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Fairness in animals: Where to from here?

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Abstract

In the last decade, there has been an explosion of work investigating non-human species' behavior as it relates to the human sense of fairness and justice. This work has provided a much-needed evolutionary perspective on humans, and highlighted ways in which humans' behavior is both similar to and different from that of other species. In this concluding paper, we outline the major threads of the work highlighted in this and the previous special issues of *Social Justice Research* and provide thoughts on future directions for the field. This is a very exciting time in our exploration of the evolution of human justice and fairness, and we eagerly await the developments of the next decade.

Humans are extremely invested in fairness and justice. This is apparently a human universal; although specifics may vary, some interest in fairness crosses cultures (Henrich et al., 2001). To what degree is this unique to humans? As this and the previous special journal issues of *Social Justice Research* indicate, there is mounting evidence that at least some comparison-of-rewards and aversion to unequal rewards are found across a wider variety of species than just ourselves, or even non-human primates. Although no other species thus far shows the inclusive sense of fairness seen in humans, aspects are present in a wide variety of species and situations.

One of the challenges, of course, is attempting to uncover these responses in species that are unable to verbally report their reactions. For instance, there is a difference between a failure to *respond* and a failure to *notice*, yet it is difficult to empirically disentangle these possibilities amongst non-verbal species (Brosnan, Newton-Fisher, & van Vugt, 2009). Moreover, it is hard to determine what differences between species might mean. If, for instance, we find a sex difference in one species, but not another, is this due to a cognitive difference, and ecological difference, or a combination of the two, and what does this mean for our understanding of the evolution of fairness?

This pair of journal issues summarizes the current state of the knowledge on behaviors related to fairness, and, in particular, responses to inequitable outcomes in species other than humans. There is growing evidence from non-human primates in particular, but also from domestic dogs and fish, and we hope that this list of species and taxa will grow significantly in the coming years. While humans' sense of fairness may differ from those of other species, the differences seem quantitative rather than qualitative. What does this mean for our understanding of human behavior? As a second goal of the issue, researchers who focus on humans have attempted to put these results in this context, and suggest future avenues for research.

What do we know about justice in non-human species?

Experimental evidence of responses to inequity

Decades of research in both psychology and economics have demonstrated that humans respond negatively to inequitable outcomes between themselves and another individual (see Chen & Houser, 2012, this issue; Skitka, 2012, this issue). This can occur at two different levels: disadvantageous or advantageous (Fehr & Schmidt, 1999; Walster [Hatfield], Walster, & Berscheid, 1978). In disadvantageous inequity, subjects respond negatively to receiving a lesser valued outcome than a social partner, whereas in advantageous inequity, or overcompensation, subjects respond negatively to receiving a more valuable outcome than a social partner. Although an aversion to disadvantageous inequity may be stronger than that to advantageous inequity (Greenberg, 1982; Loewenstein, Thompson, & Bazerman, 1989), both occur in humans. Considering the evolution of this behavior, it is likely that the former preceded the latter (Brosnan, 2006a, 2006b). There is clearly an immediate fitness advantage to any individual who is able to recognize when they receive a less valuable outcome than a partner and then try to rectify the discrepancy; after all, relative outcomes are the foundation of natural selection. Nonetheless, after an ability to recognize outcomes that differ between one's self and another have evolved, there are also benefits to being able to recognize when one is advantaged relative to one's partner. For instance, recognizing and correcting inequity when one is the beneficiary demonstrates one's value as a social partner, bringing long-term benefits despite the short-term costs (Frank, 1988, 2001).

Species other than humans respond to inequity in a variety of situations. This has been particularly well documented in two species of non-human primates, capuchin monkeys and chimpanzees, as well as in domestic dogs. Although the specifics of the tasks vary, these species show negative reactions to continued inequity between themselves and a social partner, typically evidenced by refusals to continue participating in interactions in which the outcome is repeatedly less good than a partner's (see Price & Brosnan, 2012, previous issue, Yamamoto & Takimoto, this issue, and Bräuer &

Hanus, 2012, this issue, for a summary of these studies). In other contexts, individuals may refuse to continue cooperative interactions with partners who do not share access to preferred rewards (Brosnan, Freeman, & de Waal, 2006) or who do not share food rewards that are available to only one individual (de Waal & Berger, 2000). Capuchins, for instance, are so sensitive to inequity that they often decline to cooperate when rewards are clumped together and hence are monopolizable by a dominant individual (de Waal & Davis, 2002), indicating that the mere possibility of inequity is sufficient to hamper cooperation. Observing such interactions, whether in an experimental context or not, may indicate that these primates have a sense of social regularity that informs an underlying sense of justice (de Waal, 1991).

