aversion increases with age

As a first step in our model-based analysis, we confirmed our descriptive report above that IA increases with age in young children, and that disadvantageous IA develops earlier than advantageous IA, replicating previous evidence (Fehr et al., 2008; Blake & McAuliffe, 2011). Our results blend with those studies in that envy increased significantly from levels below the reference distribution ($p<.001$) in younger to average levels in middle-aged children ($p<.001$, permutation test with Bonferroni correction for the pairwise comparison, Figure 2a). Descriptively, envy increased even further to levels larger than the reference distribution ($p<.01$) in older children. We found compassion in younger children to be inside the reference distribution, while, in middle aged children, compassion was found ($p<.001$) to be significantly lower than average. This effect was already found in other studies (Sheskin et al., 2014) and might be due to the fact that the development of advantageous IA (compassion) includes overcoming an initial spiteful preference for diminishing others' relative payoff. While compassion levels did not significantly differ between younger and middle-aged children, they increased from middle-aged to older children (*p*<.001, Figure 2b) to levels significantly higher than average (*p*<.001).



(a)

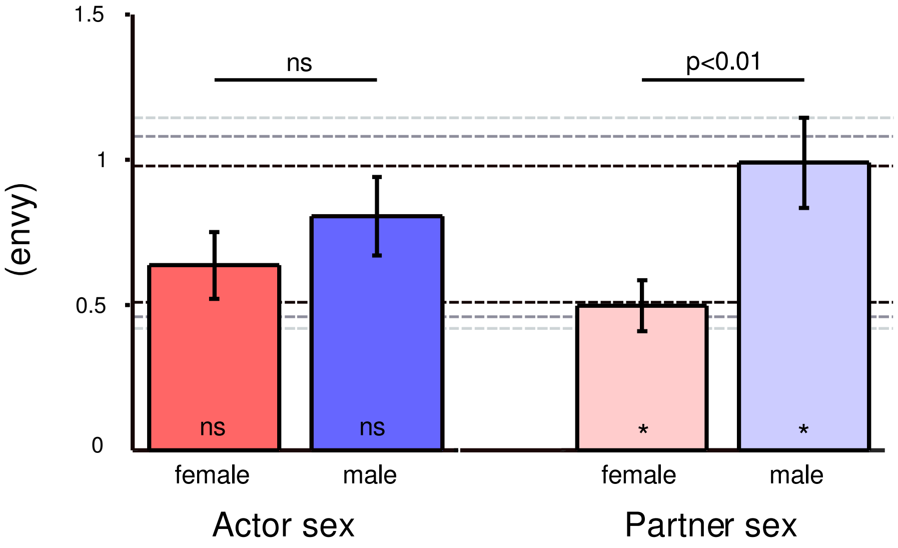


(b)

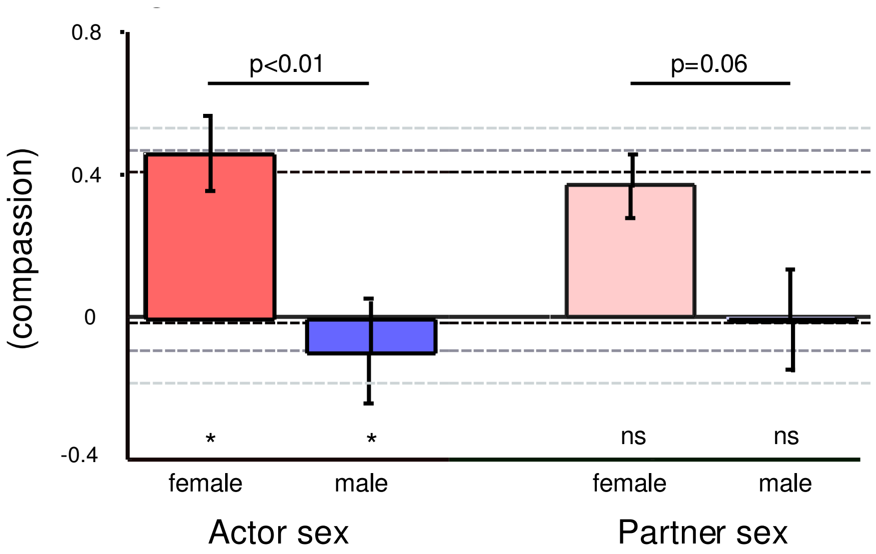
Figure 2. Development of α (envy, 2a) and β (compassion, 2b) with age (means ± standard error of the mean, s.e.m.). Distributions were compared using a pairwise permutation approach, with significance levels determined from the empirical permutation distributions and adjusted with Bonferroni-correction for multiple comparisons.

