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A comparative perspective on the human sense of justice

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ABSTRACT

Humans are not the only species that cares about inequality; individuals in some other species also respond negatively when a social partner receives a better outcome than they do and there is (limited) evidence of apes even responding when they receive more than their partner. The distribution of this reaction across species and individual's responses in experimental cooperation tasks suggests that the response to inequity evolved in the context of cooperation, potentially to help individuals recognize – and thereby avoid – partners who take more than their share. Even though this might cost individuals an absolute gain in the short term, they ultimately benefit by not being relatively disadvantaged. Thus, while clearly there are cultural influences on humans' responses to inequity, the basic response is biologically rooted, and comparative work will help us better understand why and in what contexts the responses evolved so that we can better understand how our moral and legal systems evolved in the way in which they did and thereby work to design institutions and outcomes that better benefit everyone.

One day, you witness a bully run up to Emily and attempt to take her treat. She screams and holds out her hand, asking for support. Several others join her, also screaming at the bully, who slowly retreats, while Emily resumes eating. Perhaps this is not that surprising. But if I told you that I watched this play out among a group of chimpanzees? Perhaps that would surprise you. Humans, of course, have strong intuitions about justice in such circumstances, assuming intent (the bully tried to *steal* the treat) and empathizing with the victim (poor Emily!). We carry this a step further with our formalized legal system, which dictates and enforces consequences for breaking the rules that are (in principle) consistently applied across all individuals. But where did this tendency to justice come from? Do humans alone possess it, or are there elements of this that are shared with other species, like Emily and her friends? If it is the latter, we can use a comparative approach to understand how and, potentially, why these behaviors evolved in humans, which provides a stronger framework for understanding our own behavior.

Emerging research suggests that indeed, species other than humans share some of these elements and that they are informative about the evolution of justice or morality (Bekoff, 2009; Brosnan, 2014; Flack & de Waal, 2000). For instance, other species appear to have expectations about how they (and possibly others) should be treated and they respond negatively when those expectations are violated. Chimpanzees show third-party interventions, in which one member of the group intervenes in an interaction among others in a way that suggests that they are not doing so for their own immediate benefit (de Waal, 1982; von Rohr et al., 2012) and several species show policing behavior, in which powerful or dominant (they usually coincide) individuals in the group intervene in a non-partisan way to stop aggression or conflict (i.e., Flack, Girvan, de Waal, & Krakauer, 2006). Of course, policing benefits the dominant in the long run by maintaining group cohesion and peace, but there are not immediate benefits, and individuals even police their own kin and allies, suggesting that this is not simply a way to curry favor with supporters. Indeed, apes may even recognize if they "deserve it"; bonobos' calls soliciting help after being attacked are acoustically different depending on whether or not they were the ones who instigated (Clay, Ravaux, de Waal, & Zuberbühler, 2016).

These examples are certainly suggestive, but causality is difficult or impossible to determine from observations. Thus, psychologists and economists have turned to experimental paradigms to determine how humans respond to unfairness and how their reaction changes across contexts. Since the early 2000s a line of work has explored how other species respond when they are treated inequitably and, in particular, if they get less than a conspecific partner (Brosnan & de Waal, 2003). In a typical task, two individuals take turns completing a task, or work together to complete it, for which one gets a more preferred reward than the other. We then measure how the animals respond to the unequal outcome. Their responses suggest that humans are not the only species that cares about their outcomes relative to others; other animals may

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refuse to participate, or even turn down otherwise preferred rewards, when they get less than a partner (Brosnan & de Waal, 2014). Moreover, chimpanzees may also respond when they get *more* than a partner (Brosnan, Talbot, Ahlgren, Lambeth, & Schapiro, 2010). In humans, these reactions form the basis of the sense of fairness, which permeates our lives and is at the foundation of our legal systems, suggesting that studying them will help us understand how this sense of fairness evolved. In particular, understanding what conditions selected for the sense of fairness, and what social, ecological and contextual factors influence it, will give us a better understanding of the contexts in which we might expect to see reactions to fairness and how it will influence when and how people do – or do not – respond (Brosnan, 2006; Brosnan & de Waal, 2014).

1. A comparative approach to studying behavior

What can we learn about humans from studying other species? Every species has unique selective pressures that shape their behavior, but humans' advanced cognitive abilities and distinctive traits, such as complex language and culture, seem to set us apart. Nonetheless, we evolved from the same ancestors and studying other species is vital to help us understand how our behavior evolved to the forms we see today (Boehm, 1999). If we find a trait shared among multiple species, we can start to unpack how and under what circumstances it evolved. Humans are primates, so there is a tendency to focus on other primates to study the evolution of human behavior, but it is important to study all animals, not just the primates, in order to gain a broader understanding of how ecological and social contexts can shape species' behaviors.