Of course, these examples focus on disadvantageous inequity, or how individuals respond if their outcome is worse than anticipated based on a social partner's outcome. The flip side, as discussed above, is recognizing when one is advantaged (i.e. advantageous inequity). In non-human species, this is typically studied under the rubric of prosocial behavior, or whether individuals will help others to achieve outcomes that they cannot achieve on their own. This is most typically addressed by evaluating whether individuals will choose options that reward conspecifics at no cost to themselves (Bräuer & Hanus, 2012, this issue; Yamamoto & Takimoto, 2012, this issue). As with responses to inequity, this is variable across both species and contexts. Of those species tested to date, capuchin monkeys, again, seem to be among the most prosocial of the primates. These monkeys typically choose to bring food rewards to partners in both barpull- and exchange-based tasks (de Waal, Leimgruber, & Greenberg, 2008; Lakshminarayanan & Santos, 2008), and will do so even when their efforts bring their partner better rewards than they themselves receive (Brosnan et al., 2010; Lakshminarayanan & Santos, 2008). Other species of monkeys, in particular the cooperatively breeding callitrichids, are equally prosocial (Burkart, Fehr, Efferson, & van Schaik, 2007; Cronin, Schroeder, & Snowdon, 2010), although apparently not in all situations (Cronin, Schroeder, Rothwell, Silk, & Snowdon, 2009; Stevens, 2010). More recent studies indicate that macaque species are both prosocial (Massen, van den Berg, Spruijt, & Sterck, 2010) and sensitive to inequity (Hopper, Lambeth, Schapiro, Bernacky, & Brosnan, in review; Massen, Van den Berg, Spruijt, & Sterck, 2011), showing that even among monkeys with more despotic social systems, there is an interest in others' outcomes in relation to one's own.

Evidence is more mixed in the apes. The vast majority of studies have involved chimpanzees, who seem to demonstrate prosocial behavior in some contexts more than others. In particular, while they do not behave prosocially in the barpull studies at which capuchins excel (Jensen, Hare, Call, & Tomasello, 2006; Silk et al., 2005; Vonk et al., 2008), they do prefer to reward their partners in exchange tasks (Horner, Carter, Suchak, & de Waal, 2011). In one study which allowed for an investigation of both inequity and prosocial responses within the same study, chimpanzees reacted to both receiving more and less than their partner, although their reactions to receiving more than a partner were only about a third as strong as their responses to receiving less (Brosnan, Talbot, Ahlgren, Lambeth, & Schapiro, 2010). Thus, it may be that, like humans, while these species dislike inequity in their favor, they are even more distressed by inequity that is not in their favor (Dana, Weber, & Kuang, 2003; Greenberg, 1982; Loewenstein, et al., 1989).

Unfortunately much less work has been done on non-primate species; however the data that exist are quite informative. For instance, while dogs do respond negatively to inequity that is not in their favor (Range, Leitner, & Viranyi, 2012, previous issue), there is no evidence that they respond negatively to inequity in their favor (Horowitz, 2012, previous issue). This latter study involved a situation in which they could react, but could not change outcomes, similarly to Brosnan et al (2010), so more "prosocial-style" studies in which dogs choose between distributions will be required to make a full comparison. Fish, too, have been tested for inequity responses. The focus thus far has been on cleaner fish, a highly cooperative fish species that not only work together on cooperative cleaning tasks (Bshary, Grutter, Willener, & Leimar, 2008), but also show punishment of individuals who do not

cooperate (Raihani, Grutter, & Bshary, 2010). Cleaner fish did not respond to inequitable outcomes in an analogous task (Raihani, McAuliffe, Brosnan, & Bshary, 2012), leading to the hypothesis that sensitivity to inequity may be one pathway through which species can evolve stable cooperation, but that other pathways, such as the punishment behavior seen in cleaner fish, may be equally successful (Raihani & McAuliffe, 2012).