Sex and dyad-sex-dependent differences in inequity aversion

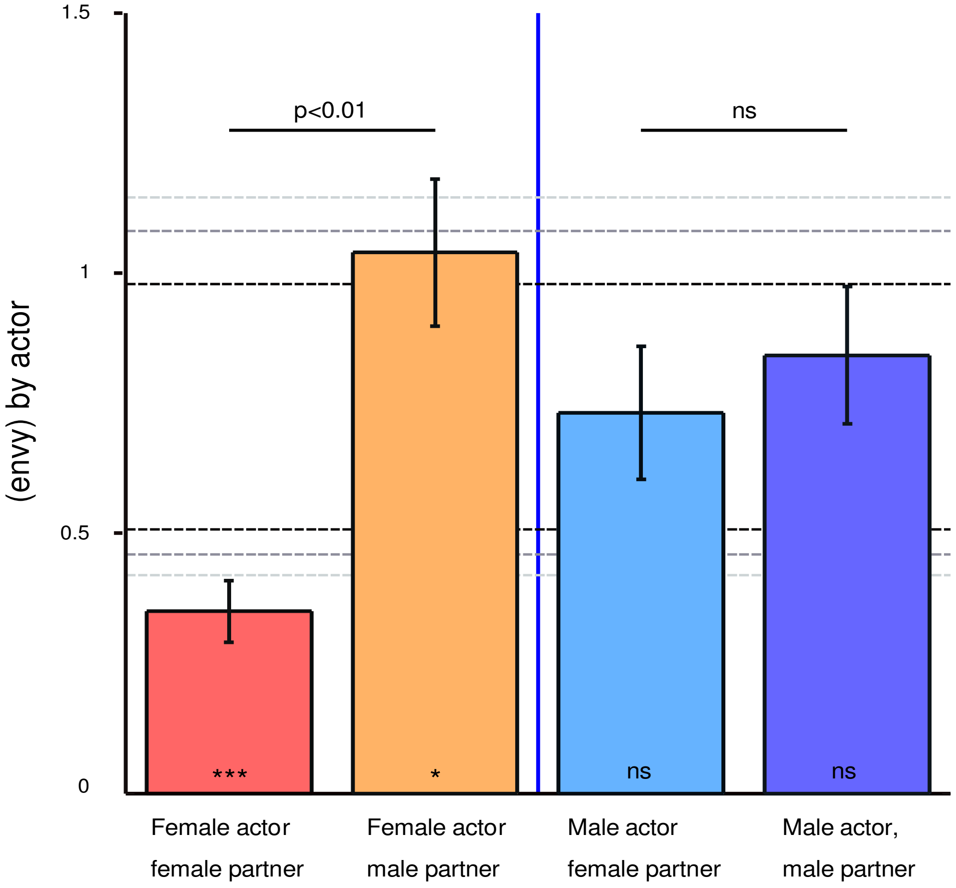
To investigate sex-differences in IA, we re-organized our sample according to the biological sex of the actor (child making the decision) and the recipient (partner). We found that female and male actors did not differ on envy (Figure 3a) and showed envy levels falling within the reference distribution. However, female actors were more compassionate (*p*<.05) and male actors were less compassionate (*p*<.05) than average, and a pairwise comparison revealed that female actors were significantly more compassionate than male actors (*p*<.01, Figure 3B). Male partners were treated with more envy than average (*p*<.05) and female partners with less (*p*<.05). Here, the pairwise contrast revealed that male partners were treated with more envy than female partners (*p*<.01, Figure 3a). Compassion scores broken down by partner fell within the reference distribution; here, the opposite trend emerged with descriptively higher compassion towards female partners (*p*=.06, Figure 3b).



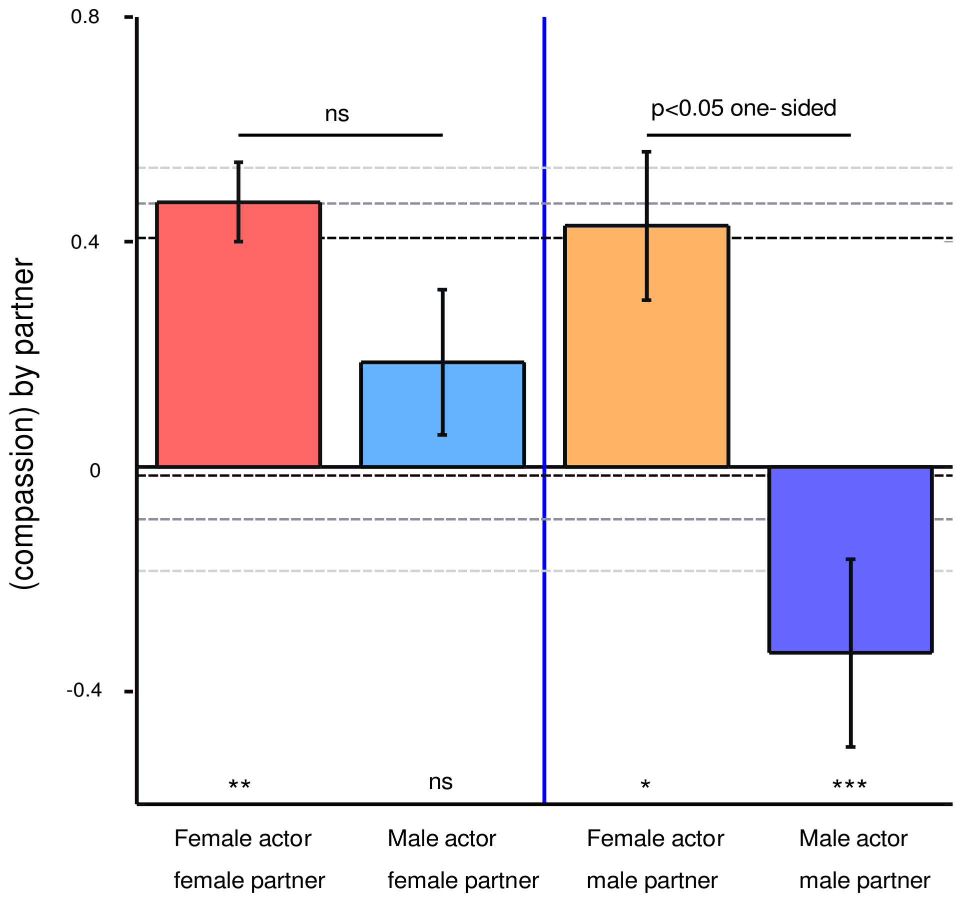
(a)


0.8
0.4
0
-0.4
(compassion)
p<0.01
p=0.06
*
*
ns
ns
female
male
female
male
Actor sex
Partner sex

(b)


1.5
1
0.5
0
(envy) by actor
p<0.01
ns
***
*
ns
ns
Female actor female partner
Female actor male partner
Male actor female partner
Male actor, male partner

(c)



(d)

