

Are Nonhuman Animals Averse to Inequity?

A Meta-Analysis

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Note: this preprint has not been peer reviewed.

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Abstract

Inequity aversion, a negative response to receiving less (or more) than others, is a key building block of the human sense of fairness. While some theorize that inequity aversion is widespread across the animal kingdom (shared by species as diverse as crows, mice, dogs, chimpanzees and humans), others believe that it is an exclusively human evolutionary adaptation to the selective pressures of cooperation among nonkin. Essential to this theoretical debate is the empirical question of whether nonhuman animals are averse toward unequal distributions of resources. Over the past two decades, researchers have reported that species across a wide range of taxa object to unequal treatment. These results, however, have been questioned on both conceptual and empirical grounds. In the largest empirical investigation of inequity aversion in nonhuman animals conducted to date, we synthesize the data from 23 papers, covering 60,430 observations of 18 species. We find no evidence for inequity aversion in nonhuman animals. Alternative interpretations of the data and implications for the evolution of fairness are discussed.

Many people object to the degree of economic inequality prevalent across the world. Underlying this concern is a sense of fairness, which tracks patterns of distributions of resources and prompts a set of emotional, cognitive, and behavioural responses when allocations diverge from mutually agreed-upon norms of justice¹⁻⁶. In the behavioural sciences, the dominant view holds that inequity aversion [IA] represents the central psychological element of the sense of fairness^{2,7,8}. An individual is said to be inequity averse when they object to inequitable resource distributions that either favour others over self (so-called disadvantageous IA) or self over others (so-called advantageous IA). Cultural and individual differences in its manifestation notwithstanding^{9,10}, IA appears to be a robust feature of human sociality¹¹. In every culture studied to date, children as young as four years of age incur costs to reject distributions that put them at a disadvantage (thus exhibiting disadvantageous IA)^{7,12}. Furthermore, in resource allocation contexts, a preference for equal distributions has been found to emerge by middle childhood and to persist into adulthood¹³⁻¹⁵. This apparent universality of disadvantageous IA in humans raises the possibility that our sense of fairness is an evolutionary adaptation.

Theorizing on the evolutionary origins of fairness has pointed to its pivotal role in stabilising cooperation^{13,16,17}. To establish and maintain mutually beneficial cooperative endeavours, collaborators must reliably solve two key challenges: the generation and distribution of benefits¹⁸. The sense of fairness likely evolved as a proximal mechanism addressing the latter, by guiding the distribution of generated benefits among collaborating partners. Fairness concerns typically manifest in contexts in which agents hold conflicting cooperative and selfish motives. For example, following a successful collaborative hunt, the evolutionary fitness of each hunter depends on their ability to maximize their own reward while simultaneously maintaining a collaborative relationship with their partners (who, in turn, aim to maximize their own rewards). Fairness allows agents to strike a balance between these mixed motives, representing a “cooperativisation of competition”¹⁹. From an evolutionary perspective, a sensitivity to inequity may thus function to stabilise cooperative relationships in the face of competing interests. Humans are not the only species in which individuals depend on stable patterns of cooperation for survival and reproduction²⁰⁻²⁴. This raises the question: Is IA shared with other animals?

The year 2003 marked a transition from more than two thousand yearlong philosophizing about the evolutionary roots of fairness in the Western intellectual tradition (Aristotle famously believed that animals lack fairness because they lack speech²⁵) to

empirically investigating whether nonhuman animals show a concern with inequity. In what has become one of the most famous studies (and videos²⁶) of animal behaviour, dyads of capuchin monkeys participate in a token exchange task. An experimenter first hands a cucumber to one monkey in exchange for the token. The experimenter then repeats this procedure with the second monkey, but, instead of a cucumber, hands over a grape – a capuchin delight – in exchange for the token. The disadvantaged capuchin monkey reacts in ways that suggest dissatisfaction with the inequitable treatment: they protest by failing to consume the cucumber or throwing it at the experimenter, and, in some cases, even refusing to participate in the task altogether. Quantitatively, a reduced willingness to exchange in these inequitable conditions (compared with equitable conditions, in which both monkeys receive the same cucumber reward) were taken as evidence that the monkeys display disadvantageous IA (which we will refer to as the *IA hypothesis*, see below)²⁷.

This publication spawned several lines of research attempting to replicate and extend its findings. Using both token exchange paradigms and other procedures, researchers published experimental results raising the possibility of IA across a wide range of taxa. Corvids²⁸, parrots²⁹, mice³⁰, rats³¹, dogs³², marmosets³³, tamarins³⁴, and chimpanzees^{35–37}, among other species, have all been shown to exhibit an aversion to inequitable treatment. At the same time, however, several studies failed to replicate these findings^{37–42}, and both the robustness of the effect and the validity of its interpretation have been questioned^{6,43}.

The central point of contention is whether subjects' response is grounded in social comparison: Are subjects rejecting the lower-quality food specifically because a partner is receiving higher-quality food? Or are subjects simply disappointed because they received a lower- instead of a higher-quality food reward?

The *IA hypothesis* maintains that increased rejection rates in inequitable conditions are indeed grounded in social comparison – the subject sees a partner receiving a better reward and protests the disparity by refusing to participate in the task. The main rival hypothesis – the *disappointment hypothesis* – questions the presence of IA in nonhuman animals and suggests that the observed condition differences are the result of disappointment driven by mechanisms unrelated to social comparison. Thus, subjects may not be responding to inequity, but rather experiencing simple frustration that they are not getting the more valuable reward that is presented to them (also referred to in the literature as “individual contrast effects”)^{38,39,44,45}.

The key difference between the *IA hypothesis* and the *disappointment hypothesis* is thus that only the *IA hypothesis* posits a specific effect of social comparison. Empirically, in

the context of the paradigmatic IA studies, the presence of social comparison concerns should manifest in higher rejection rates when the partner receives a higher quality reward than the subject – compared with conditions in which the experimenter merely draws the subject’s attention to a higher quality reward (without handing it to a partner), inducing disappointment without creating inequity. The importance of this distinction has been acknowledged by much of the literature on IA in nonhuman animals, and most studies investigating IA in animals included conditions designed specifically to rule out the *disappointment hypothesis*. Typical examples of these are conditions in which the experimenter hands a high quality reward to an empty cage^{27,46–48}, and conditions in which the experimenter holds up a high quality reward prior to exchanging but then hands both subject and partner a low quality reward^{49–55}. Some studies successfully demonstrated an effect of social comparison above and beyond disappointment^{27,37,52,56,57}, while others did not^{37,46,47}. In yet other studies, the difference in rejection rates between equitable and inequitable conditions failed to replicate altogether^{37–42}.