Traits shared across species can come about in one of two ways. Homologous traits are shared because they were present in a common ancestor. A good example of this is winged flight in birds, which evolved from a common ancestor to modern birds and is broadly present across the avian taxon, but is not present in non-avian reptiles, dating the emergence of the trait. Convergent traits are shared because the species faced similar selective pressures. In keeping with our above example, bats, (most) birds, and (some) insects have winged flight, but obviously do not share a common ancestor that had winged flight. Instead, these different species reacted to similar pressures (i.e., finding food, escaping predators) with the same solution. Convergence is particularly useful in identifying what ecological or social factors shared by the species may have been the underlying selective pressure for the trait in question. This can be tested by seeking out species (especially those that are closely related) that differ on the factor in question and seeing if the trait differs in the predicted way. Finally, homology cannot be assumed just because species are relatively close phylogenetically; for example, although large brains relative to body size are common in the primate family, some primates, such as chimpanzees and capuchin monkeys, have particularly large brain-to-body ratios even for primates (Jerison, 1985; Rilling & Insel, 1999), suggesting convergence within the taxon.

The same solution, however, does not mean the same underlying mechanism; birds' and bats' wings are based on a modified forelimb in a quadruped, whereas insects' flight is the result of a modified exoskeleton. This is a critical point, as each trait has both a function and a mechanism. Niko Tinbergen outlined four question that are essential to understanding any behavior: causation, ontogeny, evolution and survival value (Tinbergen, 1963). The first two of these relate to the underlying mechanisms, that is, how the trait develops, whether it is learned and, if so, how, and the neural, endocrine, cognitive, and other physiological mechanisms that help instantiate the behavior in organisms. The latter two relate to function: from what previous trait did it evolve and why is it beneficial? When looking at the evolution of behavior, then, it is important to recognize that two animals can share a trait with a similar function, but different underlying mechanisms, and the same mechanism can evolve to solve different functions.

Finally, species may manifest the same trait differently, or have experienced distinctive selective pressures on a shared trait. Thus, what we are often looking for is related behaviors that may be an aspect of or a precursor to the trait in question. To continue our example of wings, fossils indicate that feathers came first, and may have initially evolved for thermoregulatory or ornamental function and were later adapted for flight. Similarly, when looking for behaviors such as fairness, we do not expect to see a sense of fairness in other species, but we may see related behaviors that tell us something about the context in which it evolved or for what purposes these behaviors emerged.

2. Inequity response in non-humans

In humans, a sense of fairness is the set of norms via which we compare outcomes between ourselves and others, or among others, and judge whether they meet some standard of equitability. This standard is typically socially determined and for most situations will require language to develop. Complex traits such as these will not manifest in the same way in other species as they does in humans. Thus, as has been so successfully done with other complex traits, such as language or culture, we study fairness by breaking it down into a series of simpler questions that are experimentally tractable. The most basic division is between so-called disadvantageous inequity, or receiving less than others, and advantageous inequity, or receiving more than others. Most studies of other species to date have focused on disadvantageous inequity. It seems intuitive that getting less than another is more frustrating than getting more, because selection should always favor behaviors that ultimately benefit oneself relative to others, making it more likely to elicit a response. However, one of the experimental challenges of testing other species is that we are not testing whether they *notice* inequity, but whether they are sufficiently upset by it to respond behaviorally to it. Of course, disadvantageous inequity in and of itself isn't a sense of fairness; we would consider that an interest in everyone's wellbeing, not just one's own, is needed for a true sense of fairness. Thus, while it is less commonly studied, we are also interested in how subjects respond when they get more than a social partner.