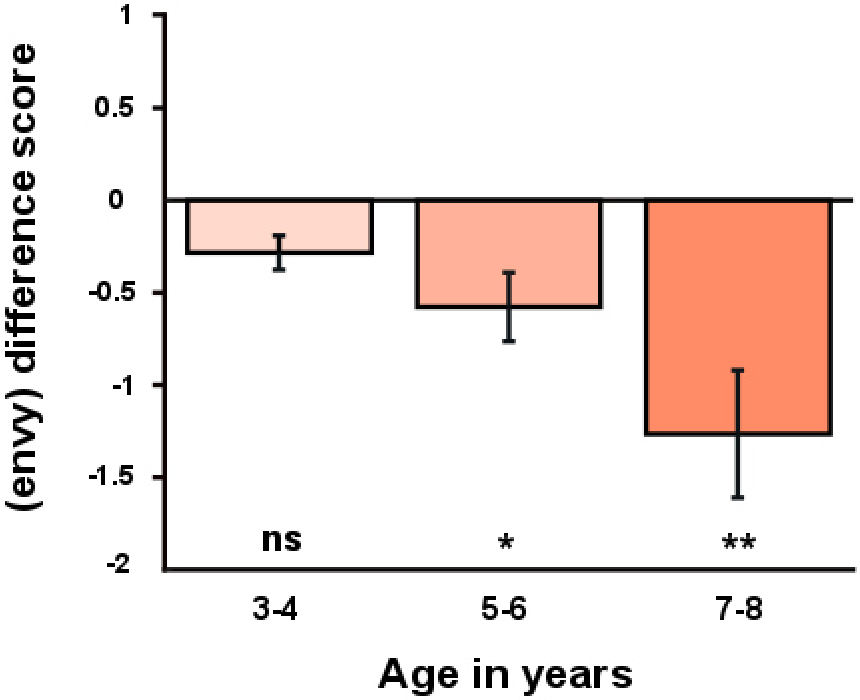
Figure 3. Main effects for actor and partner sex and for envy (3a) and compassion (3b), and differences in envy (3c) and compassion (3d) dependent on the dyad sex composition. Bars indicate the median of the bootstrapped population scores (N=5000). Error bars indicate the standard deviation of the bootstrapped population and thus act as s.e.m. Significance was assessed through permutation analyses.

Unpacking these main effects of sex, we found that actors did not treat all partners equally. Lower envy, i.e. generosity towards female partners (Figure 3a), originated from female actors only: while male actors showed similar and average envy levels towards partners of both sexes, female actors were markedly less envious with female (*p*<.001), and more envious with male partners (*p*<.05) compared to the reference distribution. In addition, they discriminated significantly between partners based on their sex (*p*<.001, Figure 3c). Thus, girls showed an envy bias as they were selectively more generous (less envious) with other girls, aligning their envy level with that of their partner. Conversely, girls were unconditionally compassionate with partners of all sexes: they showed significantly elevated levels of compassion, compared to the reference distribution, independent of the partner´s sex (*p*<.01 towards girls, *p*<.05 towards boys). By contrast, the same analysis with boys revealed that they showed spite (negative compassion, Sheskin et al., 2014) when the partner was male (*p*<.001), but average compassion when the partner was female. Indeed, the pairwise comparison of compassion levels towards male partners supports this notion and shows significantly higher compassion levels in female actors, as expected from the actor sex main effect (*p*<.05, one-sided). In other words, while boys aligned their levels of compassion, or spite respectively, to the partner's sex, girls surprisingly were unconditionally compassionate with partners of all sexes, resulting in a mismatch between female and male compassion in cross-sex interactions.

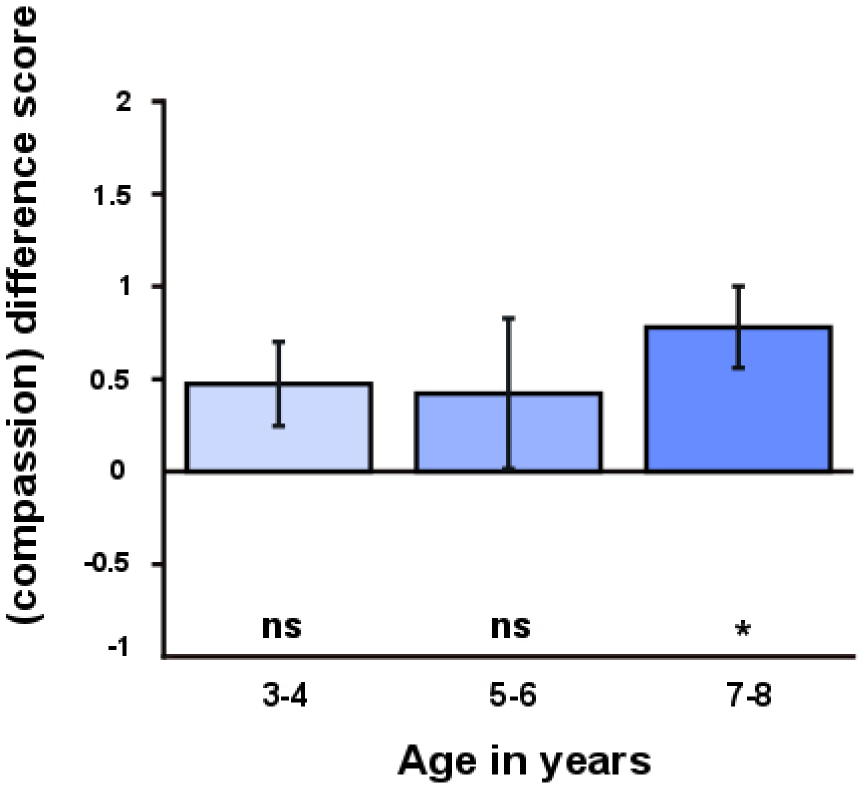
Development of dyad-sex-dependent differences in fairness preferences

Finally, we asked how these dyad-sex-dependent differences in egalitarianism develop across the age groups. We hypothesized that dyad-sex composition effects might not exist in very young children, but that dyad-sex differences in envy and compassion should become gradually more pronounced with age, fostered by social interaction experience and, possibly, exposure to gendered social roles. Indeed, we found that the envy bias in female actors against cross-sex partners became stronger with age. While we observed no envy bias in the youngest children, it appeared in middle-aged (*p*<.05) and peaked in older children (*p*<.01, Figure 4a).

