



Contents lists available at [SciVerse ScienceDirect](#)

Journal of Economic Behavior & Organization

journal homepage: www.elsevier.com/locate/jebo



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

Gregory DeAngelo^{a,*}, Sarah F. Brosnan^b

^a Rensselaer Polytechnic Institute, Department of Economics, 110 8th Street, Troy, NY 12180, USA

^b Georgia State University, Department of Psychology, PO Box 5010, Atlanta, GA 30302, USA

ARTICLE INFO

Article history:

Accepted 30 November 2012

Available online xxx

CTSNet classification:

D01

D81

Z13

Keywords:

Inequity

Risk

Prosocial behavior

Other-regarding behavior

Non-human primates

Comparative research

ABSTRACT

Researchers studying human and non-human primates have begun exploring deviations from the canonical model of expected utility. Additionally, researchers have examined the role of inequality in decision-making across the taxa. However, these two research programs are rarely combined. In this paper we offer an examination of the role and impact of risk and inequity on decision-making in both human and non-human primates. We also offer insights into what drives these observed differences, considering a range of explanations from biological to methodological.

© 2012 Elsevier B.V. All rights reserved.

1. Introduction

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 et al., 2009b), 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, prosocial decision-making and elicit negative reactions to inequity.

* Corresponding author. Tel.: +1 518 867 1284.

E-mail addresses: deangg@rpi.edu (G. DeAngelo), sbrosnan@gsu.edu (S.F. Brosnan).

The last decade of empirical human research pertaining to prosocial 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, 2004a,b; Pirttila and Uusitalo, 2008; Kroll and Davidowitz, 2003; Amiel and Cowell, 2001).

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 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 et al., 2005; Jensen et al., 2006; Vonk et al., 2008). This was even true when there was the opportunity to increase one's overall outcomes through reciprocity (Brosnan et al., 2009a). However, it soon became clear that there was more to the story. Capuchin monkeys, for instance, routinely provided benefits to partners (de Waal et al., 2008), even when their partner stood to gain more than they did (Lakshminarayanan and Santos, 2008; Brosnan et al., 2010a). Moreover, cooperatively breeding callitrichids, who share parental duties among the mated pair as well as with unweaned offspring, typically behaved prosocially (Burkart et al., 2007; Cronin et al., 2010) (although this is not always the case – see Cronin et al., 2009; Stevens, 2010). Finally, despite the fact that chimpanzees did poorly in the barpull-based prosocial tasks at which capuchins and callitrichids excelled, they were prosocial in exchange-based tasks (Horner et al., 2011) and routinely provided assistance, including targeted helping, to one another in experimental contexts (Warneken and Tomasello, 2006; Warneken et al., 2007; Melis et al., 2010; Yamamoto 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 et al., 2008), reciprocity (de Waal, 2000; Gomes et al., 2008; Schino and Aureli, 2008; Gomes and Boesch, 2009), reputation (Russell et al., 2008; Subiaul et al., 2008), and aversion towards inequity (for a review, see Brosnan, 2011, 2012; Price and Brosnan, 2012). Primates are also sensitive to risk (McCoy and Platt, 2005; Heilbronner et al., 2008; Rosati and Hare, 2010), differing in their risk tolerance, presumably due to the evolutionary pressures each species has faced. 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.

2. 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.¹ 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 his or her 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.

¹ The dictator and ultimatum games are characterized by two players, one that is allocated an initial amount of money and is tasked with the job of splitting the money between themselves and the other participant. In the dictator game, the individual making the offer is dubbed the dictator, and makes an offer to the receiver, which cannot be rejected. Thus, the receiver's role is passive and whatever split the dictator offers is the final split. In the ultimatum game, however, the individual receiving the split of the money has the option to accept or reject the split of the money. If the individual rejects the split of the money, then neither party receives any money.

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.² 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.³ 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 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

² Five cards were utilized to depict the state of the world and each subject drew a card, with replacement.

³ In the behind the veil treatments, the subjects drew from the five cards, but without replacement.

for the hypothesis that greater inequality—due to a larger disparity in the distribution of profits – generates greater conflict amongst groups.

3. 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 from those used in humans, 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 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 et al., 2013). 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 et al., 2013 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 et al., 1998; Yamagishi 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 et al., 2013 for a procedure that avoids this issue).

One drawback with this procedure, 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 behavior 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 et al., 2006; Proctor et al., 2013).