Despite the fact that researchers have explored contrast effects, or how subjects respond when their outcomes differ from what they expected, for nearly a century (Tinklepaugh, 1928), the first experiment explicitly aimed at determining whether those expectations could be based on what others received is fairly recent. Frans de Waal and I paired capuchins monkeys with a member of their social group and gauged their reactions when they received a less preferred reward than a partner for trading a token with the experimenter (Brosnan & de Waal, 2003). The monkeys were more likely to refuse the less preferred food, a piece of cucumber, when their partner got a more-preferred grape than when both received a cucumber piece. Moreover, we needed to rule out the possibility that they refused the cucumbers more often because their attention was repeatedly called to the grape (i.e., a contrast effect), but not because their partner got the grape per se. Thus, we included a control condition in which grapes accumulated each trial in the partner's (empty) enclosure to determine how seeing grapes that they could not access influenced responses. In later experiments, to control for social dynamics, our control condition included both the subject and partner being shown a grape prior to exchanging for a cucumber (monkeys may be uneasy when they are alone since they are typically with their group; see e.g., Brosnan, Schiff, & de Waal, 2005; Talbot et al., 2018). In neither control condition was there a strong effect, suggesting that the response was specific to having observed the partner's previously received food.

Since that time, researchers have demonstrated inequity in at least some cases in a variety of species (discussed in The Evolution of Fairness, below), including other primates, dogs (Brucks et al., 2017; Brucks, Range, & Marshall-Pescini, 2017; Range, Horn, Viranyi, & Huber, 2009; but see Horowitz, 2012), wolves (Essler, Marshall-Pescini, & Range, 2017), several species of birds (Wascher & Bugnyar, 2013; see Massen, Ritter, & Bugnyar, 2015 for a related task; but see Heaney, Gray, & Taylor, 2017; Di Lascio, Nyffeler, Bshary, & Bugnyar, 2012), and rats

(Oberliessen et al., 2016). Aside from expanding our understanding of the phylogeny of inequity responses, variability in outcomes has been very informative about the environmental, cognitive, and personal factors that may impact responses to inequity, clarifying the factors that are necessary for the expression of inequity responses and the conditions that likely selected for precursors to fairness.

Subsequent to the initial study, there were a flurry of similar studies on capuchins and chimpanzees that did not include a task to complete to obtain the reward; instead, subjects were simply handed the rewards for “free” (Brauer, Call, & Tomasello, 2006; Dubreuil, Gentile, & Visalberghi, 2006; Roma, Silberberg, Ruggiero, & Suomi, 2006). In these studies, subjects accepted lower value rewards, suggesting that something about completing a task affected their responses. However, there were other differences in the procedures, not to mention that the subjects were from different labs and therefore had different experiences and histories, so we could not be certain that the task was the critical factor. Thus, we followed up with a study in which this “gift reward” condition was included in the same study with a task-based inequity condition and the aforementioned control conditions (Brosnan et al., 2005, 2010; van Wolkenten, Brosnan, & de Waal, 2007). Subjects participated less often in the inequity condition, but never refused in the gift reward condition, indicating that a task was needed to elicit the inequity response.

There are (at least) two possible explanations for this (Brosnan et al., 2010). More prosaically, captive primates routinely are handed food, and who has access is strongly impacted by social factors, such as rank. Thus, in this context without a task, subjects may have expected to get a different reward than a social partner based on their history of typical feeding interactions. Of more theoretical interest, fairness in humans is hypothesized to be a mechanism by which individuals recognize good cooperation partners (Brosnan, 2006; Brosnan & de Waal, 2014; Fehr & Schmidt, 1999). If this is the case in other species, too, it may be that working side-by-side on a task triggered a sense of cooperation that made inequity more salient. As I will discuss later, inequitable outcomes impact the success of cooperative tasks, supporting this interpretation.

Humans also care about the fairness of procedures (Lind & Tyler, 1998), not just the outcome of the interaction. Indeed, humans will accept an unequal outcome if the procedures that led to the outcome are deemed fair. While other species appear to view “free rewards” differently from those that they must work for, no effect of procedure has been found in primates’ responses; they are no more likely to refuse rewards if their partner has to do less work to get the reward than they do (i.e., the subjects must complete fewer trades, or has to do a task whereas their partner gets the reward for free; Brosnan et al., 2010; van Wolkenten et al., 2007). In addition, primates’ behavior does not change if they, but not their partner, have a delay inserted between completing the task and receiving the reward (Brosnan et al., 2010; Brosnan, Flemming, Talbot, Mayo, & Stoinski, 2011; Sosnowski et al., 2021). While of course there may be other situations in which the procedure is salient, evidence thus far suggests that primates are more focused on outcomes than how those outcomes were achieved. This may be because outcomes are observable and quantifiable, whereas it may be difficult to know whether procedures were fair without a knowledge of unobservable underlying factors such as motivation and intent (c.f. Brosnan & Bshary, 2016; Packer, 1988).