In a similar vein, the sex spite gap of boys against other boys, in comparison with female partners, statistically manifested significantly only in the oldest age group (*p*<.05, Figure 4b).



(a)



(b)

Figure 4. Development of envy bias and spite gap. Panels show the difference in parameter estimates for female minus male actors/partners. Female actors exhibited lower levels of envy against other female than male partners (4a). This envy bias became gradually more pronounced with age. Spite gap, the difference in compassion between female vs. male actors towards male partners, manifested only in the oldest children (4b). Scores indicate the difference between two bootstrap populations with respect to partner sex (4a) or actor sex (4b). Error bars indicate the standard deviation of the difference between these contrasted populations across bootstraps. Significance levels were assessed with a permutation analysis at the level of actor/partner/age as indicated.

Discussion

With this study, we provide evidence for the emergence of sex biases in egalitarian preferences during development. We found that girls were more compassionate than boys, and that boys were treated with more envy, and less compassion, than girls. Notably, girls exhibited an envy bias, i.e., they were envious with boys, but generous with other girls. We also observed a sex spite gap, revealing that boys were treated with compassion by girls but with spite (the inverse of compassion) by other boys. Finally, girls revealed unconditional compassion, i.e., they were equally compassionate towards girls and boys alike, disregarding the boys' indifferent or even malevolent manner.

Interaction experiences and gender stereotypes

Our data offer insights into the development of social fairness preferences and gendered biases in these preferences. Reinforcement learning (King-Casas, Tomlin, Anen, Camerer, Quartz & Montague, 2005) and evolutionary models of cooperation (Rand & Nowak, 2013; Trivers, 1971) predict that social intuitions are fashioned by past interaction experiences (Rand et al. 2014; Trivers, 1971). According to this idea, children gradually acquire a social response pattern that reflects their previous positive and negative experiences with other children in social exchange situations (Rand et al. 2014). Since social attitudes differ between sexes, actors' fairness preferences should be congruent with the interactions partner's expected fairness attitude, dependent on the partner's sex, and as learned by experience (e.g. female compassion, male competitiveness, Sutter & Rützler, 2010); for instance, experienced or predicted male envy should be met with similar envy, and experienced or predicted female compassion should be met with equal compassion. This explanation is supported by our observation that the children's fairness attitudes were generally aligned to that of their interaction partner, dependent on his or her sex, as demonstrated by the girls' envy bias, or the boys' switch from spite to (moderate) compassion when dealing with boys and girls, respectively.

Importantly, however, girls also showed unconditional compassion; that is, their compassion levels were not different between interactions with female and male partners. The fact that girls did not adjust their compassion downwards when interacting with boys (who, on average, exhibited significantly lower levels of compassion) is difficult to reconcile with a pure experience-based model of social preferences. Instead, this mismatch between social preferences and interaction experiences seems more consistent with the notion that fairness preferences were also shaped by elements beyond experience, as for instance by a compliance to social gender norms that could dictate unconditional compassion even with non-reciprocating partners. This would imply that gendered stereotypes of social behavior could, under some circumstances, work against settling mutual social preferences on levels matching interaction experiences. Especially in cross-sex interactions, social norms prescribing, for example, female unconditional kind-heartedness could inflate female compassion to levels divorced from those expressed by males in these interactions (Eagly, 1987; Heilman & Chen, 2005). A putative influence of such internalized social roles is also supported by the fact that effects of dyad-sex-composition were weak or absent in the very young children of our sample, but developed during childhood. Thus summarizing, our data suggest that the emergence of gendered fairness preferences in childhood is unlikely the consequence of a single developmental process alone. Instead, the pattern of our children's egalitarian choices seem to reflect a mix of past interaction experiences and acquired social gender norms.

Biological pre-disposition or demographics cannot sufficiently explain dyad-sex differences in IA

Another possibility is that the development of these dyad-sex-specific social interaction patterns are not due to accumulating experience or the influence of gender role stereotypes, but the result of a biological pre-disposition that becomes gradually expressed with age. In consonance with this idea, differences between the sexes in adult decision making have often been explained with reference to natural selection in evolution (Buss, 1995). Indeed, in our study, the observed higher prosociality in females as well as higher competitiveness among males could reflect differences in the challenges faced by different sexes over the course of evolution. Females may have benefitted from the display of greater altruism towards non-kin to facilitate cooperative breeding and allomaternal care (Burkart, Allon, Amici, Fichtel, Finkenwirth, Heschl, et al., 2014) and shield against potential conflicts, whereas males had to compete with other males for access to limited resources, including mating opportunities with females, and act as protectors against male enemies (Trivers, 1971). Thus, it might well be that such evolutionary pressures promoted higher levels of compassion in females and higher levels of competitiveness – leading to envy or even spite – in males. Precursors of these tendencies already could have manifested in our sample of young children and further develop with age.

However, though it is safe to say that biological sex plays a role in social preferences and decision making, it cannot fully explain the findings reported here. We found a double dissociation of partner-sex sensitivity in the current experiment: girls only differentiated between male and female partners within the “typical male” competitiveness/ envy context (disadvantageous distributions), showing significantly more generosity when paired with same-sex partners. By contrast, boys were treated differently within the “typical female” prosociality context (advantageous distributions): female actors showed high compassion with boys, while male actors showed dramatically lower levels of compassion, and even spite when paired with same-sex partners. In addition, there is no obvious reason why such behavioral patterns should change during development in a phase where sex hormones and putative partner selection do not yet play a major role. Therefore, we consider it more plausible that the social choice patterns reported here are in line with the acquisition of sex-specific and gendered social roles, that come to override interactive experiences (Rand, 2016).