To date, the topics of interest in studies of animals have differed substantially from those that have been the focus of the human work in psychology and economics. Research to date has largely focused on three aspects of other species' responses to inequity, the first being a comparative approach aimed at understanding why the reaction has evolved, the second a more mechanistic focus on the conditions that elicit this response, and the third an exploration of the connections between the inequity response and the well-known contrast effects seen by most species. Regarding the first of these, it had been proposed for humans that responses to inequity are a way by which individuals can discriminate between beneficial and not-so-beneficial cooperative partners (Fehr & Schmidt, 1999). The comparative approach has been used to test this hypothesis in other species. The main approach has been a phylogenetic analysis, showing that the inequity response is more common in those species that are highly socially cooperative (e.g., form coalitions and alliances, group hunt) than in those that do not, irrespective of other potentially important characteristics, such as brain size or social organization (Brosnan, 2011b). Moreover, while the typical inequity test does not involve explicit cooperation, in tests in which individuals had to work together for unequal rewards, monkeys are generally willing to do so as long as the benefits are traded off, and not dominated by one individual (Brosnan, et al., 2006). Additionally, when inequity is intermittent, rather than occurring on every trial (as is typical in inequity tests), chimpanzees only respond when the frequency of inequitable outcomes is 50% or greater, indicating that occasional inequity does not cause the same response (Hopper et al., in review). This latter point may be critical given that payoffs in natural interactions are highly unlikely to ever be completely equal on any given interaction, but may often even out over time. While many more species need to be tested to provide additional evidence (see Future Directions, below), the data thus far indicate that inequity responses may have evolved to support successful cooperation.

Regarding the second two research foci, there has been a great deal of interest in what conditions elicit inequity responses. Although early work found responses to inequity in primates (Brosnan & de Waal, 2003; Brosnan, Schiff, & de Waal, 2005), later replications that did not require a task in order to receive the reward failed to do so (Bräuer, Call, & Tomasello, 2006; Roma, Silberberg, Ruggiero, & Suomi, 2006). This was true even when comparing studies of the same group of animals in situations in which they did (Brosnan & de Waal, 2003; van Wolkenten, Brosnan, & de Waal, 2007) and did not (Dindo & de Waal, 2006) have to work for their unequal rewards. This led to the hypothesis that a task of some sort was required in order to elicit the negative response to getting different rewards, possibly because the inequity response evolved to assess the value of a cooperative partner, hence requiring a situation involving cooperation, which may have been triggered by the alternating task (van Wolkenten, et al., 2007). Since that study, both between-subjects (Neiworth, Johnson, Whillock, Greenberg, & Brown, 2009) and within-subjects (Brosnan, Talbot, et al., 2010) studies have demonstrated that individuals who respond to inequity when they have to work for rewards do not do so even for the same outcomes with the same partners if the rewards are handed out for free. The mechanism for this remains unknown (although see Brosnan et al, 2010, for some possible explanations), but it is intriguing that a task is required despite the lack of evidence that animals respond to inequalities in effort in these tasks (see Data from Other Contexts, below).

Finally, there has been a debate about whether these tasks are actually social. The response to inequity is, at root, a violation of an expectation that is set by one's partner's outcomes. This is very similar to the contrast effect, in which individuals respond when their outcomes differ from a previous offer (Reynolds, 1961; Tinklepaugh, 1928). What is debated is the degree to which the inequity

response relies on a social referent. Some scholars have argued that the response is nothing more than a contrast effect, and that the presence of another individual is irrelevant (Roma, et al., 2006; Silberberg, Crescimbene, Addessi, Anderson, & Visalberghi, 2009; Wynne, 2004; see also Bräuer & Hanus, 2012, this issue). However in within-subjects designs, the same animals that respond by refusing to participate when a partner gets a better reward do not respond when more preferred rewards are offered, but then are replaced with less preferred ones, irrespective of what their partner receives (e.g., Brosnan et al, 2010; van Wolkenten et al, 2007). While it is extremely likely that these two types of comparisons, termed individual and social comparisons, share similar cognitive underpinnings and appear to be linked ontogenetically (Hopper, Lambeth, Schapiro, Bernacky, et al., in review), this does not mean that the social partner is irrelevant in inequity studies. The presence of a social partner clearly affects responses as compared to individual contrast effects. Future work is needed not only to explore how these social interactions affect comparisons, but also how human responses differ between individual and social comparisons, a topic that has received very little attention to date (see Brosnan, 2012, previous issue, for a discussion of the human literature).

What does this mean for the human sense of fairness?

