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The importance of risk tolerance and knowledge when considering the evolution of inequity responses across the primates

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Deviations from the standard expected utility (von Neumann and Morgenstern, 1944) model to include concern for equity, reference points, reciprocity, envy, malice and the like have become commonplace. Other regarding preferences are used to explain why individuals will take action that appears to, at least in the short run, be costly to one's self in order to treat others in a particular manner. Research in the area of inequality has benefited greatly from the attention that others regarding preferences has garnered. Of late, such interest has spread beyond humans in to other species, notably primates and dogs (for a review, see *Social Justice Research*, volume 25, issues 2 and 3, edited by S.F. Brosnan). Recent empirical research has found interesting analogies between humans and these populations, leading to speculation about how these behaviors may have evolved (Brosnan and De Waal 2012). However, some noteworthy differences in human versus nonhuman behavior pertaining to inequality have also been seen (Christen and Glock 2012; Skitka 2012), some of which are difficult to explore due to dissimilar methodologies between the taxa. Although to some degree these are unavoidable due to practical constraints (e.g., Brosnan, Newton-Fisher et al. 2009), we propose that one specific area of research that would provide insight into commonalities, or lack thereof, is a comparison of attitudes toward inequality and risk. This combination stands to broaden our understanding of the conditions and environment that encourage, or discourage, pro-social decision-making and elicit negative reactions to inequity.

The last decade of empirical human research pertaining to pro-social behavior has displayed violations of the canonical model with self-interested, material payoff maximizing actors (see Ledyard, 1995; Camerer, 2003; Henrich et al., 2001). The justifications for behavior that violates standard assumptions about material maximizing include warm-glow (Andreoni, 1990; Bierhoff, 2002), reciprocity (Bolton and Ockenfels, 2000; Falk and Fischbacher, 2006; Fehr and Schmidt, 1999), reputation (Frank, 2001), envy (Beckman et al., 2002) and aversion to inequality (Beckman et al., 2012; Beckman et al., 2004a, 2004b; Pirttila and Uusitalo, 2008; Kroll and Davidowitz, 2003; and Amiel and Cowell, 2000).

While researchers have actively been seeking explanations for behavior that is inconsistent with the canonical model, nonhuman research has begun to explore some of these topics as well. In particular, the last five years have seen an explosion in work on prosocial behavior in nonhuman primates (Silk 2007). Initial studies indicated that chimpanzees were much less prosocial than are humans, with the apes not appearing to notice or care (these are difficult to distinguish experimentally) about opportunities to bring rewards to the partner at very little, or no, cost to themselves and despite the fact that their partner received no more than they did (Silk, Brosnan et al. 2005; Jensen, Hare et al. 2006; Vonk, Brosnan et al. 2008). This was even true when there was the opportunity to increase one's overall outcomes through reciprocity (Brosnan, Henrich et al. 2009). However, it soon became clear that there was more to the story. Capuchin monkeys, for instance, routinely provide benefits to partners (de Waal, Leimgruber et al. 2008), even when their partner stands to gain more than they do (Lakshminarayanan and Santos 2008; Brosnan, Houser et al. 2010). Moreover, cooperatively breeding callithrichids, who share parental duties among the mated pair as well as unweaned offspring, typically behave prosocially (Burkart, Fehr et al. 2007; Cronin, Schroeder et al. 2010) (although this is not always the case – see Cronin, Schroeder et al. 2009; Stevens 2010). Finally, despite the fact that chimpanzees do poorly in the barpull-based prosocial tasks at which capuchins and callithrichids excel, they are prosocial in exchange-based tasks (Horner, Carter et al. 2011) and routinely provide assistance, including targeted helping, to one another in experimental contexts (Warneken and Tomasello 2006; Warneken, Hare et al. 2007; Melis, Warneken et al. 2010; Yamamoto, Humle et al. 2012). Thus what appears to be the case is that non-human primates do behave in prosocial ways, however this behavior is sensitive to both the species in question (e.g., the evolution of this behavior was undoubtedly influenced by the species' ecologies, see, for example, Van Schaik and Burkart 2010) as well as the context of the interaction.