In addition, demographic factors, such as socio-economic status, number and sex of siblings, or birth order have been shown to influence egalitarian preferences (Fehr et al., 2008). However, our sample was recruited in middle- to upper-middle class urban childcare facilities and was, thus, socio-economically homogeneous. In addition, while socio-economic status, siblings or birth order might relate to fairness attitude as a (relatively stable) personality trait, these factors are not easily suited to explain our children’s flexible, dyad-dependent adjustment of egalitarian preferences to the sex of the interaction partner. We therefore consider it unlikely that socio-economic status, birth order or siblings explain the sex-dyad-dependency of egalitarian preferences found in our children.

The influence of gender roles

In other domains, it has become better understood how gender stereotypes influence the young child´s mind during development. Recent evidence unveiled that attitudes towards intellectual abilities of girls and boys are strongly modulated by gender stereotypes associating high-level intellectual abilities more with men than with women (Bian et al., 2017). Critically, these stereotypes did not reflect children´s actual abilities and emerged only between years 5 and 6 in development, implying that younger children were still unaffected by gender stereotypes. Our results suggest the same: 3-4 year-old children did not discriminate between male or female partners when deciding between unequal and equal outcomes; dyad-sex-specific social preference patterns emerged only later in development.

Gender stereotypes permeate today’s society. Our study highlights the pervasiveness of gendered differences in social behavior, even in young children, possibly leading to the emergence of gender stereotypes later in adult life. However, as our study shows, at least in the field of fairness preferences, gendered differences develop over an extended period. This observation paves the way for new educational interventions aimed at preventing social stereotype development by promoting gender-non-stereotyped attitudes during this critical period.

Author contributions

Lina Oberliessen designed the study, conducted the experiments, pre-analyzed the data, developed the first concept of the article, wrote the article, and revised the article. Marijn van Wingerden analyzed the data, wrote the article, and revised the article. Tobias Kalenscher revised the data analysis, wrote the article, and revised the article. Lina Oberließen and Marijn van Wingerden contributed equally to this work.

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General Discussion

During my PhD thesis, my co-workers and I elaborated on the phenomenon of inequity aversion (IA) and its development using a multifaceted approach. The main findings of the current thesis should be discussed in this section. Furthermore, limitations and implications of our results should be pointed out. As the review (Chapter 1) already covers some parts of the general discussion from a content-related perspective, e.g. the comparison of different IA theories, the phenomenon of advantageous IA, a detailed comparison between impunity-like and choice-based IA tasks, or neural substrates of IA, I decided to not repeat these aspects within this section. I will rather focus on cross-references between chapters, and implications for future research. But first, the contributions of the single chapters and a secret hidden chapter shall be briefly summarized.

In Chapter 1, we reviewed the research of IA in non-human animal species. Interestingly, the results are quite heterogeneous, which stimulated several different theories on (or against) IA (Brosnan, 2006, 2011; Engelmann, Clift, Herrmann, & Tomasello, 2017; Roma et al., 2006; Bräuer et al., 2006; Dubreuil et al., 2006; Neiworth et al., 2009; Chen & Santos, 2006). Some of these theories are mutually exclusive, but others are not necessarily contradictory. Besides different theories, we had a closer look at moderator variables that seem to influence the IA response and might therefore explain some of the heterogeneity. We identified the experimental setup as one crucial moderator and concluded that the use of non-costly choice-based IA paradigms might supplement the more common impunity-like tasks in which animals have to forgo own rewards to express IA. With these suggestions we hope to promote research on non-human IA as the use of different paradigms would help to detangle genuine IA from paradigm-dependent interferences.

In Chapter 2 and 3, we put our own suggestions into practice and studied IA in rats, wolves, and dogs by implementing choice-based paradigms. We provided evidence for disadvantageous IA in rats for the first time (Chapter 2). They were tested in a social maze (Hernandez-Lallement et al., 2015; Hernandez-Lallement et al., 2016), and could choose between equal and unequal food rewards in a social versus non-social control condition. Furthermore, we could identify an influence of social hierarchy on IA. This was also found in other species (Essler et al., 2017; Brosnan et al., 2010; but see Massen et al., 2012). More dominant rats showed stronger IA compared to submissive individuals. On a content level, our study supports the idea that different taxa are equipped with a similar mechanism to detect inequity, respectively, to avoid it. On a methodological level, we established a new paradigm to test IA in rodents.

In contrast to rats, wolves and dogs had already been tested in impunity-like IA tasks before (Range et al., 2009; Brucks et al., 2016; Brucks et al., 2017; Essler et al., 2017). It could be found that they responded to reward inequity (at least in some studies), i.e. they stopped earlier to perform a command without being rewarded when a partner still received a reward, compared to a control condition without any partner present (Range et al., 2009, Brucks et al., 2016; Essler et al., 2017; but see Brucks et al., 2017). However, a response to quality inequity, i.e. receiving a reward of lesser value compared to a partner, was only found in pack-living dogs and wolves and turned out to be weaker (Essler et al., 2017). That is why we implemented a new touchscreen-based choice task for wolves and dogs (Chapter 3) to test their response to quality inequity in a non-costly setup. However, we could not demonstrate IA in this new paradigm. We assume that the animals´ previous experience with discrimination tasks on the touchscreen as well as the complexity of the current task could be two reasons why our animals did not show a preference for an equal payoff. Nevertheless, our study provided helpful methodological insights to establish a promising touchscreen-based IA paradigm in the future.

With a study on children (Chapter 4) we aimed at addressing the development of IA also from an ontogenetic perspective, in addition to the phylogenetic approach, which is covered by our animal studies. In this experiment, we especially focused on the influence of the sex-dyad of decision-maker and partner on (disadvantageous and advantageous) IA. To our knowledge, this potential moderator of IA has not been studied before as previous studies only took the sex of the decision-maker or recipient into account (e.g. Soutschek, Burke, Beharelle, Schreiber, Weber, Karipidis, et al., 2017; Rand, Brescoll, Everett, Capraro, & Barcelo, 2016;

Croson & Gneezy, 2009; Saad & Gill, 2001a, 2001b). Indeed, we found evidence that not only the sex of the decision-maker but also the dyad-sex composition influences the IA response. Interestingly, fairness attitudes were often (but not always) congruent with that of the partner in the particular dyad. This is in line with the idea that sex-specific fairness preferences could be influenced by same- and cross-sex past interaction experiences, but possibly also by gendered social norms. Thus, our study uncovers another important moderator of IA and consequently also of cooperation.