How, then, do primates' responses to receiving more or less preferred outcomes than a partner relate to the human sense of fairness? To first define some terms, in the Introduction (Brosnan, 2012), 'fairness' was operationally defined as an interest in the equity of outcomes, both one's own and others', reflected in an ideal of fairness against which outcomes are compared. This definition importantly includes several components. First, there is a focus beyond one's own outcomes to those of others; in other words, in a true sense of fairness, individuals must be as distressed by receiving more than a partner as by receiving less than that partner. Additionally there is the, often implicit, assumption of an ideal to which comparisons are made. This may be extremely difficult to determine in species without language, although we emphasize that this does not mean that such an idea does not exist.

There are two major research foci related to this question in the non-human literature. First, there are studies on how individuals respond to getting less than a partner (the inequity studies), and second, there are those exploring they respond to getting more (the prosocial studies; see above). These relate to two very different aspects of the human sense of fairness (see Figure 1). The first is getting less than a partner, which is clearly aversive and has an obvious evolutionary advantage, as discussed above. We consider this to be "first order fairness." The second is almost certainly a derived property of the first, as it is not in and of itself a bad outcome. The only negative aspect is that the partner, who is getting less, may react negatively to the distribution, which could lead to a bad outcome for the individual in question (e.g., the partner refusing to participate, leading to no rewards for either individual). Thus, in order to prevent conflict within close or beneficial relationships, the advantaged individual will benefit from either protesting or rectifying the situation. This we consider second order fairness. We also note that, as with the response to advantageous inequity discussed above, this is likely to be a weaker tendency and result in weaker responses as it is an indirect, rather than a direct, benefit. As Thomas Hobbes once said, "Every man is presumed to seek what is good for himselfe naturally, and what is just, onely for Peaces sake, and accidentally¹." Thus, we predict both stronger responses in inequity studies than in prosocial studies and more variable reactions in prosocial studies, in which the value of the relationship should influence an individual's willingness to react.

¹ Hobbes, T. (1991 [orig. 1651]). *Leviathan*. Cambridge: Cambridge University Press.

Considering the data to date, there is evidence for reactions to both advantageous and disadvantageous inequity, although typically not within the same study, or even within the same context (but see Brosnan et al., 2010). This makes it difficult to compare the magnitude of responses. Additionally, it is challenging to compare non-humans' and humans' responses, as the procedures typically vary dramatically. Studies of humans often focus on self-report outcomes, which are not possible in non-human species, and may use more complicated designs involving significant instruction. Although there are some excellent studies of children that are comparable to those for non-human primates (i.e., those using non-verbal paradigms), these suffer from their own limitations with respect to comparison. In particular, the typical lack of an individual contrast condition to verify that responses to inequity involve a social referent, considered essential in the non-human literature (see Introduction, Brosnan, 2012, previous issue, for additional discussion of this problem).

So, do non-human species have a sense of fairness? We believe that the answer is a qualified "yes." They do show behaviors indicative of both a sensitivity to their own and others' outcomes, however these responses are neither as consistently elicited as those seen in humans, nor do they appear to be as strong, particularly in the case of second order fairness (e.g., prosocial outcomes). However, this does not mean that they are any less important. Instead, what appears in non-human species are precursors to the human sense of fairness. These allow us to understand the pathways through which our own sense of fairness evolved and the contexts and environments that selected for this important human behavior. With this in mind, we now turn to the future of the study of fairness in other species.

What can the evidence from non-human species tell us about humans?

Despite the burgeoning literature on responses to inequity in other species, the different foci of such research mean that comparisons with humans are only now emerging. As evidenced by the authors in this pair of journal issues, however, there is great interest in this merger from both the human and non-human researchers. The study of inequity was begun in the field of psychology, with work on Equity Theory (e.g., Walster [Hatfield], et al., 1978). This literature largely focused on distributional inequity, as has been true of the work on experimental economics and is true of the non-human research today (see Skitka, 2012, this issue; Christen & Glock, 2012, this issue). However, the work with humans, having had decades to mature, addresses a host of issues that may be relevant for non-human researchers, such as how procedural differences influence subjects' responses. One fruitful avenue for non-human researchers looking to expand the field is to explore the questions being addressed in psychology and economics and consider ways in which they might be relevant to other species as well.