Not only do prosocial behaviors emerge in other primates, but there is also evidence for some of the same underlying mechanisms for prosocial behavior that have been discussed for humans, although these have often not been considered in the context of prosocial behavior. For instance, authors have argued for evidence, in non-human primates, of the warm-glow (de Waal, Leimgruber et al. 2008), reciprocity (de Waal 2000; Gomes, Mundry et al. 2008; Schino and Aureli 2008; Gomes and Boesch 2009), reputation (Russell, Call et al. 2008; Subiaul, Vonk et al. 2008), and aversion towards inequity (for a review, see Brosnan in revision). Primates are also sensitive to risk (McCoy and Platt 2005; Heilbronner, Rosati et al. 2008; Rosati and Hare 2010; Proctor, de Waal et al. in prep). In fact, primates differ in their risk tolerance, presumably due to the evolutionary pressures each species has faced (Mulcahy and Call 2007; Penn and Povinelli 2007). Thus it seems possible that these behaviors share continuity between humans and other species, either due to homology of similar cognitive mechanisms, or convergence of similar behaviors, albeit with potentially differing cognitive mechanisms. A better understanding of this would help to understand the conditions under which these behaviors evolved in humans. Although the literature on this taxon is vast, particularly in the case of humans, we here

summarize work relevant to laboratory experiments on inequity to provide a framework for comparison.

Inequity in human experiments

Inequality aversion in human research typically refers to differences in acquired compensation for similar activities or varying abilities to alter an outcome, which is largely connected to financial capabilities. However, inequality can also result from chance that results in differences in payouts that are out of the control of subjects. The experimental research in this area generally falls into two procedural categories – the use of dictator/ultimatum games and some other type of redistribution game. Fehr and Schmidt (1999), Bolton and Ockenfels (2000), and Goeree and Holt (2000) have all used the dictator/ultimatum games (or a similar game) and found that individuals who were motivated by their own monetary payoffs tend to perform poorly in these games. Schildberg-Horisch (2010) adapted the dictator game to allow a veil of ignorance and behavior toward risk. The original dictator game was modified with a 50% efficiency loss for any funds the dictator transfers to the receiver. If the assignment of dictator and receiver was made before the dictator chose to transfer the funds, then the treatment was with positions/states of the world known. If the assignment of role was made after the transfer decision, then a veil of ignorance had been imposed. Behavior toward risk was modeled by removing the second player. Each subject then decided how much to transfer and was subsequently randomly assigned to be dictator or receiver given their own choice. No other subject is involved. This research finds a small but statistically significant increase in the amount transferred behind a veil of ignorance than in the risk treatment indicating inequality aversion. The effect is strongly moderated by a gender effect with women being both more risk averse and more inequality averse.

Other research has focused on the ability to create equality by allowing participants to pay for equality. Carlsson et al. (2001) found that left-wing voters and women were both more risk- and inequality averse in their choice of paying for more equal societies. Dana et al. (2006) designed a clever experiment whereby individuals could incur a \$1 loss (payment of \$9 instead of \$10) to avoid playing a dictator game and consequently prevented the would-be receiver from finding out that they were playing a dictator game. The majority of participants opted out of the game with a payout of \$9 and no money being allocated to the would-be receiver, despite the fact that a payout of \$9 to the dictator and \$1 to the receiver was possible if the dictator game was carried out. Alternatively, in a “private” dictator game where the receivers were aware that they were playing the dictator game, the dictator rarely exits the game and, as seen in past research, tends to allocate some money to the receiver. Thus, the popularity of entertaining the option to opt out of playing the dictator game with a \$1 penalty shows evidence that subjects are averse to inequality, or at least are averse to being the cause of inequality, but are more inclined to entertain inequality if they can reduce their interaction with the less fortunate.

Use of a veil of ignorance (Frohlich and Oppenheimer, 1992; Rawls, 1971; Harsanyi, 1953) in understanding individual attitudes toward inequality has become a generally accepted baseline. Kroll and Davidowitz (2003) made use of a ‘common game’ and ‘individual game’ in order to induce a veil. In the common game, the individuals received the same payout from a single, mutual gamble whereas the payouts differed for each participant in the individual game. The experiment was carried out with children living in a communal environment and also with children living in a city. In short, they found that for small payouts, half of the children preferred the common game, but as the payout increased, the desired game changed in the direction of the individual game. The finding that individual behavior changed with increases in payoffs is supported in Holt and Laury (2002). Additionally, children who were raised in a communal environment tend to make more prosocial choices (favoring the common game).