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 et al., 2005, 2010b), capuchin monkeys (Brosnan and de Waal, 2003; Van Wolkentem et al., 2007; Fletcher, 2008; Takimoto et al., 2010), macaques (Massen et al., 2012), and, possibly, bonobos (Bräuer et al., 2009), respond to inequity while other, often closely related (Talbot et al., 2011) and equally large-brained species (Brosnan et al., 2011; Bräuer 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 *moreso* (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, *Labroides dimidiatus*, punish other individuals who cheat in cooperative interactions (Raihani et al., 2010), indicating that they recognize differences in behavior, yet do not respond to inequity in an experimental paradigm (Raihani 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 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 et al., under review). However, the vast majority of the human literature involves strangers, often in anonymous interactions, 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 et al., 2009; Brosnan et al., 2010b), group membership (Brosnan et al., 2005), and sex (Brosnan et al., 2010b). 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 et al., 2005), a stronger response by males than females (Brosnan et al., 2010b), and a stronger response by females than males (Hopper et al., under 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, but is nonetheless essential. Understanding how factors such as sex, rank, age, personality and relationship interact 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.

4. 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 et al., 2011a,b; Proctor et al., 2013 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, and so bring 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 et al., 2011a, b, 2013). 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 require additional work by some individuals (Brosnan et al., 2010b). In fact, thus far there is no evidence that differences in effort lead to inequity responses in non-human primates (Fontenot et al., 2007; Van Wolkenten et al., 2007), although it is clear that responses to inequitable outcomes do not occur unless individuals had to perform a task in order to receive those outcomes (Brosnan et al., 2010b; 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). However, there is evidence that they notice the discrepancy (Brosnan et al., 2010b), so it may be that our experimental designs are not conducive to eliciting such prosocial responses. In particular, as discussed above, despite chimpanzees' apparent disinterest in their partners' outcomes (Silk et al., 2005; Jensen et al., 2006), capuchin monkeys are quite responsive to their partner's needs (de Waal et al., 2008), even to the point of bringing their partner more than they will receive (Lakshminarayanan and Santos, 2008; Brosnan et al., 2010a). Thus, future work is needed to delineate the magnitude of this apparent difference between humans and other primates.

5. 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 et al., 2008; Rosati and Hare, 2010) 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 et al., 2012). It is possible that different phenomenon are being conflated in comparisons between the human and non-human literatures. 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 each other's fields.

6. 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.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.jebo.2012.12.014>.

References

- Abbink, K., Masclet, D., Mirza, D., 2012. Inequality and Inter-Group Conflicts – Experimental Evidence. Working Paper.
- Amiel, Y., Cowell, F.A., 2001. Attitudes Toward Risk and Inequality: A New Twist on the Transfer Principle. Distributional Analysis Paper 56, STICERD, London School of Economics, London WC2A2AE.
- Anderson, L.R., Mellor, J.M., Milyo, J., 2008. Inequality and public good provision: an experimental analysis. *The Journal of Socio-Economics* 37, 1010–1028.
- Andreoni, J., 1990. Impure altruism and donations to public goods: a theory of warm-glow giving. *The Economic Journal* 100, 464–477.
- Beckman, S.R., Formby, J., Smith, W.J., Zheng, B., 2002. Envy, malice and Pareto efficiency: an experimental examination. *Social Choice and Welfare* 19, 349–367.
- Beckman, S.R., Formby, J., Smith, W.J., Zheng, B., 2004a. Efficiency, equity and democracy: experimental evidence on Okun's leaky bucket. In: Frank, C. (Ed.), *In: Research on Economic Inequality*, vol. 11. Emerald Group Publishing Limited, pp. 17–42.
- Beckman, S.R., Formby, J., Smith, W.J., Zheng, B., 2004b. Risk, inequality aversion and biases born of social position: further experimental tests of the leaky bucket. In: John, B., Yoram, A. (Eds.), *In: Research on Economic Inequality*, vol. 12. Emerald Group Publishing Limited, pp. 73–96.
- Beckman, S.R., DeAngelo, G.J., Smith, W.J., Wang, N., Zheng, B., 2012. Social Behavior Toward Risk and Inequality. Working paper.
- Bierhoff, H.W., 2002. *Prosocial Behaviour*. Taylor and Francis Publishing, New York, NY.
- Bolton, G.E., Ockenfels, A., 2000. ERC, a theory of equity, reciprocity and competition. *The American Economic Review* 90, 166–193.
- Bolton, G.E., Katok, E., Zwick, R., 1998. Dictator game giving: rules of fairness versus acts of kindness. *International Journal of Game Theory* 27, 269–299.
- Bräuer, J., Call, J., Tomasello, M., 2009. Are apes inequity averse? New data on the token-exchange paradigm. *American Journal of Primatology* 7, 175–181.
- Brosnan, S.F., 2006. Nonhuman species' reactions to inequity and their implications for fairness. *Social Justice Research* 19, 153–185.
- Brosnan, S.F., 2012. Introduction to Justice in Animals". *Social Justice Research* 25, 109–121.
- Brosnan, S.F., 2011. A hypothesis of the co-evolution of inequity and cooperation. *Frontiers in Decision Neuroscience* 5, 43, <http://dx.doi.org/10.3398/fnins.2011.00043>.
- Brosnan, S.F., Beran, M.J., Parrish, A.E., Price, S.A., Wilson, B.J., 2013. Comparative approaches to studying strategy: towards an evolutionary account of primate decision-making. *Evolutionary Psychology*, in press.
- Brosnan, S.F., de Waal, F.B.M., 2003. Monkeys reject unequal pay. *Nature* 425, 297–299.