On the other hand, primates may be more influenced by the magnitude of the reward than are humans. Most studies suggest that humans’ decisions in the context of inequity are only marginally influenced by reward level. In the Ultimatum Game, an economic game in which the subject must decide whether to accept a proposed distribution, or refuse, blocking both themselves and the proposer from getting any money, human participants generally do not change their behavior depending on the amount at stake (Larney, Rotella, & Barclay, 2019), or may even be *more* likely to refuse when greater amounts of money were involved (Hoffman, McCabe, & Smith, 1996). Primates, however, are more likely to refuse lower value rewards. A recent study comparing various combinations of low, medium and high value rewards found that subjects only refused when they got a low value reward, irrespective of what the partner received, suggesting that they will not give up a reward that is too high value (Talbot et al., 2018).

There are two important ramifications to the impact of rewards on behavior. First, this may explain some of the variability in the non-human inequity literature; although most authors pre-test to ensure that their subjects prefer the better reward(s), we do not know how well individuals like the rewards relative to one another. Thus, some subjects may be tested with “low-value” rewards that are less preferred – but are nonetheless too good to refuse. Second, and related to this, what we are measuring in other species is whether they are willing to give up rewards, not whether they *notice* inequity. Thus, we may be underestimating the contexts in which other species notice inequity because we measure their behavioral responses rather than asking how they feel, and responding is costly, requiring them to sacrifice a food that, under other circumstances, they like well enough to accept. Indeed, while children and dogs accept rewards that are less valuable than a partner’s, children verbally express dissatisfaction with the outcome (LoBue, Nishida, Chiong, DeLoache, & Haidt, 2011) and dogs spend less time with both the experimenter and the other dog subsequent to this (Brucks, Essler, Marshall-Pescini, & Range, 2016). While there is no similar study in primates, new techniques that allow us to measure physiology non-invasively, such as infra-red thermography (measuring changes in facial temperature, which is believed to correlate with changes in affect; Barrault et al., 2022), eye tracking (Sosnowski, Kano, & Brosnan, 2022), and non-invasive sampling of hormones that change over relatively short timeframes (e.g., salivary cortisol; Verspeek et al., 2021) may allow us to explore this question more deeply.

Compounding these issues, primates’ experiences with food outside of the context of the experiments also appears to influence their behavior in these studies. A recent analysis suggests that food restricted subjects are less likely to refuse in inequity tests than those with freer access, particularly to high value foods (Schweinfurth & Call, 2021). Thus, refusing to participate because of inequity may be a luxury afforded those who have enough resources to easily give up a moderately valued food item, but even those monkeys who are well resourced are unlikely to give up too valuable of a food.

Individual factors may be influencing subjects’ responses above and beyond these procedural issues. Dominant individuals sometimes respond differently than more subordinate ones, with more dominant animals showing a stronger reaction to receiving less (Brauer et al., 2006; Brosnan et al., 2010), although this is not consistent across studies. This is perhaps not surprising, both because more dominant animals are used to receiving better outcomes and because, from an evolutionary perspective, more dominant animals have more to lose. Moreover, intuitively one would expect subjects’ relationships to impact responses. Humans, for instance, are more likely to respond negatively to inequity with individuals with whom they do not have a close relationship, yet accept it with close social partner (Clark & Grote, 2003). This may also be true with chimpanzees. A previous study found that individuals who had been in the same group for their entire lives rarely responded to inequity, whereas those from a group that had been created after they were adults did so (Brosnan et al., 2005). While this is suggestive, especially since the chimpanzees were housed at the same facility and tested by the same experimenters, it is a still correlational. Moreover, counter examples exist; male (but not female) marmosets are more likely to respond to inequity when paired with their mate than when with a stranger (possibly because no offspring were housed with them; Mustoe, Harnisch, Hochfelder, Cavanaugh, & French, 2016). Unfortunately this has been hard to test because most studies involve voluntary participation; a previous study meant to do so found that chimpanzees who had better relationships were more likely to pair for the study, but that meant that it was impossible to test how relationships influenced responses to inequity. Instead, variability in this study was related to subjects’ personalities, with subjects who were more social (i.e., ranked highly on the dimensions of extraversion and agreeableness) showing stronger reactions to inequity whereas those who were more human-oriented responded more strongly to contrast (Brosnan et al., 2015). New studies are testing subjects with the entire social group present to try to capture data on those pairs who may be willing to occasionally work together, but will not separate from the group together (Vale et al., 2022).