Due to the limited subject populations that researchers can access, animal behaviour studies generally use small samples⁵⁸. Over the past decade, the field of psychology has been reckoning with a replication crisis, which has spotlighted the need to re-evaluate key findings^{59,60}. A particularly valuable tool for estimating the strength of the evidence in a field is meta-analysis⁶¹. The plurality of small-sample studies using comparable methodologies and equivalent outcome measures makes the question of IA in animals uniquely suited for meta-analytic investigation. The present study is an individual participant data [IPD] meta-analysis investigating IA in most non-human species studied to date. In IPD meta-analyses, researchers collect the primary, participant-level data of the original studies and draw new inferences from the combined dataset (rather than synthesizing effect size estimates, as in conventional meta-analytic approaches). This approach is considered the “gold standard” of meta-analysis^{62,63}. Since many of the original studies used non-parametric tests, an IPD meta-analysis is particularly suited to the present question. To allow a meaningful comparison of results, we narrowed our investigation to experiments investigating inequity in settings with one subject and one partner and reporting a binary outcome measure (acceptance or rejection of an offered distribution; this criterion precluded inclusion of the literature on IA in dogs). We contacted the authors of 30 eligible publications and received data for 23 of them, covering 18 species and 60,430 observations. To analyse the data, we used a series of pre-registered and exploratory mixed-effects models, which represent the key experimental features hypothesized to elicit IA while allowing generalisation across studies. The models’ random effects structures allow us to account for the variability between and within species,

studies, and subjects, thereby providing a stringent test of the population-level effect. The result is the most comprehensive account yet of the current state of evidence on the evolutionary origins of fairness.

The *IA hypothesis* and *disappointment hypothesis* make divergent empirical predictions. The *IA hypothesis* predicts higher rejection rates only when a partner is treated better than the subject; the *disappointment hypothesis* predicts higher rejection rates when a higher quality reward is presented, regardless of how the partner is treated. The goals of the present meta-analysis are twofold: first, to test the statistical robustness of the evidence in favour of the *IA hypothesis*, using a series of pre-registered analyses (see Prediction 1 below); and second, to examine how well the disappointment hypothesis fits the data, using complementary exploratory models (see Predictions 2 and 3 below). The analyses reported in this meta-analysis were thus designed to test three predictions:

- *Prediction 1*: Preferential treatment of a conspecific will increase rejection rates (this represents the main goal of this meta-analysis: testing the replicability of the *IA hypothesis*)
- *Prediction 2*: The presentation of a higher quality reward will increase rejection rates (testing the replicability of the *disappointment hypothesis*)
- *Prediction 3*: A partner receiving a higher quality reward than the subject will increase rejection rates over and above the mere presentation of a higher quality reward (*direct comparison of the IA and disappointment hypotheses*)

Methods

1. Protocol and registration

Apart from analyses marked as exploratory, search strategy, eligibility criteria, variable coding, models, and inferential criteria were pre-registered and made available online prior to data collection (<https://osf.io/q8ajw>) in accordance with PRISMA-IPD reporting guidelines⁶³. Unless stated otherwise, analyses conform to the pre-registration.

2. Inclusion criteria

2.a. Study type and design

Only experimental studies that include a manipulation designed to induce disadvantageous IA in the context of a dyadic interaction were included. We did not include studies in which IA was investigated in a group context (e.g.⁶⁴).

2.b. Species

All non-human species were included.

2.c. Manipulation

For a study to be included, the manipulation must create clear contrasting conditions where IA behaviour is either hypothesized to occur or not. This can be operationalized in one of three ways, (i) equal vs. unequal reward distribution (i.e., “reward inequity”); (ii) equal vs. unequal effort (i.e., “effort inequity”); (iii) presence vs. absence of a partner given an unequal reward distribution (another operationalization of reward inequity). Only conditions in which the subject receives some reward in each trial, and studies which include such conditions, were included. In studies that vary the value of the reward received by the subject, only low value reward conditions were included.

2.d. Outcome measures

Only studies with a clear, binary behavioural outcome variable that corresponds to whether or not the subject accepted an offered distribution were included. We did not include studies with nonbinary outcome measures (such as much of the literature about IA in dogs³²), since their trial-level data would not have been meaningfully comparable with the paradigmatic IA studies included in our dataset. We also excluded studies with other outcome variables, such as choice of fair vs. unfair experimenter⁶⁵, choice between two distributions³¹, neuronal signals⁶⁶, or cooperative behaviour⁶⁷.

3. Search strategy and study selection

We conducted our bibliographic searches in March 2021 on Web of Science and PubMed, for papers published from 2003 onwards (the year the first study reporting the existence of IA in animals was published²⁷), using the following queries:

Web of Science: ALL=((fairness OR inequity OR inequality) AND (animals OR “non-human” OR primates OR dogs OR monkeys OR birds))

PubMed: inequity aversion

Duplicates were removed using EndNote⁶⁸, after which the entries were imported into Covidence⁶⁹ for screening. Two relevant papers were published after the search was conducted and screened when their authors notified us of their existence^{47,53}. The first author undertook the preliminary title and abstract screening; the first and fourth authors both conducted full text review of papers identified as potentially eligible.

4. Data collection

The primary data of two eligible papers was available online^{46,51}. We contacted the authors of the remaining papers requesting access to the primary data of the relevant conditions. In doing so, we explained the goal of the study and linked to the pre-registration. We sent all authors our first request in April 2021, with the initial goal of ending data collection by September 2021. Since some authors required additional time to prepare the data, we extended this deadline to November 2021. We have not received any additional datasets between November 2021 and the submission of this meta-analysis.

5. *Variable Coding*

5.a. Outcome variable

rejection: In typical token exchange paradigms, which represent most of the studies included in this meta-analysis, a rejection could occur when the subject either (1) failed to provide the token to the experimenter or (2) did not accept the offered reward. Accordingly, we coded the variable “rejection” as 1 in either of those cases and 0 otherwise. In tray pulling and spoon holding paradigms, the variable “rejection” was coded as 1 for any trial in which the subject did not carry out the task or did not accept the reward, and 0 otherwise.