Beckman et al. (2012) proposed an experiment whereby individuals made choices over 5 potential states of the world (payoffs). Three treatments were carried out – behind the veil of ignorance, risk and positions known – in the experiment. Beckman et al. (2012) allowed the subjects to make pairwise redistributions of funds across five states of the world in order to invoke the subject’s desired distribution of income. In the risky environment, the subjects were ex ante informed that each of the five payoffs was equally likely to be realized and the individual’s redistribution governed their actual payoff.¹ In the behind the veil treatment, subjects again redistributed the funds to their liking, but the median transfer between states of the world for all subjects governed the actual payoffs that the individual received. Additionally, each state of the world was not equally likely.² In the positions known treatment, subjects again redistributed funds but their state of the world was known ex ante, and the median transfer from the group governed the individual payoffs. Examining the differences in redistribution between the behind the veil and risk treatments allowed the teasing out of inequality aversion by examining an environment with both risk and inequality (behind the veil treatment) and a simply risky environment. The impact of pure risk on redistributions is also directly examined by comparing redistributions in the risk and positions known treatments. Thus, the experimental design allowed the researchers to disentangle the impacts of risk aversion and inequality aversion separately (see also Kroll and Davidowitz (2003) and Carlsson (2001)). Moreover, when individuals were asked to reallocate funds across the five potential payoffs in the positions known treatment where there were three subjects who would not be impacted by the redistribution, they found that individuals who were not impacted by the outcome of the reallocation voted in favor of a more equitable redistribution.

While Beckman et al. (2012) found that individuals favored a more equitable world when placed behind a veil of ignorance, the composition of redistribution displayed two interesting trends. First, and consistent with the findings in Kuziemko et al. (2010), individuals were averse to “last place” such that they did not want to end up with the smallest payoff. In fact, those

¹ Five cards were utilized to depict the state of the world and each subject drew a card, with replacement.

² In the behind the veil treatments, the subjects drew from the five cards, but without replacement.

individuals who were receiving the second smallest payoff desired reallocations that ensured that the individual receiving the smallest payoff did not end up with a payoff larger than their own. Second, in both the behind the veil and risk treatments, females tended to desire more equitable redistributions of payouts than did males. Only when positions were known did males begin desiring a redistribution that favored a higher degree of equity, which might be an aversion to showering the rich with greater payoffs. However, this research did not directly examine the role that group dynamics played in the redistribution of payoffs.

There has also been work that examines the effect of inequality on cooperation in groups. Anderson et al. (2008) examined the impact of inequality on cooperation in contributing to a public good. Inequality, in this context, came in the form of manipulating the levels and distributions of fixed payments given to subjects for participating in the experiment. In comparison to public goods contributions, when all individual's contributions were equal, when individual's rank within the experiment is made salient, the contributions decreased significantly as a result of the known ranks.

The absence of contributions to the public good often generates conflict within groups, especially if the lack of contributions is due to inequality. Abbink et al. (2012) examined this issue directly by determining how much conflict arose in a rent (profit) seeking experiment where groups could prevent profit generation when unequal shares of the profits existed. In short, if a group was set to obtain a smaller share of the profits generated from a profit raising activity, they might take actions to prevent the "advantaged" group from obtaining greater profits. Surprisingly, though, the authors find little support for the hypothesis that greater inequality – due to a larger disparity in the distribution of profits – generates greater conflict amongst groups.

Inequity in non-human primates (and other species)

Inequity has also been explored in other species, primarily non-human primates. However, the paradigms used to investigate it have differed rather substantially, in large part due to the difficulties of giving complex scenario or decision-making tasks to non-verbal species for whom instruction cannot be given (thus making it difficult to determine if they understand experimental contingencies). Because of this, there has been far less focus on the Dictator or Ultimatum games in non-human primates. In fact, to date only two studies have explored this game, and only in chimpanzees. The first found that chimpanzees were rational maximizers in an ultimatum game, with respondents accepting any offer made by the proposer (Jensen, Call et al. 2007). However, additional work showed that the paradigm used with the chimpanzees resulted in the same outcome in humans, indicating that the procedure was too dissimilar from the typical human procedure to be compared to the existing human literature (Smith and Silberberg 2010). A more recent study, comparing "dictator-like" responses to ultimatum game responses found that chimpanzees and children both responded by offering a more equal split when the partner had the option to refuse, despite the fact that neither children nor chimpanzees ever refused in the

game (Proctor, Williamson et al. in review). This may indicate that only the threat of a refusal is needed in order to promote more equitable behavior, both in children and chimpanzees. This work also highlights the need for careful consideration of “equivalent” procedures to make sure that they really are so (see below and Brosnan, Beran et al. in review for a more detailed discussion of this problem).