Please cite this article in press as: DeAngelo, G., Brosnan, S.F., The importance of risk tolerance and knowledge when considering the evolution of inequity responses across the primates. *J. Econ. Behav. Organ.* (2013), <http://dx.doi.org/10.1016/j.jebo.2012.12.014>

- Brosnan, S.F., de Waal, F.B.M., 2012. Conclusion to Justice in Animals. *Social Justice Research* 25, 336–351.
- Brosnan, S.F., Flemming, T.E., Talbot, C., Mayo, L., Stoinski, Tara, S., 2011. Responses to inequity in orangutans. *Folia primatologica* 82, 56–70.
- Brosnan, S.F., Freeman, C., de Waal, F.B.M., 2006. Partner's behavior, not reward distribution, determines success in an unequal cooperative task in capuchin monkeys. *American Journal of Primatology* 68, 713–724.
- Brosnan, S.F., Henrich, J., Mareno, M.C., Lambeth, S., Schapiro, S., Silk, J.B., 2009a. Chimpanzees (*Pan troglodytes*) do not develop contingent reciprocity in an experimental task. *Animal Cognition* 12 (4), 587–597.
- Brosnan, S.F., Houser, D., Leimgruber, K., Xiao, E., Chen, T., de Waal, F.B.M., 2010a. Competing demands of prosociality and equity in monkeys. *Evolution and Human Behavior* 31, 279–288.
- Brosnan, S.F., Newton-Fisher, N.E., van Vugt, M., 2009b. A melding of the minds: when primatology meets social psychology. *Personality and Social Psychology Review* 13, 129–147.
- Brosnan, S.F., Parrish, A.R., Beran, M.J., Flemming, T., Heimbauer, L., Talbot, C.F., Lambeth, S.P., Schapiro, S.J., Wilson, B.J., 2011a. Responses to the Assurance game in monkeys, apes, and humans using equivalent procedures. *Proceedings of the National Academy of Sciences*, <http://dx.doi.org/10.1073/pnas.1016269108>.
- Brosnan, S.F., Schiff, H.C., de Waal, F.B.M., 2005. Tolerance for inequity may increase with social closeness in chimpanzees. *Proceedings of the Royal Society* 1560, 253–258.
- Brosnan, S.F., Talbot, C., Ahlgren, M., Lambeth, S.P., Schapiro, S.J., 2010b. Mechanisms underlying the response to inequity in chimpanzees, *Pan troglodytes*. *Animal Behavior* 79, 1229–1237.
- Brosnan, S.F., Wilson, B.J., Beran, M.J., 2011b. Old World monkeys are more similar to humans than New World monkeys when playing a coordination game. *Proceedings of the Royal Society* 279, 1522–1530.
- Burkart, J., Fehr, E., Efferson, C., van Schaik, C.P., 2007. Other-regarding preferences in a non-human primate: common marmosets provision food altruistically. *Proceedings of the National Academy of Sciences* 104 (50), 19762–19766.
- Christen, M., Glock, H.-J., 2012. The (limited) space for justice in social animals. *Social Justice Research* 25 (3), 298–326.
- Clark, M.S., Grote, N.K., 2003. In: Millon, T., Lerner, M.J. (Eds.), *Close Relationships. Handbook of Psychology Personality and Social Psychology*, vol. 5. John Wiley & Sons, New York, pp. 447–461.
- Cronin, K.A., Schroeder, K.K.E., Rothwell, E.S., Silk, J.B., Snowdon, C.T., 2009. Cooperatively breeding cottontop tamarins (*Saguinus oedipus*) do not donate rewards to their long-term mates. *Journal of Comparative Psychology* 123, 231–241.
- Cronin, K.A., Schroeder, K.K.E., Snowdon, C.T., 2010. Prosocial behaviour emerges independent of reciprocity in cottontop tamarins. *Proceedings of the Royal Society* 277, 3845–3851.
- de Waal, F.B.M., 2000. Attitudinal reciprocity in food sharing among brown capuchin monkeys. *Animal Behavior* 60, 253–261.
- de Waal, F.B.M., Leimgruber, K., Greenberg, A.R., 2008. Giving is self-rewarding for monkeys. *Proceedings of the National Academy of Sciences* 105, 13685–13689.
- Fehr, E., Schmidt, K.M., 1999. A theory of fairness, competition, and cooperation. *The Quarterly Journal of Economics* 114, 817–868.
- Fletcher, G.E., 2008. Attending to the outcome of others: disadvantageous inequity aversion in male capuchin monkeys (*Cebus apella*). *American Journal of Primatology* 70, 901–905.