5.b. Predictor variables

In order to generalize across studies, we coded two new predictor variables, which correspond to the *IA hypothesis* and the disappointment hypothesis, respectively:

ia_condition: For IA to emerge, a trial should include a partner receiving a higher quality reward (“reward inequity”) or the same reward for less effort (“effort inequity”). Therefore, corresponding to the IA hypothesis, we coded the variable “ia_condition” as 1 when a partner was present and receiving a higher quality reward, or receiving the same reward for less effort, and 0 otherwise.

disappointment_condition: In order for food disappointment effects to emerge, a higher quality reward than the one the subject is offered must be saliently presented in the trial. Therefore, we coded the variable “disappointment_condition” as 1 for conditions in which a higher value reward was either: (1) handled by the human experimenter; or (2) handled by the partner (relevant to conditions where the reward was dispensed by a machine); and 0 otherwise. Note that every condition with inequity may also induce disappointment, but the reverse is not the case. For example, as addressed in the Introduction, many studies included conditions in which both subject and partner were shown a high value reward prior to exchanging but given a low value reward after returning the token. Since both participants are treated the same, these conditions are not inequitable, but the presentation of a higher

quality reward may be hypothesized to trigger food disappointment. In such conditions, *ia_condition* was coded as 0 and *disappointment_condition* as 1 (see SI Table 1 for a full breakdown of all conditions in the dataset and their respective coding).

6. *Data analysis*

All analyses were carried out in R⁷⁰ using RStudio⁷¹. We used the tidyverse package for data wrangling and visualization⁷². Generalized linear mixed effects models were run using the lme4 package⁷³. To test our hypotheses, we compared the full models with a respective null model lacking the test predictors but maintaining the same random effects structures using a likelihood ratio test. All reported p-values are two-tailed, with results considered significant at $p < 0.05$.

7. *Models*

All models are mixed-effects logistic regressions that predict the likelihood of a rejection in a given trial based on characteristics of the experimental condition. In order to address the fact that both IA and disappointment effects are likely to operate differently in different species, we included a random intercept for species as well as within-species random slopes. This allows the models to account for between-species differences in both overall rejection rates and the effect of the experimental manipulations. Similarly, we also included random intercepts and slopes for study and subject. As pre-registered, we ran each model separately for (1) all species included in the dataset; (2) all species reported to exhibit IA; (3) all primate species reported to exhibit IA; (4) chimpanzees; and (5) capuchin monkeys (see SI Note 1 for a list of species included in each category). These subsets of the data were included to avoid a population-level effect in some species being “washed out” by species never hypothesized to exhibit IA, and to assess the state of the evidence concerning the two species tested most often for IA (chimpanzees and capuchins). Note that for these last two populations we removed the random terms for species.

We chose to subset the species based on the reported rather than hypothesized existence of IA since only the former provides a clearly defined criterion. For example, while the cooperation hypothesis suggested that IA should only emerge in cooperative species, it is unclear what level of cooperation suffices; thus, while gorillas do cooperate with nonkin, it has been argued that their failure to exhibit IA supports the cooperation hypothesis since they are less cooperative than chimpanzees⁵³. Furthermore, since the cooperation hypothesis is

based on the empirical findings included in this meta-analysis⁵⁰, it is unclear whether one can meaningfully distinguish between the two.

Results

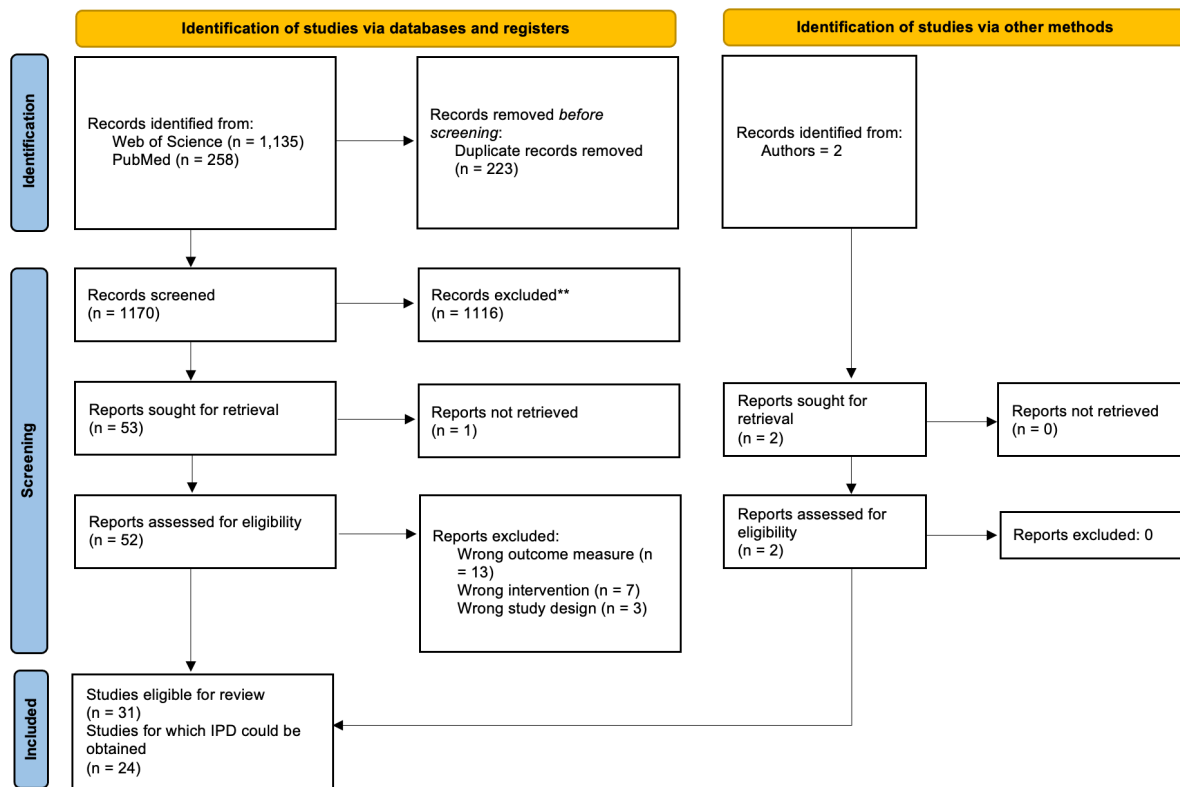
1. Data

We identified 29 eligible papers in the literature search (see Figure 1 for a PRISMA flow diagram of the selection process). One paper and one preprint were published after we conducted the literature search and added after their publication was brought to our attention^{47,53}. After requesting primary data from the authors of the eligible papers, we obtained the data for 24 studies.

Participation in an effortful task, such as exchanging a token for a food reward, has been identified as a necessary precondition for the emergence of IA⁸. Therefore, in the pre-registration, we intended to explicitly examine the effect of whether the subject had to carry out a task – as opposed to simply being handed a reward – on rejection rates, as well as the interaction between task and condition type. However, since only one of the studies in our dataset included both equitable and inequitable conditions without a task, obtaining a reliable estimate of the interaction effect would have been impossible. Therefore, in all analyses reported below, we only included conditions in which the subject had to carry out a task. This resulted in the exclusion of one out of the 24 studies⁴¹. The final dataset included 18 species, 302 subjects, and 60,430 observations. The included papers are listed in Table 1; the number of subjects and studies per species is summarized in Table 2.