Finally, as I mentioned above, a true sense of fairness requires that individuals also notice when they are *advantaged* relative to a social partner. Little evidence exists for advantageous inequity aversion in primates, which is not necessarily surprising as this behavioral reaction requires giving up a highly preferred reward, which, as discussed earlier, is challenging. However, an exception is chimpanzees, who are more likely to refuse a high value reward if their partner gets a lower one than if both receive the high value food (Brosnan et al., 2010). As with humans, however, they are even more likely to refuse if they get a less preferred reward than a partner, suggesting that they are more likely to respond to disadvantageous than advantageous inequity; one cross-cultural study of children that used a similar paradigm (albeit with stickers as rewards) found a robust response to disadvantageous inequity that increased with age across seven cultures, but only children in three cultures showed a response to advantageous inequity, and even those were of a lower magnitude than their own responses to disadvantageous inequity (Blake et al., 2015). Hopefully the aforementioned techniques - IR thermography, eye-tracking, and behavioral endocrinology - will allow us to assess subjects' reactions without relying on costly refusals so that we can determine if subjects are aware of their advantage even if they do not respond behaviorally.

3. Cooperation and inequity

Why would we have evolved to respond negatively to inequity? After all, isn't having something better than having nothing at all? Perhaps not, if someone else has more. Indeed, economists have argued that recognizing inequity allows us to more easily identify good cooperative partners (Fehr & Schmidt, 1999). This can be quite useful for both partner control, wherein individuals may try to change the partner's behavior, and partner choice, wherein individuals may leave a subpar partner and try to find a new one. However, there is very little evidence of partner control (i.e., punishment) in the animal kingdom (Jensen, 2010; although see Raihani, Grutter, & Bshary, 2010) and indeed, it may be difficult in many cases for animals to control others, making partner choice their only practical mechanism (Brosnan & Bshary, 2016). Moreover, this may be sufficient; if you and I are working together and you consistently take advantage of me, I am likely better off finding a new partner – even if I must pick one at random (Darden, James, Cave, Brask, & Croft, 2020) – than continuing to work with you and being relatively disadvantaged (Brosnan, 2006).

As this hypothesis predicts, cooperation declines in the context of inequality. Capuchin monkeys are, from the very first trial, far less likely to cooperate to pull in a counterweighted tray when the rewards are adjacent to one another in the center rather than dispersed to the ends of the tray, where the monkeys can easily grab them. This suggests that the monkeys understand that the more dominant monkey may grab both rewards in the clumped condition and, therefore, they avoid that situation (de Waal & Davis, 2003). Monkeys may also avoid coordinating if their partner gets more benefit from coordinating than they do in an Assurance game (Robinson et al., 2021), a coordination game derived from experimental economics. In this game, subjects chose between a token representing a "safe" option (*Hare*) that gives them a single reward regardless of what their partner picks and an option (*Stag*) that rewards them with a greater number of rewards if the partner also chooses it or nothing if their partner chooses the safe option. When the benefit for coordinating is identical, capuchins routinely coordinate on *Stag* (Brosnan, Wilson, & Beran, 2012). In this study, however, one monkey got four rewards for coordinating on *Stag* whereas the other got only two. Monkeys continued to coordinate on *Stag* when working for a highly preferred food, Cheerios, no matter what their partner got. However, when we switched to a less preferred reward, flavored pellets, they played *Stag* less often (they also quit participating at all, likely because they did not wish to work for such low value food). As in earlier tasks, the monkeys were not willing to sacrifice a high value reward for equity. More broadly, these results highlight the important role of reward value in affecting behavior and suggest that differences among rewards used might explain some of the variation seen across studies of inequity and cooperation.

Aside from avoiding unequal situations, monkeys may avoid specific individuals. In another barpull task, monkeys could choose whether to work together to pull in the tray (Brosnan, Freeman, & De Waal, 2006). Sometimes rewards were equal, but sometimes one side of the tray contained a more preferred reward than the other. The monkeys weren't separated and had to choose who would work on which side. Reward equity did not affect success, but their partner's behavior did. In pairs in which the dominant monopolized the better reward in the unequal condition, success was low, irrespective of whether the rewards were equal or unequal. However, in pairs in which both monkeys got the grape equally often in the unequal condition, success was high, even on those unequal trials. Indeed, even the dominants did better, in terms of overall rewards and high value rewards, because of the much higher rate of success. While this is a correlation, it suggests that willingness to cooperate is based as much on the partner's behavior as the inequity of any given interaction; they seem to accept lower value outcomes sometimes as long as the overall benefit is equal.