Rather than the ultimatum game procedure, work in non-humans has relied more on a paired task reminiscent of an Impunity Game (Bolton, Katok et al. 1998; Yamagishi, Horita et al. 2009). In the commonly used non-human primate version of this game, pairs of individuals alternately interact with a human experimenter, who sometimes pays them the same (e.g., a baseline control), sometimes pays one individual more (e.g., an inequity condition) and sometimes offers higher amounts, but then returns a lower payoff (e.g., an individual contrast condition). Subject responses in the inequity and individual contrast conditions are compared to their response to the same lower-value reward in the baseline control, in which both individuals were given the less preferred payoff (for reviews of this procedure, see Brosnan 2006; Price and Brosnan 2012). Thus, individuals cannot change either their own or their partners' outcomes by any action of theirs, but they can refuse to participate. Unlike in a human impunity game, however, the experimenter sets the payoffs, rather than the partner, a procedure necessitated largely by the problems associated with showing that the primates understand that their payoffs are contingent upon their partner's earlier actions (although see Proctor, Williamson et al. in review for a procedure that avoids this issue).

One drawback with this procedure, of course, is that the inequity experienced by the animals is caused by the *experimenter* rather than a social partner. Of course, the response are still illustrative for showing that the primates both notice and react to their partners' outcomes, nonetheless the lack of clarity over the actual referent of the primates' distress means that it is challenging to say whether the frustration is caused by the partner's behavior, the experimenter's behavior, or the partner's outcome. Some research has addressed this by looking at how the primates respond when their partner's outcome determines their reward, for instance when the partner has to choose a distribution or when the two individuals have to repeatedly negotiate which reward each will receive for a cooperative task. Both of these procedures indicate that the non-human primates, at least, are highly sensitive to the conspecific's behavior (Brosnan, Freeman et al. 2006; Proctor, Williamson et al. in review).

Nonetheless, despite the differences in procedure, the work in non-human subjects has been critical for understanding the evolution of inequity responses across the primates, including humans.

There are three key findings with respect to the primate work. First, these results demonstrate that responding negatively to inequity in experimental laboratory conditions is not a homology shared across the primates (Brosnan 2011). In particular, work with ten primate species spread across the great apes, Old World monkeys, and New World monkeys

demonstrates that inequity is most common in species that show high levels of cooperation with non-kin, non-pair social group members (Brosnan 2011). That is, primates that routinely form coalitions and alliances for support, rank acquisition or territory defense, cooperatively hunt, or otherwise socially cooperate, including chimpanzees (Brosnan, Schiff et al. 2005; Brosnan, Talbot et al. 2010), capuchin monkeys (Brosnan and de Waal 2003; van Wolkenten, Brosnan et al. 2007; Fletcher 2008; Takimoto, Kuroshima et al. 2009), macaques (McCleam and Harlow 1954; Beran, Rumbaugh et al. 2007), and, possibly, bonobos (Bräuer, Call et al. 2009), respond to inequity while other, often closely related (Talbot, Freeman et al. 2011) and equally large-brained species (Meyer, Polidora et al. 1961; Bräuer, Call et al. 2009) do not. Moreover, these results do not map on to other distributions, such as those based on brain size, performance on cognitive tasks, or extent of sociality (Brosnan 2011).

Thus, the non-human primate results seem to support the hypothesis in humans that responding to inequity is a mechanism by which individuals may recognize when a cooperative partnership is no longer beneficial and find a new partnership which is more so (Fehr and Schmidt 1999). We note here, too, that this may be one of several mechanisms used by other species, including humans, to support successful cooperation. For instance, cleaner fish, *Laibroides dimidiatus*, punish other individuals who cheat in cooperative interactions (Raihani, Grutter et al. 2010), indicating that they recognize differences in behavior, yet do not respond to inequity in an experimental paradigm (Raihani, McAuliffe et al. 2012). This has led to the hypothesis that this species utilizes punishment rather than partner choice as a mechanism to promote successful cooperation, a mechanism which may be present in humans as well (Raihani and McAuliffe 2012).