Figure 1

PRISMA flow diagram for new systematic reviews



Note. Papers excluded prior to retrieval were deemed clearly irrelevant based on title and abstract screening. Wrong outcome measure included nonbinary outcome variables and behavioural measures not corresponding to acceptance of a distribution (such as affective responses and preference towards a more equitable experimenter). Wrong intervention included studies which investigated IA in nondyadic (e.g., group) settings, and studies which included collaborative tasks. One paper was found eligible according to our pre-registered criteria but excluded from the analyses following our decision to simplify the models and only include conditions in which the subject had to carry out a task, leading to the final count of 23 papers included in the dataset.

Table 1

Studies included in the combined dataset.

Study	Species	N	Task	IA found?
Bräuer et al., 2009 ⁴⁰	bonobos	5	token exchange	no
	chimpanzees	6		no
	orangutans	4		no

Brosnan & de Waal, 2003 ²⁷	capuchins	5	token exchange	yes (only females were studied)
Brosnan et al., 2005 ³⁵	chimpanzees	20	token exchange	only in some subjects
Brosnan et al., 2010 ³⁶	chimpanzees	16	token exchange	only in males
Brosnan et al., 2011 ⁴⁹	orangutans	5	token exchange	no
Brosnan et al., 2015 ³⁷	chimpanzees	24	token exchange	only in some subjects
Engelmann et al., 2017 ⁴⁶	chimpanzees	9	token exchange	no
Freeman et al., 2013 ⁵⁰	marmosets	10	token exchange	no
	owl monkeys	8		no
	squirrel monkeys	14		no
Heaney et al., 2017 ⁵¹	kea	4	token exchange	no
Hopper et al., 2013 ⁵⁷	rhesus macaques	20	token exchange	only for some subjects/ages
Hopper et al., 2014 ⁵²	chimpanzees	18	token exchange	only in females
Krasheninnikova et al., 2019 ⁴⁸	grey parrot	8	token exchange	no
	blue-throated macaw	6		no
	blue-headed macaw	6		no
	great green macaw	8		no
Laumer et al., 2020 ²⁹	Goffin's cockatoos	9	token exchange	only effort inequity
Massen et al., 2012 ⁷⁴	long-tailed macaques	15	tray pulling	only with moderate effort
McAuliffe et al., 2015 ⁴²	capuchins	6	tray pulling	no
Silberberg et al., 2009 ³⁸	capuchins	7	token exchange	no

Sosnowski et al., 2021 ⁵³	gorillas	8	token exchange	no
Talbot et al., 2011 ⁵⁴	squirrel monkeys	24	token exchange	no
Talbot et al., 2018 ⁷⁵	capuchins	15	token exchange	yes (only when subject received low value reward)
Titchener et al., unpublished ⁴⁷	long-tailed macaques	12	token exchange	no
van Wolkenten et al., 2007 ⁵⁵	capuchins	13	token exchange	yes
Wascher & Bugnyar, 2013 ²⁸	crows	6	token exchange	yes
	ravens	4		
Yasue et al., 2018 ³³	marmosets	6	spoon holding	yes

Note. “Token exchange” refers to the token exchange paradigm referenced throughout the paper. In “tray pulling” tasks, subjects need to pull a rope to make a tray with the reward accessible. In the “spoon holding” task, subjects held a spoon for 2 seconds before being handed a reward.

Table 2

Number of subjects and studies per species

Species	N	K
chimpanzees	81	6
capuchins	43	5
squirrel monkeys	38	2
long-tailed macaques	27	2
rhesus macaques	20	1
marmosets	16	2
Goffin’s cockatoos	9	1
orangutans	9	2
gorillas	8	1
great green macaw	8	1

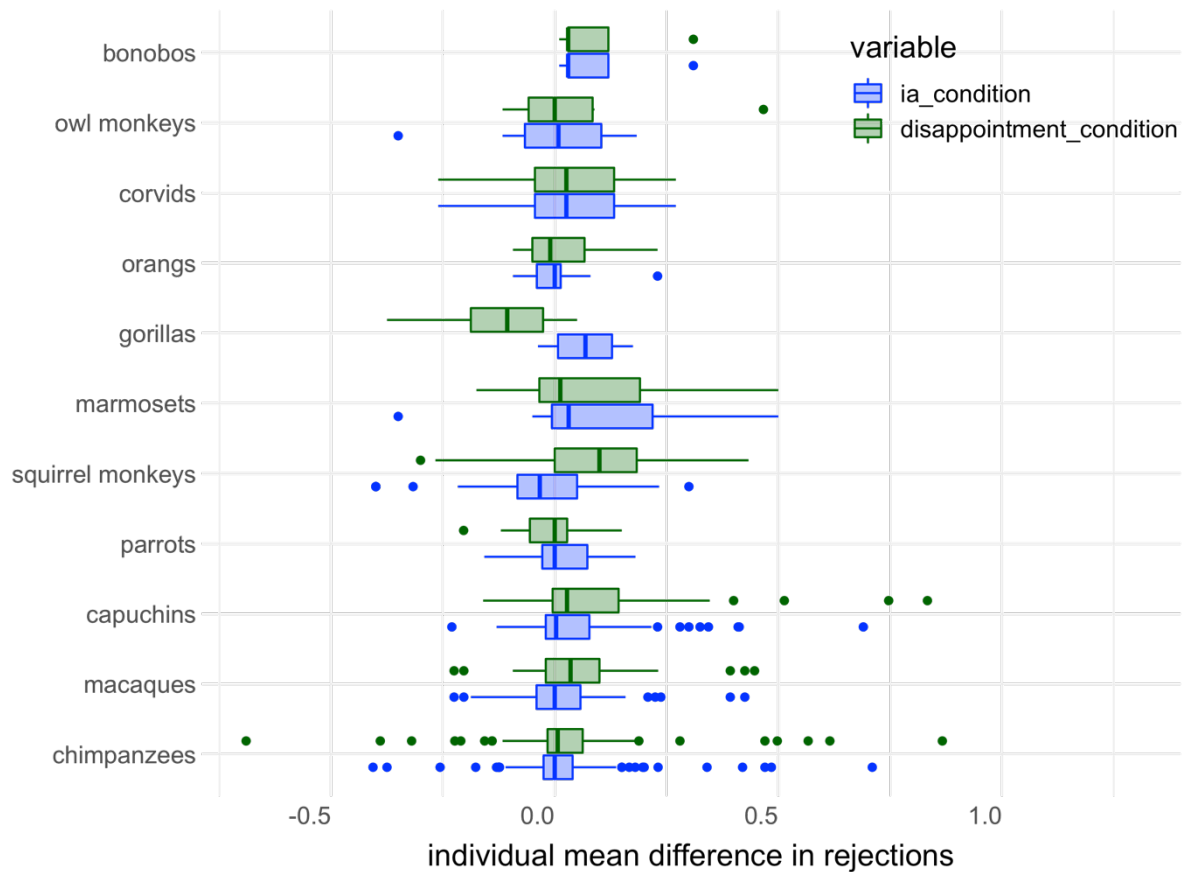
owl monkeys	8	1
grey parrot	8	1
blue-throated macaw	6	1
blue-headed macaw	6	1
crows	6	1
bonobos	5	1
kea	4	1
ravens	4	1

Note. Some subjects participated in multiple studies, and some studies included multiple species (see Table 1). N refers to number of subjects and K refers to number of studies.