Chimpanzees, too, succeed more often in cooperative tasks with compatible partners (Melis, Hare, & Tomasello, 2006a) and, when allowed to choose their partner, actively choose the one who shared rewards more fairly in a previous task (Melis, Hare, & Tomasello, 2006b). Capuchins share more with a partner whose help they needed to access a food reward (that only they get) than when they can access it by themselves (de Waal & Berger, 2000). Moreover, partners who don't get food from the subject after assisting help less often in future trials. Chimpanzees also recognize intent, more often punishing their partner when their partner "stole" food than when the experimenter moved it to the partner, despite the latter resulting in the same outcome (Jensen, Call, & Tomasello, 2007). Capuchins show a similar spite-like behavior, although they do not seem to discriminate whether it was intentional (Leimgruber, Rosati, & Santos, 2015).

4. The evolution of fairness

There are two predictions if inequity is linked to cooperation; first, as discussed above, individuals should be particularly sensitive to inequity within a cooperative context and second, more cooperative species should have evolved to be more likely to respond negatively to inequity than those that do not routinely cooperate (Brosnan, 2011). This is what we find. Across the primates, species that generally cooperate, for instance hunting cooperatively, sharing food, or participating in group defense, are more likely to respond to inequity in these experiments. Capuchins mob predators (Perry, Manson, Dower, & Wikbert, 2003), coordinate movement (Boinski, 1993), alloparent (Baldovino & Di Bitetti, 2008), and reciprocally share food (de Waal, 2000), grooming (di Bitetti, 1997), and support (Gros-Luis, Perry, & Manson, 2003; Perry, 1996). Experimental cooperation tasks suggest that they understand at least something about their role and that of their partner (Brosnan, 2010). As predicted, the majority of task-based inequity studies find a negative response to inequity (Brosnan & de Waal, 2003; Fletcher, 2008; van Wolkenten et al., 2007; Talbot et al., 2018; but see Fontenot, Watson, Roberts, & Miller, 2007; Silberberg, Crescimbene, Addessi, Anderson, & Visalberghi, 2009; McAuliffe et al., 2015). Chimpanzees also reciprocally exchange services and food (de Waal, 1989; Gomes & Boesch, 2009; Gomes, Mundry, & Boesch, 2009; Watts, 2002), form coalitions (Watts, 1998) and engage in complex cooperative hunting (Boesch, 2002), and also respond to inequity in task-based studies

(Brosnan et al., 2005, 2010, Brosnan et al., 2015; Hopper, Lambeth, Schapiro, & Brosnan, 2014; but see Bräuer, Call, & Tomasello, 2009). Responses to inequity are also seen in bonobos (Verspeek & Stevens, 2023, see also Bräuer et al., 2009), who are also highly cooperative (i.e., Parrish, 1996). Finally, inequity responses are seen in several species of macaque (Hopper, Lambeth, Schapiro, Bernacky, & Brosnan, 2013; Laumer et al., 2020; Massen, Van Den Berg, Spruijt, & Sterck, 2012), a taxon that often cooperates to obtain and maintain high rank (Chapais, 1991; Higham & Maestripieri, 2010).

Of course, the reverse should also be true; species that do not routinely cooperate should not respond negatively to inequity. So far, this pattern holds for primates; gorillas and orangutans, great apes that show less evidence of cooperation than chimpanzees, do not respond negatively to inequity in these tasks (Bräuer et al., 2009; Brosnan et al., 2011; Sosnowski et al., 2021). This also rules out that the response is a homology, either within the primates or the great apes, or that the response is a side effect of large brains and complex cognition. Likewise, squirrel monkeys, who are confamilial with capuchin monkeys, neither cooperate extensively nor show evidence of inequity in dyadic contexts (Freeman et al., 2013; Talbot, Freeman, Williams, & Brosnan, 2011). Squirrel monkeys are sympatric with capuchins and live in even larger social groups, suggesting that neither ecology nor sociality are sufficient for inequity responses. Intriguingly, however, evidence suggests that female Bolivian squirrel monkeys show more cooperative behavior than other demographics (Boinski & Cropp, 1999; Mitchell, Boinski, & van Schaik, 1991; Vale, Williams, Schapiro, Lambeth, & Brosnan, 2019) and a more recent inequity study looking at female Bolivian squirrel monkeys in a group context found evidence suggestive of more sensitivity to inequity, indicating that more nuance may be needed in considering the level at which to correlate behavior for these analyses (Vale et al., 2022).