On the flip side, the comparative work in non-human species provides a much needed evolutionary perspective that is missing in the human fields (see Skitka, 2012, this issue; Christen & Glock, 2012, this issue; Chen & Houser, 2012, this issue; Pierce & Bekoff, 2012, previous issue). Without this comparative perspective, we cannot hope to understand why some of these behaviors evolved, nor can we provide coherent predictions for all of the variations seen in human behavior (i.e., Brosnan, Jones, Gardner, Lambeth, & Schapiro, 2012; Jones & Brosnan, 2008). This approach is embraced by many in the field. For instance, as argued by Chen and Houser in this issue, the non-human literature provides support for understanding the foundations of human institutions, such as the ways in which record keeping may have developed. While it is clearly true that the responses seen in other species, even closely related apes, are not the same as those seen in humans, this approach of using other species' behavior to understand the foundations of human behavior can tell us both about the evolutionary trajectory of these responses and their evolutionary function (Brosnan, 2011a). It is our hope that this comparative approach will provide a robust way to generate novel hypotheses for human researchers rather than being relegated to simply demonstrating that other species can do the same

things that humans do. It is only in this way that the true power of the comparative approach is evidenced.

What is needed now

We have learned a great deal about non-human species' reactions to unequal outcomes in the nine years since the publication of the first paper on the topic (Brosnan & de Waal, 2003), but there is still a great deal more to explore. Below we outline a wish list of future research directions, including both our own thoughts and those outlined by the authors in this pair of journal issues.

Data from additional species

One urgent need is data from a wider variety of species. Right now, the majority of species tested have been non-human primates, but given the ubiquity of individual contrast effects in animals (e.g., Friedan, Cuello, & Kacelnik, 2009), and the apparent links to cooperate (Brosnan, 2011b; Fehr & Schmidt, 1999), it seems unlikely that social contrast will not be present in other species, particularly those that are gregarious and routinely cooperate. Broadly, there is a need for both data across the spectrum of species that socially cooperate and those that do not, as well as data that might be able to test other hypothesis, such as species that differ in cognitive abilities or social ecologies. Moreover, species that may face ecological situations in which loss is a serious pressure may help to disentangle non-social origins of inequity (e.g., foraging; M. K. Chen & Santos, 2006) from more social origins (for experimental attempts to separate these possibilities, see Hopper, Lambeth, Schapiro, & Brosnan, in prep). Thus far, tests have extended to two cooperative species, domestic dogs (Horowitz, 2012; Range, Horn, Viranyi, & Huber, 2008; Range, et al., 2012) and cleaner fish (Raihani & McAuliffe, 2012; Raihani, et al., 2012), highlighting the potential for expanding this research to additional species.

Data from other contexts

Thus far, virtually all of the data on inequity comes from experimental paradigms with two procedures; either subjects' responses are compared when they receive the same versus different outcomes than their partners, or their choices are compared when they receive the option to reward only themselves, only their partner, or both themselves and a partner. While these paradigms are clearly useful, both because they provide an objective, quantifiable way to measure responses, and because they are at least roughly analogous with the human economic literature, additional contexts are needed to more fully understand the breadth and nuance of this response. In particular, it is necessary to understand how this response is related to species natural behaviors (for a review of this question, see Brosnan, 2006b)

Some progress has been made in this direction. Most obviously, there are studies, not always linked explicitly to inequity, showing that individuals who are cooperating are less likely to do so with partners who do not share outcomes than with those who do (Brosnan, et al., 2006; de Waal & Berger, 2000; Melis, Hare, & Tomasello, 2006a). In fact, when given a choice between partners who tolerantly share rewards and those who do not, chimpanzees actively choose the more tolerant partners (Melis, Hare, & Tomasello, 2006b). Capuchins will often avoid potential situations of inequity by refusing to cooperate when rewards are monopolizeable, even when working with kin (de Waal & Davis, 2002). This line of research is critical as it shows that it is not only the *distributions* that are important, but also the *partner's behavior*. These studies draw a bit closer to the human psychology literature on equity, which demonstrates that people are upset by more than just distributions.

In fact, this returns to an earlier important point, highlighted by several authors in this issue. The non-human literature, possibly because it grew out of experimental economics paradigms, has been largely focused on distributional inequity, while the human literature recognizes many different types of equity (see Christen & Glock, 2012, this issue; Skitka, 2012b, this issue). In particular, social psychology

of late has focused on procedural inequity (Skitka, 2012b, this issue), or differences in the way individuals are treated rather than differences in outcome, a topic that could very easily be studied in other species. There is only one study to date which specifically attempts to manipulate procedure. Brosnan and colleagues (2010) found that chimpanzees' responses did not change when they got the same rewards as partners, but underwent a slightly different procedure to acquire them. Chimpanzees either received rewards immediately upon completing a task, or faced a 10 second delay² after completing the task prior to receiving their rewards.