Figure 2 offers a descriptive overview of the distribution of mean between-condition differences in individual rejections for ia_condition and disappointment_condition, respectively.

Figure 2

Boxplot of individual differences in mean rejection rates for ia_condition and disappointment_condition



Note. For each subject, we calculated the difference in mean rejection rates between condition types for ia_condition and disappointment_condition. Thus, e.g., for ia_condition, each data point is the mean rejection rate for ia_condition == 1 subtracted by the mean rejection rate for ia_condition == 0 for a particular subject. Numbers above 0 thus speak descriptively in favour of the respective hypothesis. For the purpose of this representation (but not the analyses), different parrot, macaque, and corvid species were grouped together. Species are arranged by sample size. Only conditions in which the subject had to carry out a task were included. Boxes extend from first to third quartile, with the line in the middle representing the median; whiskers represent quartile ± 1.5 x interquartile range; points represent outliers.

2.a. Model 1 (pre-registered): Does preferential treatment of a conspecific increase rejection rates in IA paradigms?

Our first model offers a straightforward test of the statistical robustness of the IA effect. According to the IA hypothesis, rejection rates should be higher in inequitable conditions. As described in section 5.b of the Methods, the variable ia_condition corresponds to whether the condition creates inequity between the subject and the partner, and therefore served as the predictor variable.

Model 1, which predicts the likelihood of an unsuccessful exchange in a given trial, thus took the following form:

$$\text{rejection} \sim \text{ia_condition} + (\text{ia_condition} \mid \text{species}) + (\text{ia_condition} \mid \text{study}) + (\text{ia_condition} \mid \text{subject})$$

The results of Model 1 are presented in Table 3. The IA effect was not significant for any of the species or species combinations investigated. It approached significance only in the model investigating all species (including those species not previously reported to exhibit IA). Contrary to what the IA hypothesis would suggest, in no other subset of the data did a statistically significant effect emerge. The model estimates for the by-species random effects are presented in Figure 3. Equivalent models investigating only reward inequity and only effort inequity are reported in SI Tables 2 and 3 and reveal no effect.

Table 3

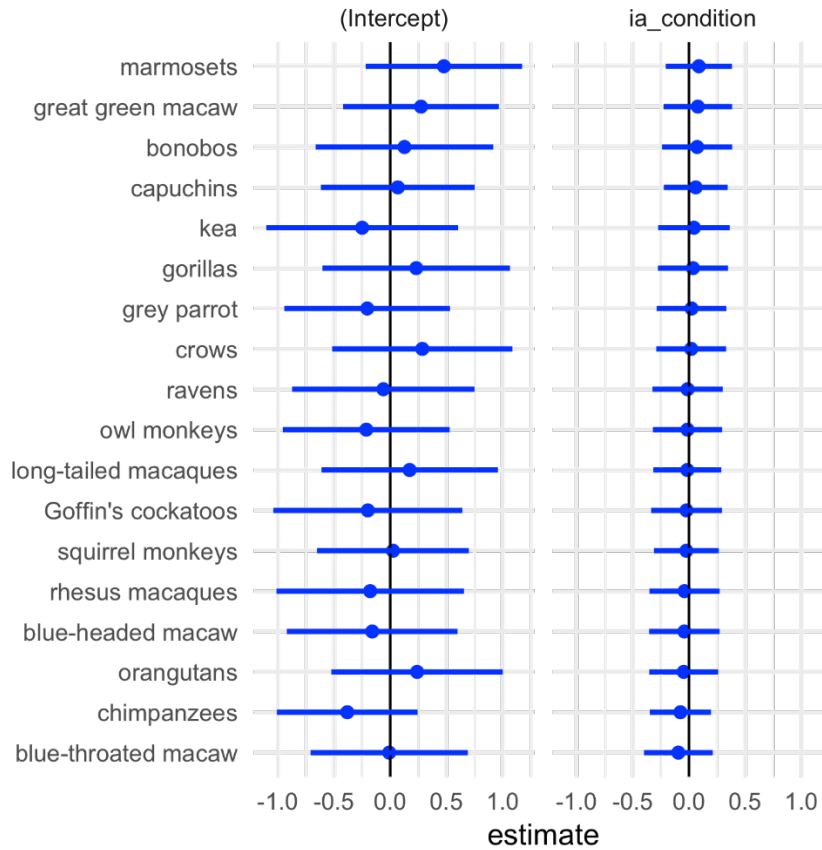
Overview of results from Model 1

Population	K	N	$\beta_{\text{ia_condition}}$	$p(\text{full-null comparison})$
All species	23	302	0.2565 [-0.0285; 0.5432]	$\chi^2(1) = 2.83, p = 0.0923$
IA reported species	18	204	0.1995 [-0.1849; 0.5712]	$\chi^2(1) = 1.34, p = 0.2478$
IA reported primates	16	5	0.2146 [-0.1465; 0.5942]	$\chi^2(1) = 1.22, p = .2692$
Chimpanzees	6	81	-0.0748 [-0.6397; 0.5143]	$\chi^2(1) = 0.05, p = 0.8133$
Capuchin monkeys	5	43	0.3747 [-0.2940; 0.9785]	$\chi^2(1) = 1.12, p = 0.2902$

Note. P-value for full-null comparison corresponds to a likelihood ratio test comparing the full model with a model consisting of the same random effects structure but no fixed predictors. N refers to number of species and K refers to number of studies.

Figure 3

Caterpillar plot of by-species random effects for Model 1 – all species



Note. By-species random intercepts and slopes for Model 1 – all species. Dots represent model estimates; error bars represent the predictor $\pm 2 \times \text{SE}$, approximating 95% confidence intervals. Predictors are centred at 0.