Other taxa show the same pattern. Some cooperative corvids respond negatively to inequity (Wascher & Bugnyar, 2013), as do rats (Oberliessen et al., 2016), who are also cooperative (Daniel, 1942). More work has focused on canids, who are both highly cooperative and, across numerous studies, show evidence of responding negatively to inequity (reviewed in McGetrick & Range, 2018). Unlike monkeys, dogs only refuse in the absence of a reward (Range et al., 2009), however they respond to differences in reward quality by changing their interactions with the experimenter (Brucks et al., 2016; Essler et al., 2017), as do pack-living dogs and wolves, suggesting that this response is not an artifact of domestication (Essler et al., 2017). As with chimpanzees, there are personality differences in which dogs respond to inequality (Brucks, Range, & Marshall-Pescini, 2017), reiterating the importance of individual differences. Finally, several species that do not respond to inequity also show a more equivocal understanding of cooperation (Heaney et al., 2017; Jelbert, Singh, Gray, & Taylor, 2015).

Biparental care species, in which both the male and female raise the young (if older siblings or others also help it is called cooperative breeding), are an interesting exception. Given the high degree of cooperation in this social system (and on cooperative tasks; Cronin, Kurian, & Snowdon, 2005), I originally predicted that biparental care species would respond to inequity, but they have not (Freeman et al., 2013; Mustoe et al., 2016; Neiworth, Johnson, Whillock, Greenberg, & Brown, 2009). Most studies, however, have tested mated pairs, often with offspring present, and if inequity responses really are a mechanism for partner choice, the intrinsic interdependence in these relationships may make the cost of protesting inequality too high; individuals cannot raise offspring on their own, so sacrificing a rearing partnership over the difference between a grape and a cucumber is likely not worth it. If so, I have predicted enhanced responses to inequity when relationships are being established, when such information about the partner might be particularly useful and the costs of finding a new partner are much lower (Brosnan & de Waal, 2014). Supporting this, callitrichid males show greater responses to inequity with their mate when no offspring are present (Mustoe et al., 2016). Finally, cleaner fish mated pairs, who also are highly interdependent, do not show evidence of responding negatively to inequity (Raihani, McAuliffe, Brosnan, & Bshary, 2012).

We have proposed that fairness evolves in a two-step process (Brosnan & de Waal, 2014). First, individuals develop an aversion to receiving less than a partner in the context of cooperation. Disadvantaged individuals benefit from searching for more equitable cooperative partners, even if they sacrifice some absolute gains, by improving relative outcomes. We suspect this aversion will be common across many or all cooperative organisms. Subsequently, some species may have evolved a tendency to avoid benefitting at the expense of partners, a short term cost with the long term benefits of both maintaining and building the cooperative relationship and, potentially, providing reputational benefits that could lead to even more partners. Of course, they need not understand it in this way as long as there is some proximate trigger to refuse excessive benefit. Nonetheless, the immediate cost of giving up a benefit, not to mention the cognitive load of inhibition, suggests that this will be less common than reacting against disadvantageous inequity. Among non-human species, it has thus far only been seen in chimpanzees, although I anticipate that it may occur in other large brained, long lived social species that routinely cooperate and would, therefore, benefit from establishing and maintaining strong partnerships. Humans, of course, take this even further; we plan far into the future, understand the consequences of our interactions, and can even manipulate others' perceptions to improve our reputation. However, while we may be the only species to show a robust sense of fairness, the roots go much deeper and understanding how fairness evolved will help us understand our own behavior in the face of inequity.

5. Unanswered questions

As much as we know, there is more that we do not. Relationship quality impacts inequity responses in humans (Clark & Grote, 2003), but little is known about its impact in other species because it is difficult to test pairs who do not choose to work together. We also do not know how much variability there is across the animal kingdom because we have tested only a small number of species. Finally, as mentioned above, we are likely underestimating the impact of unequal outcomes, perhaps dramatically, as we are only measuring behavioral responses to inequity, which are costly and require inhibition, rather than whether they notice and/or care about inequity. Fortunately, these challenges are being addressed. For instance, testing the group together, rather than separating out dyads, allows for a greater number of potential partners to willingly interact (Burkart & van Schaik, 2013) and emerging non-invasive techniques, such as IR thermography, eye-tracking, and the ability to track relatively more short term changes in hormones non-invasively, provide alternate ways of measuring what animals notice rather than relying solely on their behavioral responses.