Hidden chapter: Inequity aversion in marmosets

Admittedly, one other social animal species had been omitted in the current thesis so far, even though they diligently participated in another choice-based inequity task based on the study of Mustoe, Harnisch, Hochfelder, Cavanaugh, and French (2016). We are talking about marmosets (*Callithrix jacchus*). I consider it important to also briefly report about this unsuccessful yet revealing experiment. It unveils important information about factors that can prevent a valid measuring of IA and further stimulates the discussion of paradigm-influenced results which was one main topic of our review (Chapter 1). Furthermore, a similar methodological issue occurred in our wolf-dog study (Chapter 3), even though we tried to prevent it after the experience with the marmosets. But before I start those discussions, the setup of the marmoset study shall briefly be summarized.

Similar to Mustoe et al. (2016) and Burkart, Fehr, Efferson, and van Schaik (2007), we used an apparatus that consisted of two transparent sliding trays (one above the other). By pulling one of two handles to either move the upper or lower tray, marmosets could make their choice. Each tray was equipped with two small plastic bowls containing the rewards. One of the plastic bowls was accessible for the subject and the other for the partner. Dependent on the subject´s choice, the distribution of rewards was equal (one piece of marshmallow for both animals) or unequal (one piece of marshmallow for the subject and four pieces for the partner). As all rewards were always visible for the animals, we decided against an extensive training procedure. This might have raised certain reward expectations which could have had an influence on test performance and decision behavior. That is why we just trained the marmosets how to pull the lever to access food. Against our expectations, and different to Mustoe et al. (2016) who used qualitatively different rewards, we found no preference for the equal option in our nine male subjects. Their choice behavior was on chance level. A subsequent magnitude discrimination task revealed that they could not discriminate between 1/1 versus 1/4 and still performed on chance level when they could access both rewards. This was untypical as marmosets as well as other monkeys are generally capable of discriminating between a higher versus lower quantity of the same food, and prefer the higher quantity (Stevens, Wood, & Hauser, 2007). Possibly, their inability to choose a quantitatively higher reward for themselves was due to the fact that all subjects were completely naïve and had no prior test and (too?) little training experience. Regardless of the actual reasons, we apparently never measured IA in the marmoset task as already the magnitude discrimination seemed to be too complex for our subjects.

The monkeys´ (bad) advice to canids

To avoid this particular issue in the wolf-dog study, which was carried out after the marmoset study, we adapted the experimental design accordingly. First of all, we opted for qualitatively rather than quantitatively different rewards to make the difference more obvious, i.e. we used low value dry food and high value meat instead of one piece of meat versus more pieces of meat. Furthermore, an extended training procedure prior to the actual test was implemented. By doing so, we wanted to make sure that the animals understood the different rewards associated with the particular symbols, respectively, we wanted to be able to exclude animals that did not prefer the better reward in the first place. Unfortunately, learning from mistakes is no guarantee to avoid new mistakes. As already reported in Chapter 3, the extended training procedure is suspected to have caused learning effects, i.e. one factor, amongst others, that prevented us from validly measuring IA in the wolf-dog task. Furthermore, the paradigm was apparently still too complex for our wolves and dogs, as they presumably did not understand the altered reward contingencies between subject and partner, an aspect that could not be covered by the applied training procedure. Although this is a bitter reflection in the first place, I consider it as highly valuable to gain such experiences in the experimental sciences. They sharpen the awareness for the many factors that might play a role next to the one factor that one has in mind.

Cross-references between studies

The strengths, but also limitations, and potential weaknesses of the single studies were already discussed in detail in the particular chapters. At this point it should rather be focused on cross-over aspects and challenges of measuring (especially non-human) social preferences in general and IA in particular.

Cognitive abilities and task complexity

As already mentioned above, task complexity is one important aspect that might, at worst, prevent the measuring of social preferences like IA (my formal apologies to the marmosets). However, it is also conceivable that results are biased by cognitive abilities, e.g. in a way that smarter animals show higher social preferences in a certain task, not because they are genuinely more social, but because they have a better understanding of the test processes. This is difficult to verify and could also have happened in any IA study, as well as in our rat study (although less obvious compared to the wolves and dogs that were already pre-selected by training performance). To minimize such effects, it should be opted for social paradigms that are as simple as possible and adapted to a species´ characteristics. A token exchange task is for example nicely suitable for monkeys but would be rather difficult for rats.

On the other hand, it might also well be that there is a task-independent correlation between cognitive abilities and social preferences. Such a link is supported by some human studies (e.g. Chen, Chiu, Smith, & Yamada, 2013; Ben-Ner, Kong, & Putterman, 2004; Brandstätter & Güth, 2002; Jones, 2008; but see Benjamin, Brown, & Shapiro, 2013). However, less is known about such a connection in animals. That might be due to the fact that measuring an animal´s intelligence is not trivial (even the predictive value of human IQ tests must be treated with caution, see e.g. Sternberg, Grigorenko, & Bundy, 2001). Nonetheless, there are studies that attempted to assess individual cognitive abilities, e.g. in mice (Matzel, Han, Grossman, Karnik, Patel, Scott, et al., 2003; Matzel, Grossman, Light, Townsend, & Kolata, 2008), or primates (Herrmann & Call, 2012; Vonk & Povinelli, 2011). Even though measurements of cognitive abilities also have their limitations, e.g. a connection of motivation and performance (see Marshall-Pescini, Virányi, Kubinyi, & Range, 2017, for an example of wolves´ and dogs´ problem solving abilities), it might be worthwhile to further investigate the link between cognitive abilities and social preferences like IA in animals. Ideally, the same animals would be tested in both social and cognitive tasks.