This is also reminiscent of the extensive literature on how effort affects responses to inequity (see above). In fact, in all studies that have been done to date, no non-human primate has been shown to modify their responses to outcomes dependent upon whether their level of effort to achieve the outcome is different than their partners (Fontenot, Watson, Roberts, & Miller, 2007; Brosnan et al, 2010; reviewed in Price & Brosnan, 2012, this issue; Bräuer & Hanus, 2012, this issue). This is true even for those individuals who alter their behavior dependent upon distributional inequity. Instead, effort seems to influence responses in two ways. First, inequity of effort seems to exacerbate responses to inequity of distribution, causing subjects to respond negatively with a greater frequency to these unequal outcomes, despite the fact that effort alone does not cause a change in reaction when outcomes are otherwise equal (van Wolkenten, et al., 2007). Second, some sort of effort seems to be required to elicit a response to inequity. No study with inequitable outcomes that lacked a task has ever found evidence of inequity, and within-subjects studies have shown that a task is required to elicit inequity (e.g., Brosnan, 2010). This has led to the argument that a task of some sort is required, regardless of what that task is (Freeman et al., in review). Nonetheless, future work is needed to understand exactly what the role of effort is, especially in light of the extensive human literature indicating that humans are quite sensitive to unequal procedures.

A species-centric perspective

Moreover, while the above suggestions all seek to explain how non-humans respond as compared to known human responses, in order to understand these responses for each species it is necessary to take a more ethological approach. That is, how have inequity responses diverged across different species with different social and ecological environments, and how might responses to inequity manifest in different species? There are a wide variety of behaviors seen in the natural world that, at least on the surface, seem to be related to inequity (reviewed in Brosnan, 2006b). Many of these behaviors may be very dissimilar from the typical experimental procedures for assessing inequity. Only one study to date has examined inequity in a species-specific context. Van Leeuwen and colleagues explored gorillas' play interactions, and discovered that they seemed to be very focused on the social inequalities during these play bouts (van Leeuwen, Zimmermann, & Davila Ross, 2010). Gorillas who had the upper hand in an interaction worked hard to maintain this inequality, indicating that for gorillas, social interactions may be particularly important. Unfortunately, it is unknown how gorillas would respond to a more typical distributional inequity paradigm, nor is it known how other species' social negotiations may reflect a focus on equity (although see de Waal, 1991).

Gorillas are not the only species for which play and social interaction are clearly an arena in which equity considerations are important. One area that has been explored in canids is so-called fair play (see also Bekoff, 2004; Pierce & Bekoff, 2012, previous issue). Juveniles routinely play with one another, and during these play bouts they must make decisions about how hard to bite, when to "apologize" after excessively rough play, and whether to continue playing with individuals who are routinely overly aggressive. Canids that are overly rough during social play are excluded from play

² Ten seconds represents a long delay for chimpanzees, particularly as this is two to three times the length of the typical exchange interaction, and the partner was getting their food immediately.

sessions, as others fail to accept their play invitations or even leave play groups that these rough individuals join. In coyotes, there is an explicit fitness consequence for this behavior. Individuals who are excluded from play sessions as pups are far more likely to leave the group upon reaching adulthood. Those who leave the group face a mortality rate almost three times as high as their peers who remain in their natal groups.

This seems very different from the sorts of inequity experiments discussed above, as individuals are not comparing rewards with one another, but instead are comparing actions to a social norm. While it is not unreasonable to hypothesize that these situations may be unrelated or rely on entirely different mechanisms, there is a connection through the maintenance of valuable relationships. In the case of fair play, individuals are moderating their behavior in order to avoid disrupting a relationship. This may, then, be similar to the second order fairness discussed above, in which the focus is on the social relationship rather than the individual's personal outcome. Moreover, these species seem also to be sensitive to first-order fairness in the more typical distributional experiment. Domestic dogs respond negatively to disadvantageous inequity (see Horowitz, 2012, previous issue; Range et al, 2012, previous issue), opening the possibility that there is a link between an ethologically relevant natural behavior, play, and an experiment modeled on behavior seen in humans. We are very enthusiastic to see additional studies for which these links across domains can be made.