2.b. Model 2 (exploratory): Does the presentation of a higher quality reward increase rejection rates in IA paradigms?

As an exploratory follow-up analysis, we examined whether the salient presentation of a higher value reward than the one offered to the subject increases the likelihood of a rejection. Thus, we compared conditions in which a high-quality reward was either handled by a human experimenter or consumed by a partner with conditions in which the partner was either absent or received a low-quality reward (and the experimenter did not present a higher quality reward than the one given; see Section 5.b of the Methods for a detailed description and SI Table 1 for a breakdown of all conditions and their coding). To this end, we modified Model 1 by replacing `ia_condition` with `disappointment_condition` as the predictor:

$$\text{rejection} \sim \text{disappointment_condition} + (\text{disappointment_condition} \mid \text{species}) + (\text{disappointment_condition} \mid \text{study}) + (\text{disappointment_condition} \mid \text{subject})$$

The results of Model 2 are presented in Table 4. The models investigating all species, all species reported to exhibit IA, and all primate species reporting to exhibit IA revealed a significant effect of `disappointment_condition`, indicating that subjects were more likely to reject a low-quality reward when a higher quality reward was presented in the trial. The model testing chimpanzees revealed a non-significant but positive effect in favour of the disappointment hypothesis. Figure 4 represents all fixed effects estimates for Models 1 and 2.

Table 4

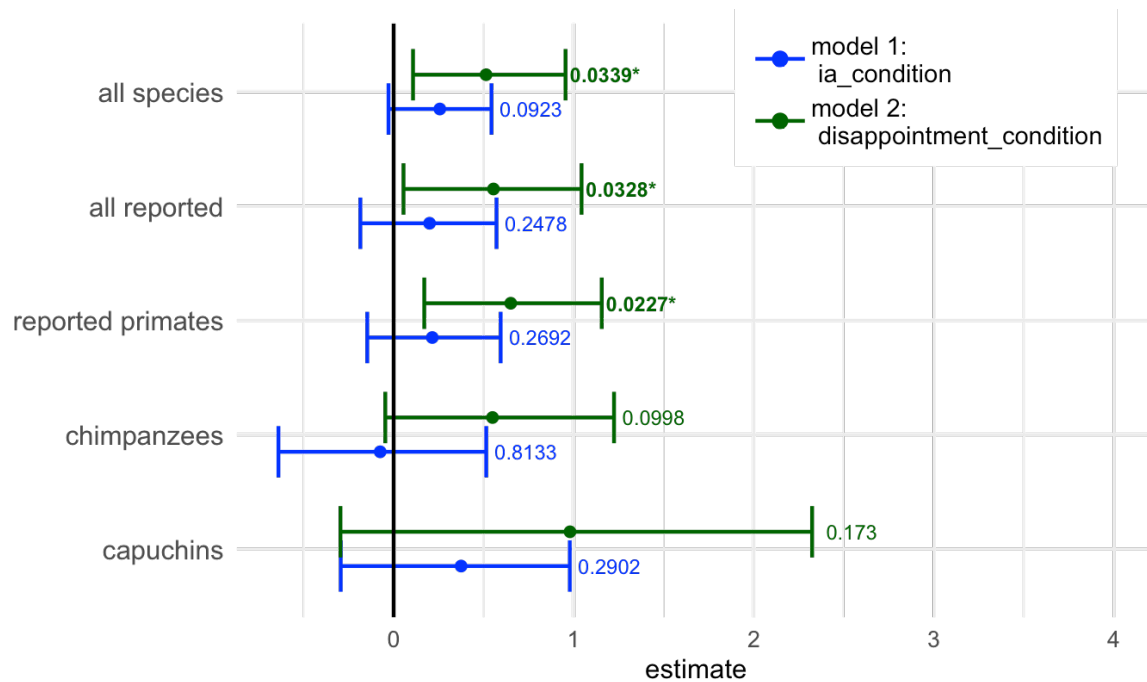
Overview of results from Model 2

Population	K	N	β disappointment_condition	p(full-null comparison)
All species	23	302	0.5131 [0.1076; 0.9545]	$\chi^2(1) = 4.50$, p = 0.0339
IA reported species	18	204	0.5544 [0.0547; 1.0435]	$\chi^2(1) = 4.56$, p = 0.0328
IA reported primates	16	5	0.6502 [0.1701; 1.1556]	$\chi^2(1) = 5.19$, p = 0.0227
Chimpanzees	6	81	0.5492 [-0.0464; 1.2239]	$\chi^2(1) = 2.71$, p = 0.0998
Capuchin monkeys	5	43	0.9796 [-0.2954; 2.3239]	$\chi^2(1) = 1.86$, p = 0.173

Note. P-value for full-null comparison corresponds to a likelihood ratio test comparing the full model with a model consisting of the same random effects structure but no fixed predictors. N refers to number of species and K refers to number of studies.

Figure 4

Model estimates for Models 1 and 2



Note. Dots represent log-scale model coefficient estimates for fixed effects (“ia_condition” for Model 1 in blue, “disappointment_condition” for Model 2 in green). Error bars represent bootstrapped 95% confidence intervals. P-values above error bars refer to full-null model comparison (see Section 4 in Methods).

2.c. Model 3 (exploratory): Does partner receiving a higher quality reward than the subject increase rejection rates over and above the mere presentation of a higher quality reward?

For our final exploratory model, we investigated whether the existence of inequity – i.e., a partner receiving a better reward, or the same reward for less effort – increases the likelihood of a rejection over and above food disappointment (the salient presentation of a higher-quality reward). To this end, we again ran Model 1, this time only including conditions in which a higher quality reward was presented (i.e., `disappointment_condition == 1`). Furthermore, to avoid confounding by study, we only included studies with conditions which induced food disappointment without inequity (all studies had conditions inducing food disappointment and inequity).

The results are presented in Table 5. In all populations tested, the models revealed no effect of inequity beyond that of disappointment. Equivalent models looking only at reward inequity are presented in SI Table 4 and show the same pattern of results.

Table 5

Overview of results from Model 3

Population	K	N	$\beta_{\text{ia_condition}}$	p(full-null comparison)
All species	17	244	-0.0011 [-0.3923; 0.3470]	$\chi^2(1) = 0, p = 0.992$
IA reported species	12	155	-0.0187 [-0.4493; 0.4035]	$\chi^2(1) = 0.01, p = 0.9253$
IA reported primates	11	146	0.0431 [-0.3402; 0.4198]	$\chi^2(1) = 0.05, p = 0.8222$
Chimpanzees	5	75	-0.0793 [-0.6779; 0.6364]	$\chi^2(1) = 0.05, p = 0.8208$
Capuchin monkeys	3	30	0.3320 [-0.1561; 0.8300]	$\chi^2(1) = 1.11, p = 0.2928$

Note. P-value for full-null comparison corresponds to a likelihood ratio test comparing the full model with a model consisting of the same random effects structure but no fixed predictors. N refers to number of species and K refers to number of studies.