In our children study, it was easier to gain information about task comprehension. The great advantage of human studies is that one is able to simply ask the participants if they understood the task correctly (at least as soon as they are able to speak). Therefore, we prepared control questions to validate if children were aware of the consequences of their choices. If they could not answer the control questions correctly, which sometimes happened in the youngest age group, subjects were excluded from the analysis. Admittedly, this could also have caused a selective sample in the children aged 3-4. Similar to the wolves and dogs, it could have been the case that only smarter (respectively more developed) individuals were finally considered.

Captivity and domestication

It became obvious that non-human IA is studied in captive animals. However, there is some evidence for behavioral and cognitive differences between wild animals and animals that live in captivity, respectively under human influence (e.g. Benson-Amram, Weldele, & Holekamp, 2013; Greene, Melillo-Sweeting, & Dudzinski, 2011; Gajdon, Fijn, & Huber, 2004; Tomasello

& Call, 2004; but see e.g. Cauchoix, Hermer, Chaine, & Morand-Ferron, 2017). We can merely speculate to what extent IA is influenced by captivity. However, with regard to the cooperation hypothesis (Brosnan, 2006, 2011), it can be reasonably assumed that IA might be less pronounced in captivity. There is usually less need for intra-specific cooperation, and, as a consequence, also less experience with cooperation. For example, our wolves do not need to cooperatively hunt together and there is no classical puppy raising, as new puppies are not introduced to the consisting packs before an age of five months. Also, our rats were fed by humans, did not raise any offspring together, and there was no need for cooperative territory defense. However, it remains elusive to what extent IA is an evolutionary response independent of concrete experiences with cooperation, and to what extent learning might modulate, respectively enhance the sensitivity to inequity. The results of our children study (Chapter 4) provide indications that past interaction experiences might indeed influence fairness preferences. There is also evidence in animals that the level of cooperativeness is dependent on past cooperation experiences (Rutte & Taborsky, 2007, 2008). To assess if this also holds true with IA, one might likewise manipulate the animals´ level of experience with previous cooperation. Additionally, it would be promising to invent tasks that would also be applicable to wild animals.

Connected to the captivity aspect, it is also worthwhile to consider domestication as a possible moderator of IA. Notably, not only the dogs but also the rats of the current dissertation project are in fact a domesticated species. IA studies that take domestication effects into account are so far limited to wolves and dogs (Essler et al., 2017). With regard to the cooperation hypothesis (Brosnan, 2006, 2011), it is known that one aspect of domestication is a reduced level of intra-specific cooperation (Marshall-Pescini, Schwarz, Kostelnik, Virányi, & Range, 2017; Feddersen-Petersen, 2007). This might subsequently result in a faded sensitivity to inequity. Essler et al. (2017) found that both wolves and dogs responded to reward inequity as well as quality inequity. However, in line with the cooperation hypothesis, dogs showed less pronounced quality inequity and needed less prompts than wolves to comply in a quality inequity condition compared to an equity condition. Essler et al. (2017) interpreted their results in a way that dogs´ relationship to humans and their will to please may foster a higher tolerance for unequal treatments, at least from humans. As the design of the current wolf-dog study (Chapter 3) is still in a maturing phase, we cannot make any reliable statements about the influence of domestication on choice-based IA tasks yet. If domestication also affects IA in other species, for example in rats, remains to be studied.

Experimenter effects

It is long known that experimenters do influence scientific results, e.g. by expectations (Rosenthal, 1976). In most non-human IA tasks, the experimenter plays a central role and is directly involved in the experimental process. In impunity-like IA tasks similar to the pioneering experiment by Brosnan and de Waal (2003), the experimenter is directly responsible for the equal, respectively unequal reward distributions. In choice-based tasks the experimenter is less involved but still present and responsible for the distribution of rewards according to the subject´s choice. The level of involvement can vary from task to task. In our wolf-dog study (Chapter 3), the experimenter was visible all the time and obviously distributed the rewards between individuals. In contrast, in our rat study (Chapter 2), the experimenter could not be seen during the whole experimental session. However, rats could still hear and smell the human presence and movements. Critically, in studies on social preferences in general and IA in particular, it remains elusive if (or to what degree) occurring IA is directed to the partner animal or the experimenter (also see McGetrick & Range, 2018). It is also conceivable that some impunity-like tasks failed to demonstrate IA because animals would only react to inequity in intra-specific encounters but attributed inequity to the human experimenter in the particular setups. Even though this can be excluded for choice-based tasks, it is still possible that animals´ decisions are influenced by the human experimenter or that they merely focus on the human experimenter and therefore pay less attention to their conspecific and its rewards. For choice-based tasks it would be beneficial to opt for automated designs to diminish experimenter effects. Automated apparatuses that measure social preferences were already implemented in rodents and apes (e.g. Avital, Aga-Mizrachi, & Zubedat, 2016; Yang, Silverman, & Crawley, 2011; Martin, Biro, & Matsuzawa, 2014; Mendonça, Dahl, Carvalho, Matsuzawa, & Adachi, 2018). For impunity-like tasks it is more challenging to reduce experimenter effects. On the one hand, one could likewise replace the experimenter by an automated food dispenser. However, I consider it more valuable to actually create a cooperation setting in which one individual disadvantages a conspecific. This would also allow to assess whether further cooperation is refused by the disadvantaged individual. So-called negotiation games offer this possibility. In such games, pairs of animals can commonly choose between an equally and an unequally baited string-pulling apparatus. It could be found that chimpanzees were able to settle conflicts of interest over resources in mutually satisfying ways (Melis, Hare, & Tomasello, 2009). To assess IA rather than coordinated cooperation, it would for example be possible to explicitly train one animal to choose the unequal option.

Implications for future research

Several implications for future research were already included in the chapters and in the previous paragraph, e.g. investigating the influence of cognitive abilities, captivity, past experience with cooperation, and domestication on IA. Furthermore, automated IA designs were discussed to prevent experimenter effects.