Second, the primate results highlight the influence of a variety of social and individual factors on responses. At the species level, the degree of interdependence seems to have influenced responses to inequity. That is, cooperative breeders, who must work together in order to raise offspring, do not respond to inequitable outcomes in these experimental conditions (Neiworth, Johnson et al. 2009), despite high degrees of cooperation. One possibility is that the level of interdependence required to raise offspring is such that responding to a small level of inequity is too costly in terms of the benefits lost (Brosnan, 2011). In fact, humans show a similar response within the species, with individuals in close relationships showing different responses than those in more contingent relationships (Clark and Grote 2003; Freeman, Sullivan et al. in review). However, the vast majority of the human literature involves strangers, often anonymously, removing the possibility of discovering the degree to which relationships may affect outcomes. Clearly more work needs to be done on different relationships, and how these relationships may affect outcomes both in humans and other species. For instance, one reasonable hypothesis is that behavior should be different at the commencement of a relationship, with subjects being more sensitive to perceived inequities, than as a relationship matures and the costs of finding a new partner increase (Brosnan 2011)

Third, and related to this, the primate results highlight the variation between individuals even within the same species and context. Considering chimpanzees for the moment, their responses are highly variable, based on factors such as rank (Bräuer, Call et al. 2009; Brosnan, Talbot et al. 2010), group membership (Brosnan, Schiff et al. 2005), and sex (Brosnan, Talbot et al. 2010). However, very little is known about what causes these differences, and they are often not consistent across studies. For instance, in various chimpanzee studies, chimpanzees have shown no sex difference (Brosnan, Schiff et al. 2005), a stronger response by males than females (Brosnan, Talbot et al. 2010), and a stronger response by females than males (Hopper, Lambeth et al. in review). This is particularly difficult to pin down given the much smaller sample sizes possible in non-human primate studies as compared to human studies. One recent study looked at sex, rank, and age as well as personality and the relationship between the partners, and found that chimpanzees' responses were best predicted by two factors, their personality and the frequency with which they had been involved in inequity studies (subjects showed stronger responses on earlier as compared to later exposures to inequity; Brosnan, Hopper et al. in prep). Thus, while the authors predicted a strong impact of relationship quality, based on both previous chimpanzee and human work, this did not turn out to be an important factor. This is not only important for understanding chimpanzees, but for exploring the evolution of these responses. There is a growing interest in how humans' responses vary across such dimensions as sex, political views, nationality, ethnicity, or culture (see above), but it may be useful to investigate other features, such as personality, relative status, and relationship with the partner as well for a fuller understanding of the underlying variability in responses to inequity in humans.

Comparing Human and Non-human Primates

As is clear by now, the non-human primate literature is not directly comparable with the human literature, which creates difficulty for a truly comparable approach. First, the form of the games for studies such as these typically differ between humans and other primates (although see Brosnan, Parrish et al. 2011; Brosnan, Wilson et al. 2011; Proctor, Williamson et al. in review for exceptions to this). Aside from the form of the game, there are other more subtle differences. In the primate games, individuals play with known (not anonymous) others from their social group, so bringing with them their previous relationships. Additionally, in all primate research thus far, the primates know what they are to receive prior to making a decision. This is likely critical as it removes any hint of risk, uncertainty, or ambiguity from the interaction, making this an area that needs to be much more fully explored. We emphasize that these subtle differences can be avoided. One of us is involved in a long-term study to compare non-human primates' and humans' responses to a series of games derived from game theory, utilizing methods that are, as much as is possible, identical across species. These results have been instrumental in highlighting ways in which humans do and do not differ from the rest of the primates (Brosnan, Parrish et al. 2011; Brosnan, Wilson et al. 2011; Brosnan, Beran et al. in review). Procedures such as these will be essential for a truly comparative approach that allows us to more fully understand the evolution of inequity responses.