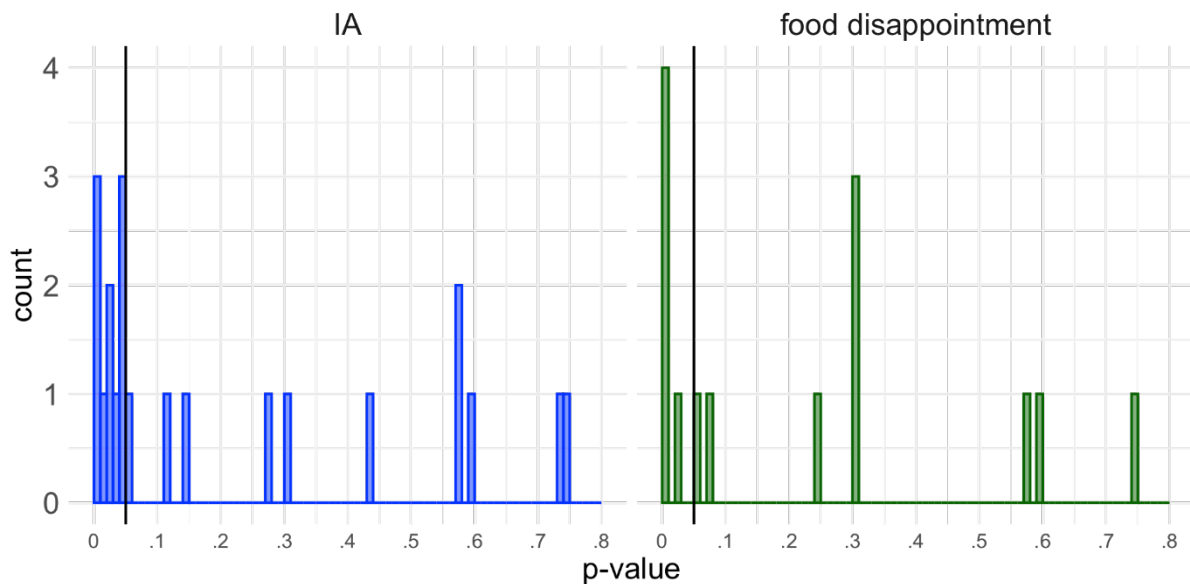
3. Estimating the risk of publication bias

To estimate the risk of publication bias, we first scanned all eligible published papers for the p-value corresponding to the strictest test reported as evidence in favour of the IA and food disappointment hypotheses. For example, in any paper that included both individual contrast and inequity conditions, we extracted the p-value of the test differentiating these conditions as the p-value in favour of the IA hypothesis (see SI Table 8 for full list of p-values). For papers that reported results from multiple species, we included one p-value for each species; otherwise, we only included one p-value from each paper to maintain statistical independence⁷⁶. Since some papers reported neither exact (or relevant) p-values, nor the test statistics required to compute such p-values, we were only able to extract 22 p-values from 19 papers for the IA hypothesis, and 14 p-values from 12 papers for the disappointment hypothesis. Of these, 10 were significant for the IA hypothesis, and 5 for the disappointment hypothesis (at $\alpha < 0.05$). This number is insufficient for reliably calculating the false discovery risk⁷⁷. However, a descriptive histogram of all p-values is presented in Figure 5.

The small number of p-values precludes any clear conclusions regarding the risk of publication bias. Nevertheless, the form of the histogram may cautiously be taken to suggest that such risk is present for the IA hypothesis. Note that the p-value at $0.05 < p < 0.06$ was extracted from a paper that reported the result as significant (as it would be in a one-tailed test). Furthermore, 30% of significant p-values are in the range of $0.04 < p < 0.05$, and there is a drop in the distribution at $p = 0.05$. For the disappointment hypothesis, the distribution appears to be left-skewed, tentatively suggesting a low false discovery risk⁷⁸.

Figure 5

Histogram of p-values in favour of the IA hypothesis and food disappointment hypothesis



Discussion

We investigated whether nonhuman animals exhibit disadvantageous IA – a main building block of the human sense of fairness – using an individual participant data meta-analysis. To generalize across studies using varying procedures, we obtained the primary data of eligible studies, and coded a new variable corresponding to whether the condition was inequitable according to the *IA hypothesis* (i.e., is a partner present and receiving better treatment?). We then used this variable as a predictor in a series of pre-registered mixed-effects logistic regressions, which we ran separately for all species in the dataset, all species previously reported to exhibit IA, all primate species previously reported to exhibit IA, chimpanzees, and capuchin monkeys. None of the tests revealed a significant effect of inequity manipulations on rejection rates. These pre-registered analyses combined two forms of IA: reward and effort inequity. Exploratory models testing these two forms separately are reported in SI Tables 2 and 3 and likewise show no significant effect. We thus find no evidence for the hypothesis that IA is shared with other species.

These findings shed new light on our understanding of the evolution of fairness. A full-fledged sense of fairness, which involves both disadvantageous and advantageous IA, is generally considered to be a uniquely human adaptation⁷⁹. What remains controversial is

whether nonhuman animals display any of the elemental strands of fairness which coalesce in comprehensive human concern for equity. Our results do not support the assumption that disadvantageous IA underlies responses to unfair distributions across species. Rather, they suggest that nonhuman species may rely on other mechanisms, such as dominance¹⁸, to solve the challenge of distributing resources. Humans may differ from other species in this respect due to high levels of interdependence with social partners¹⁷, in combination with a history of selective pressures favouring high levels of cooperation^{80,81}. Another possibility is that nonhuman animals would benefit from social comparison-based fairness, but lack the cognitive (and possibly motivational) resources to track patterns of unequal resource distributions. After all, the mechanism proposed by the *IA hypothesis* is computationally demanding (and significantly more demanding than the mechanism posited by the *disappointment hypothesis*): To protest the more favourable treatment of the partner, a subject would have to keep track of how the experimenter treats both subject and partner, compare these treatments along a principle such as equality, represent the fact that the experimenter could have treated both the same, and based on these processes infer that the experimenter wronged the subject. It is possible that at least some nonhuman species lack the working memory capacity and inferential abilities required for such a complex computation^{82,83} (although chimpanzees do appear to be able to compare alternative possibilities⁸⁴, suggesting that in some taxa motivational factors might be more important).