Aside from play, what other areas are worth considering? An obvious situation is mating, where individuals, and in particular, males, should be very focused on the frequency of their copulations as compared to those of the other males in their group. Both males and females may also be focused on the quality of their potential mates as compared to the quality of their rivals' mates (e.g., Townsend, Deschner & Zuberbühler, 2008). Outside of the mating realm, another social area in which equity considerations may play a role is in the negotiations with allies and coalition partners. In absolute terms, an alliance should only be successful if all members of the alliance are gaining more from it than they would be able to on their own, but it may also be that alliance partners focus on their *relative* gain with respect to their partner. Thus even a beneficial alliance may fall apart if one member is perceived as taking advantage of the other. Long-term observations of groups show conclusively that successful alliances may fail (de Waal, 1982). Even short-term dissolutions of the alliance may be catastrophic if this gives another individual or alliance an entrée to negotiate in to a better position. Although these two social situations would be virtually impossible to study experimentally, long-term, careful observations in both the field and in large captive social groups may uncover the ways in which equity interacts with social interactions.

A developmental perspective

Finally, it will be critically important to understand the ontogeny of fairness as a complement to our growing understanding of the evolution of fairness. Recently, new research has focused on how young human children respond to inequity and sharing. Regarding the former, children begin to recognize unfair outcomes in third-party distribution situations as young as one to two years of age (Geraci & Surian, 2011; Sloan, Baillargeon, & Premack, 2012). However, they do not actively respond to inequity until far later. As young as three years of age, children start to recognize when they are treated less well than a peer, as evidenced by changes in affect, but they do not start responding verbally to these discrepancies until around four years of age (LoBue, Nishida, Chiong, DeLoache, & Haidt, 2011). Regarding the latter, it is clear that children already show prosocial tendencies at a very young age (Eisenberg & Mussen, 1989), in some cases seeming to prefer giving objects to others rather than keeping them for themselves (Aknin, Hamlin, & Dunn, 2012). Some evidence indicates that, like adults, children prefer distributions which are equitable over those that favor either themselves or another individual (Fehr, Bernhard & Rockenbach, 2008; Blake & McAuliffe, 2011).

Unfortunately, there has been almost no work on non-human species to complement this growing field. However, recent evidence indicates a developmental trajectory for fairness in non-human primates similar to that reported for humans (Hopper, Lambeth, Schapiro, Bernacky & Brosnan, in review). Hopper and colleagues were able to follow a cohort of socially housed rhesus monkeys beginning shortly after weaning (at around one year of age), and test them, with the same partners and using the typical exchange-based procedure, at both 15 and 27 months of age. They found no response to inequity at the younger age, however by two years of age the monkeys were responding more strongly to inequity than to the equity control or to the individual contrast conditions. A follow-up study with a separate cohort of 18 month old rhesus monkeys showed that at this stage, they responded more strongly to the individual contrast condition.

This study raises a number of very interesting questions about the development of inequity. From a cognitive perspective, it is rare for human studies to include a control for individual contrast (although see Sloan, et al., 2012 for an exception to this), thus it is difficult to tease apart when individual versus social comparison come online (see Brosnan, 2012, previous issue). While it is likely that these behaviors are linked, it would be interesting to know whether this pattern is consistent with humans', as well as in other species', development. From an evolutionary perspective, as mentioned above, it is unknown what the selective pressures that led to the evolution of fairness were, or from which ancestral behavior this trait emerged. Although ontogeny does not re-capitulate phylogeny, a comparative approach, investigating the similarities and differences in the emergence of these behaviors within a developmental timeframe, will allow us to tease apart which features may have been important in which social and ecological environments.

Conclusions

A recent proliferation of studies investigating non-human species', and in particular, non-human primates', responses to unequal outcomes has greatly expanded our understanding of the evolution of these behaviors. Through these studies, we are coming to understand the contexts in which other species respond to inequity, which tell us about the selective forces that shaped the behavior, as well as the cognitive mechanisms at play. This comparative approach provides an opportunity to not only understand other animals' behaviors, but also to understand the evolution and function of our own behaviors. Given the explicit modeling of non-human studies off of those of humans, many parallels have emerged, and we are now at the point where the findings from the non-human literature can reciprocally inform the human literature, leading to new hypotheses in other fields. We are excited to see how far the field has come in less than a decade, and look forward to future developments that are sure to come.

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