We also know little about how this response manifests in natural environments. Most studies measure responses to unequal foods, but many of these species do not cooperate in food-related contexts. Under what circumstances, then, might we expect to see a response to inequity? Bonobos show expectations about equity in social contexts, with individuals who were the recipient of an aggressive attack using a different call to solicit support when they had done something to instigate the attack (i.e., they "deserved" it) than when they had not (Clay et al., 2016). Indeed, we may find more species that respond to inequity if we explore a wider variety of contexts. Data suggest reciprocity of services (i.e., grooming, support, mating privileges) in many species, so might they keep track of inequity in their social accounts? Better understanding which species respond to inequity in what contexts will help clarify its function.

6. What does this mean for human legal systems?

A comparative understanding of inequity allows us to better understand how our own sense of fairness evolved and predict in what contexts we are likely to see reactions, as well as what they will look like.

For instance, while there are cultural differences in both what is considered fair and how one responds to inequity, the sense of fairness is not just a cultural artifact; it is deeply engrained in biology. Like other species, we notice inequality, even, sometimes, when we have an absolute gain, get frustrated, and may quit participating if the inequity is too great. Indeed, given that our social and economic systems are so inextricably cooperative, it is not surprising that as a society we are sensitive to inequity; think of female suffragettes, the civil rights era, and the more recent Black Lives Matter movement. On the other hand, our economic and social systems are interdependent, and I argued that interdependence makes many interdependent species, for instance cooperative breeders, *less* likely to respond to inequalities. However, responding is not the same as noticing, and just because we don't see an immediate reaction to some inequality does not mean that it goes unnoticed, even in the case of interdependence. Presumably even cooperative breeders will respond to inequity if the cost of staying gets too high. If this is true in humans, then we need to know what that price point is so that we can re-design institutions and rules to better take into account inequality that may be endured, but not happily. Improving equality will provide more acceptance and compliance from those who currently experience the rules as unfair and, therefore, resist in subtle – and oftentimes costly – ways.

Another challenge facing humans is that what we consider 'fair' will differ among individuals, making it difficult to satisfy everyone. One reason for this is that, like chimpanzees, we react more strongly to (and presumably care more about) being disadvantaged than advantaged (Blake et al., 2015), and it may be difficult for the advantaged person to view the situation from the other's perspective. In addition, chimpanzees, at least, respond differently depending on their rank and personality (and, likely, other factors). If humans are the same, we should expect that even two people who are experiencing identical situations may view them differently (Petersen, Sznycer, Sell, Cosmides, & Tooby, 2013; Price, Kang, Dunn, & Hopkins, 2011). Both of these will make designing systems with universal acceptance challenging. Indeed, if it is impossible to do so, perhaps we should consider alternate approaches; for instance, legal rules and judgements might be accepted more readily if this variability in perception and experience were more openly discussed and acknowledged. And again, just because someone isn't protesting inequity doesn't mean that they don't notice. Data from dogs' and children's reactions to inequity suggests that they notice it, and do not like it, but they still accept the rewards. Thus, focusing on costly responses may cause us to dramatically underestimate the degree to which people are feeling inequitably treated.

Moreover, inequity impacts relationships. Dogs respond to inequity by interacting less with their social partners, which may drive a wedge in the relationship, harming future endeavors. Capuchins refuse to work with a partner who consistently takes more than their share, even when rewards are equal. This has important implications in human societies, suggesting that a history of inequitable treatment will devastate cooperation, even in contexts in which inequality is impossible or the advantaged partner offers a more fair deal. This hurts everyone, including the individual who was benefitting, as they get fewer rewards of any type over the long term than in those pairs that more fairly share the preferred outcomes. It would be interesting to know how long these social memories persist; if you start treating someone fairly, how long does it take before they trust you and a cooperative relationship can be restored? Moreover, this suggests that at least some component of our inequity response is based on our affective response to the situation or the individual. If so, in legal contexts we must focus on the emotional component as well as a purely cost-benefit analysis to find a solution that will make everyone feel satisfied.

On a more positive note, however, we can use what we know about the evolution of inequity responses to try to recognize situations in which inequity will cause a breakdown in the system and fix them before they arise. Humans have the foresight and theory of mind to predict what problems will arise and recognize how others will react; we can use this information to try to ameliorate inequalities before they start. Moreover, short-term inequity may be acceptable if the relationship is equitable over the longer term, suggesting that better framing to include (believable) long term benefits may help individuals see past the immediate inequality and maintain the relationship. Using what we have learned about other species' responses helps us better understand ourselves and design systems and institutions that lead to more mutually beneficial cooperation over the long term. That's an outcome we can all feel good about.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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