Which processes, if not IA, might explain subjects' rejection of low-quality rewards in the included studies? Two versions of the *disappointment hypothesis* – the *food disappointment hypothesis* and the *social disappointment hypothesis* – both maintain that subjects' rejections are not grounded in social comparison, but rather stem from frustration at receiving a low- rather than a high-quality reward (independent of the partner's payoffs). According to the *food disappointment hypothesis* (also referred to in the literature as “individual contrast effects”³⁶), subjects are experiencing simple disappointment in not getting the higher quality reward they were expecting. Shifting attention to the relationship between the human experimenter and the subject, the *social disappointment hypothesis* proposes that rejections are fuelled by subjects' disappointment that the human is not treating them as well as they could – regardless of what the partner is getting^{46,47,85}. Notably, social disappointment effects can emerge even in studies not specifically designed to test them, whenever the human experimenter handles a higher quality reward than the one the subject receives (e.g., by serving it either to an empty cage or to a conspecific). The only conditions that can be expected to induce food disappointment but not social disappointment are those

where rewards are dispensed by a machine. Since only two studies in our dataset included conditions with both human and machine distributors^{46,47}, we are limited in our ability to tease apart the two versions of the *disappointment hypothesis*. However, we can say that the data is consistent with both. We found a significant effect of food disappointment for all species in the dataset, all species reported to exhibit IA, and all primate species reported to exhibit IA (in the models investigating specifically chimpanzees and capuchin monkeys, effects were positive but non-significant). Models testing the social disappointment hypothesis are reported in the Supplementary Information (Tables 5 & 6) and show the same pattern of results.

Our meta-analysis has several important limitations. We were able to obtain the data for 24 out of 31 eligible studies. This is a relatively large share for an IPD meta-analysis, but nevertheless omits several relevant studies. While we have no reason to suspect any systematic bias against the IA hypothesis in the studies we could obtain the data for, it is possible that an even higher powered investigation would have led to different or perhaps stronger conclusions. Crucially, only one of the seven omitted studies reported a positive finding (i.e. a finding in line with the *IA hypothesis*, see SI Table 7). We thus believe it would be highly unlikely that the results of our meta-analysis would have qualitatively changed if we had been able to include all studies. A second limitation of the present study is that simple frustration effects (i.e., frustration that one is receiving a lower quality reward than one has previously received) have been argued to influence rejections in IA paradigms^{38,39,44}, and were not tested in this meta-analysis since our dataset lacks this information. Furthermore, to be able to meaningfully compare results, we limited our inclusion criteria to procedures with dyadic tasks (including a subject and a partner) and binary acceptance measures, which constitute the paradigmatic IA studies. This led to the exclusion of studies which used more collaborative tasks (e.g. bar pulling paradigms, where two conspecifics work together to produce mutual rewards⁸⁶ and collaborative foraging tasks in cleaner fish, where a male and a female work together to gain access to a food reward⁸⁷). Since the sense of fairness functions to support cooperation^{88,89}, an analysis of these studies could deliver further insights into its evolutionary origins. These criteria also led to the exclusion of all canine studies, which use nonbinary outcome measures (e.g., number of trials the subject participated in¹⁸), and have often reported evidence for IA^{65,90–92}. Finally, as always, the absence of evidence for IA in nonhuman animals should not be taken as evidence of absence. Even in studies reporting the existence of IA, it was often only certain individuals that responded to the manipulation, and the IA effect may be highly context dependent^{23,24}. For example, time living together³⁵,

sex^{25,26}, age²⁷, and personality dimensions such as “extraversion”²⁴ have all been reported to predict responses to inequity. Testing the effect of different contextual, demographic or personality-related variables was beyond the scope of the current study and would require an even larger dataset. Nevertheless, such a highly context- and individual-specific effect is unlikely to have played a substantial role in the evolution of cooperation, and it is questionable to what degree it could explain the emergence of such a robust phenomenon as disadvantageous IA in humans.

Our findings set the stage for further explorations of the mechanisms underlying cooperation in nonhumans. Our sense of fairness consists, to a large extent, in expectations for how we want to (and should) be treated in relation to others; it is this triadic notion of fairness that has been tested in nonhuman species⁸. It is possible that individuals in other species do not form these kinds of triadic expectations, but nevertheless form complex dyadic expectations towards specific social partners⁸⁵. Indeed, theorists have suggested that individuals across species respond with anger to violations of social expectations^{93,94}. Our understanding of the origins of fairness would benefit greatly from identifying what these expectations are, how they are formed, and which cognitive mechanisms support them. Fairness is a fundamental feature of human sociality; further work on the motivational, emotional, and cognitive underpinnings of cooperation in other species will contribute to a greater understanding of its evolutionary history.

Acknowledgments

We thank R. Mundry for statistical advice and M.C. Frank for advice on conducting a meta-analysis. We thank S.F. Brosnan for invaluable feedback on an earlier version of the manuscript and for generally contributing generously to this meta-analysis. Furthermore, we thank all authors who conducted the primary studies and shared their data with us: E. Addressi, M. Ahlgren, J.R. Anderson, A.M.I. Auersperg, B.J. Bernacky, P.R. Blake, D.R. Blanco, J. Bräuer, S.F. Brosnan, D. Brucks, N. Buffenoir, T. Bugnyar, J. Call, C. Carminito, J. Carrigan, L.W. Chang, J.B. Clift, L. Crescimbene, F.B.M. de Waal, L.A. Drayton, J.L. Essler, J. Fischer, T. Flemming, H.D. Freeman, S.D. Gosling, R.D. Gray, M. Heaney, E. Herrmann, A.N. Holmes, L.M. Hopper, T. Hüser, N. Ichinohe, N. Kawai, S. Keupp, A. Krasheninnikova, S.P. Lambeth, I.B. Laumer, K.L. Leimgruber, K.L. Leverett, M. Lorck-Tympner, J.J.M. Massen, L. Mayo, K. McAuliffe, K. Nakagaki, A. Nakagami, A.E. Parrish, A. Paukner, L. Prétôt, S. Richey, L.R. Santos, S.J. Schapiro, H. Scherberger, H.C. Schiff, N. Schultz-Darken, A. Silberberg, M.J. Sosnowski, D. Soulet, R. Spaulding, B.M. Spruijt,

E.H.M. Sterck, T.S. Stoinski, J. Sullivan, C. Talbot, A.H. Taylor, C. Thiriau, R. Titchener, M. Tomasello, L.M. Van den Berg, M. van Wolkenten, E. Visalberghi, A. von Bayern, B. Wakonig, C.A.F. Wascher, J. Watzek, L.E. Williams, and M. Yasue.

Data Availability Statement

Data is available on request (contingent upon approval from the authors of the original manuscripts).

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