Aside from procedural differences, there are also differences in foci. Thus far, the non-human primate work has been focused primarily on distributive inequity, which only represents a component of the human work (Brosnan and De Waal 2012; Christen and Glock 2012; Skitka 2012). In particular, the human work has focused on procedural justice, for which there is very little evidence in non-human primates. Only one study to date has explicitly explored procedure in non-human primates, and found that, when rewards are the same, chimpanzees do not respond to differences in procedure that result in longer delays for some individuals or for additional work required by some individuals (Brosnan, Talbot et al. 2010). In fact, thus far there is no evidence that differences in effort lead to inequity responses in non-human primates (Fontenot, Watson et al. 2007; van Wolkenten, Brosnan et al. 2007), although it is clear that a task of some sort is required (Brosnan, Talbot et al. 2010; Price and Brosnan 2012). Finally, although issues of risk, ambiguity, and uncertainty in response to inequity are beginning to be investigated in humans (see above), this is entirely unexplored in other species, and is necessary to fully understand these behaviors.

Finally, despite many similarities in outcome, there are also differences that must be considered for a full understanding of how this response evolved and what function it may play. As it stands, primates look like they lack an overall preference for equity; individuals are very concerned about what they receive, and respond negatively when they get less than a partner, but generally do not behaviorally respond when they get more (Brosnan 2012; Brosnan and De Waal 2012). There is evidence that they notice the discrepancy (Brosnan, Talbot et al. 2010), and it may be that our experimental designs are not conducive to eliciting such prosocial responses (Murphy and Miller 1955). In particular, as discussed above, despite chimpanzees' apparent disinterest in their partners' outcomes (Silk, Brosnan et al. 2005; Jensen, Hare et al. 2006), capuchin monkeys are quite responsive (de Waal, Leimgruber et al. 2008), even to the point of bringing their partner more than they will receive (Lakshminarayanan and Santos 2008; Brosnan, Houser et al. 2010). Thus, future work is needed to delineate the magnitude of this apparent difference between humans and other primates.

Future Directions

Thus we see several directions that are necessary for a full understanding of the evolution of inequity responses. Many of the more general foci are outlined in a recent special issue exploring inequity in other species (Social Justice Research, volume 25, issues 2 & 3; see specifically Brosnan and De Waal 2012). Thus here we focus on those issues most relevant to the topics at hand. First, it is necessary to gain more information about how primates would respond under the veil of ignorance, and how these results compare both to 1) their results when outcomes are known and 2) humans' behavior both when outcomes are known and unknown. This may provide more insight in to whether non-human primates, like humans, have a taste for equity, or are simply averse to receiving less than a partner.

Second, risk tolerance should be combined with inequity studies, both in humans and non-humans, to determine the degree to which risk influences responses. We know that primates vary in both their risk preferences (e.g., Heilbronner, Rosati et al. 2008; Rosati and Hare 2010; Proctor, de Waal et al. in prep) and their responses to inequity (see above), providing another possible explanation for the variation in responses to inequity seen across the species. However, nothing is known about whether and how risk preferences influence judgments of or responses to inequity.

Third, and perhaps more basically, we need additional studies that are comparable between humans and other primates. As discussed above, some such studies do exist, but they are only now becoming common. These are important for two reasons. First, different assumptions are made in the two fields, and more attention to these assumptions may highlight gaps in the existing literature. As a single example, in the non-human literature, inequity is not considered to occur unless the researcher can explicitly rule out that the mere presence of a better outcome, without a social partner receiving it, would cause a similar reaction (reviewed in Brosnan 2012). However, such a control for contrast effects (Reynolds 1961) is typically lacking in other species (although see Sloan, Baillargeon et al. 2012). It is possible that different phenomenon are being conflated in comparisons between the human and non-human literatures, and additionally, without attention to these basic processes, it is impossible to determine whether similar outcomes are due to similar or dissimilar cognitive mechanisms. Second, without a fully comparative approach shedding light on how humans and other primates are both similar to each other and different from each other, we cannot hope to understand the features that selected for humans' responses to inequity, or the function for which these responses evolved. This requires both human and non-human researchers to explore the questions that are asked in the other fields.

Conclusion

For the current paper, our goal was to synthesize the literature in light of these two main areas. To our knowledge, these questions have barely been explored in either the human or the non-human literature, thus broaching the conversation is an important first step. A second goal was to develop a series of predictions based on these hypotheses and, as a third goal, provide a series of future directions for research in order to address these important issues. We believe this is an important step in providing a more nuanced understanding of the evolution of responses to inequity in humans and other species.

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