Generally, IA in non-human animals is still a young field of research. So, first of all, replication studies would be useful to validate existing results and would help to learn more about IA and its moderating factors. Coding social behaviors during IA tasks might moreover provide insights into the animals´ state of mind. A high occurrence of agonistic behaviors could for example reflect an aversive emotional state induced by inequity; prosocial choices might be accompanied by an increased level of approaching behaviors.

Furthermore, as already mentioned, combined studies using more than one paradigm (e.g. impunity-like tasks and choice-based tasks) would offer the possibility to detangle IA from paradigm-specific effects. In addition to that, it is also highly revealing to test the same subjects with regard to different social concepts. By doing so, one could gain insight into links between various social preferences, e.g. IA, prosocial behavior, or reciprocity (see also Chapter 1). Moreover, links between social preferences and non-social concepts could shed light on underlying mechanisms of social behavior. As discussed in Chapter 1, it is for example conceivable that IA and temporal discounting (Stevens and Hauser, 2004; Kalenscher and Pennartz, 2008) are shaped by similar mechanisms.

Besides, it would be promising to design IA paradigms that are applicable for both humans and animals. Such an approach was for example chosen to compare children and animals with regard to false beliefs (Krachun, Carpenter, Call, & Tomasello, 2009; Call & Tomasello, 1999). Standard economic games (e.g. Bolton, Katok, & Zwick, 1998; Güth, Schmittberger, & Schwarze, 1982; Bolton & Zwick, 1995) that are often used to measure human IA, differ from animal tasks and are based on verbal instructions, i.e. a comparison of results is critical. However, a valid comparison of social preferences between humans and animals might offer the possibility to learn more about the influence of culture and society on IA. This would for example be interesting with regard to the dyad-sex differences that we found in our children study (Chapter 4), as there is also evidence for sex differences in animals (Brosnan et al., 2010). Furthermore, such designs would enable to study inter-specific IA, e.g. one could test if children would show similar patterns of IA when paired with a dog partner compared to a human partner, and vice versa. As there is evidence for dog-human-cooperation (Range et al., 2019; Ostojic & Clayton, 2014) it appears logical to speculate that also inter-specific IA might exist.

Conclusion

Again, plenty of research is still needed to truly understand the nature of IA. However, I am convinced that it is worthwhile to scientifically invest in this topic to eventually understand the origin of our own social nature and to promote human cooperation in the long run, on an individual as well as on a societal level. To do so, I, among many others, consider animals to be promising and suitable models to learn about ourselves (see e.g. Kalenscher & van Wingerden, 2011; Darwin, 1872). As Sarah Brosnan (2006) nicely puts it, “we see a mirror of ourselves stripped of the complications of language and complex culture” (p.181). Furthermore, I hope that by providing more evidence for the (often human-like) complexity of animals´ minds and their social structures, people become more aware of the necessity to treat and keep them accordingly.

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Declaration

I, Lina Oberließen, declare that the current thesis entitled “Inequity aversion in social species” contains no material that has been submitted previously, in whole or in part, for the award of any other academic degree or diploma. Except where otherwise indicated, this thesis is my own work. I did not use any sources other than those specified. All passages which are taken from other texts (literally or content-related) are identified as such; this applies to printed texts as well as to electronic resources. I further declare that the current thesis complies with the "Fundamental principles for safeguarding good scientific practice at Heinrich Heine University Düsseldorf".

Düsseldorf, September 2019

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Non-scientific footage (German)

Da es die Marmosets leider nicht zu einem eigenen Kapitel gebracht haben, sollen hier ein paar exklusive Eindrücke von der Arbeit mit ihnen in Reimform geteilt werden. Es war nicht immer leicht…

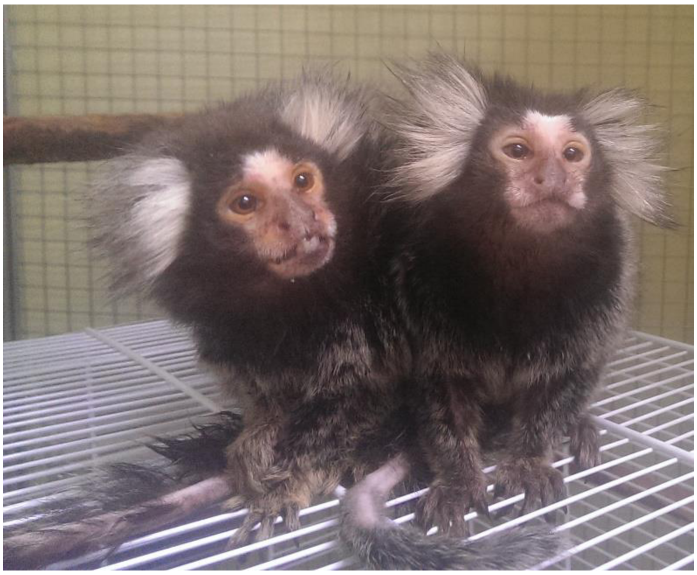

Photo credit: Lina Oberließen

Affentanz

Die mangelnde Konzentration der Affen,
macht der Lina schwer zu schaffen.
Das Futter interessiert nicht mehr,
sie wollen nur Geschlechtsverkehr.

Seit der güld´nen Morgenstund,
steht sie sich die Füße wund.
Trainiert wird fleißig das Getier,
den Doktortitel im Visier.

Die Äffchen kreischen, stinken, springen,
sodass einem die Ohren klingen.
Erst jüngst hat er sich zugetragen,
der Gipfel forscherischer Plagen.

Die Lina strebsam und geschäftig,
vor den Käfigen zugange,
auf einmal sprenkelt es recht heftig,
Urin tropft gelblich von der Wange.

Auch die Bekleidung, welch ein Graus,
schick sieht darin niemand aus.
Ein Baumwollkittel knöchellang,
mintgrün und weit ist der Behang.
Mit einem Schleifchen zugebunden,
und um das Bild noch abzurunden,
grässlich blaue Überschuh,
entstellt ist jeder Look im Nu.