- Fontenot, M.B., Watson, S.L., Roberts, K.A., Miller, R.W., 2007. Effects of food preferences on token exchange and behavioural responses to inequality in tufted capuchin monkeys, *Cebus apella*. *Animal Behavior* 74, 487–496.
- Frank, R.H., 2001. Cooperation through emotional commitment. In: Nesse, R.M. (Ed.), *Evolution and the Capacity for Commitment*. Russell Sage Foundation, New York, pp. 57–76.
- Freeman, H.D., Sullivan, S., Hopper, L.M., Holmes, A.N., Schultz-Darken, N., Williams, L.E., Brosnan, S.F. Different responses to inequity by three primate species provides support for the importance of interdependence in the selection of social behavior. *PLoS ONE*, under review.
- Gomes, C.M., Boesch, C., 2009. Wild chimpanzees exchange meat for sex on a long-term basis. *PLoS ONE* 4 (4), e5116.
- Gomes, C.M., Mundry, R., Boesch, C., 2008. Long-term reciprocation of grooming in wild West African chimpanzees. *Proceedings of the Royal Society* 276, 699–706.
- Heilbrunner, S.R., Rosati, A.G., Stevens, J.R., Hare, B., Hauser, M.D., 2008. A fruit in the hand or two in the bush? Divergent risk preferences in chimpanzees and bonobos. *Biology Letters* 4, 246–249.
- Henrich, J., Boyd, R., Bowles, S., Camerer, C., Fehr, E., Gintis, H., McElreath, R., 2001. In search of Homo Economicus: Behavioral experiments in 15 small-scale societies. *American Economic Review* 91, 73–78.
- Hopper, L.M., Lambeth, S., Schapiro, S., Brosnan, S.F. I want what you have! Female chimpanzees' response to individual loss is mediated by inequity, under review.
- Horner, V., Carter, J.D., Suchak, M., de Waal, F.B.M., 2011. Spontaneous prosocial choice by chimpanzees. *Proceedings of the National Academy of Sciences* 108, 13847–13851.
- Jensen, K., Call, J., Tomasello, M., 2007. Chimpanzees are rational maximizers in an ultimatum game. *Science* 318, 107–109.
- Jensen, K., Hare, B., Call, J., Tomasello, M., 2006. What's in it for me? Self-regard precludes altruism and spite in chimpanzees. *Proceedings of the Royal Society* 273, 1013–1021.
- Lakshminarayanan, V., Santos, L.R., 2008. Capuchin monkeys are sensitive to others' welfare. *Current Biology*, R999–R1000.
- Massen, J.J.M., Van den Berg, L.M., Spruijt, B.M., Sterck, E.H.M., 2012. Inequity aversion in relation to effort and relationship quality in long-tailed macaques (*Macaca fascicularis*). *American Journal of Primatology* 74, 145–156.
- McCoy, A.N., Platt, M.L., 2005. Risk-sensitive neurons in macaque posterior cingulate cortex. *Nature Neuroscience* 8, 1220–1227.
- Melis, A.P., Warneken, F., Jensen, K., Schneider, A.-C., Call, J., Tomasello, M., 2010. Chimpanzees help conspecifics obtain food and non-food items. *Proceedings of the Royal Society* 278, 1405–1413.
- Neiwirth, J.J., Johnson, E.T., Whillock, K., Greenberg, J., Brown, V., 2009. Is a sense of inequity an ancestral primate trait? Testing social inequity in cotton top tamarins (*Saguinus oedipus*). *Journal of Comparative Psychology* 123, 10–17.
- Price, S.A., Brosnan, S.F., 2012. To each according to his need? Variability in the responses to inequity in non-human primates. *Social Justice Research* 25, 140–169.
- Proctor, D., Williamson, R., de Waal, F.B.M., Brosnan, S.F., 2013. Chimpanzees play the ultimatum game. *PNAS*, in press.
- Raihani, N.J., Grutter, A.S., Bshary, R., 2010. Punishers benefit from third-party punishment in fish. *Science* 327, 171.
- Raihani, N.J., McAuliffe, K., 2012. Does inequity motivate punishment? Cleaner fish as a model system. *Social Justice Research* 25, 213–231.
- Raihani, N.J., McAuliffe, K., Brosnan, S.F., Bshary, R., 2012. Are cleaner fish (*Labroides dimidiatus*) inequity averse? *Animal Behavior* 84 (3), 665–674.
- Reynolds, G.S., 1961. Behavioral Contrast. *Journal of the Experimental Analysis of Behavior* 4, 441–466.
- Rosati, A.G., Hare, B., 2010. Chimpanzees and bonobos distinguish between risk and ambiguity. *Biology Letters* 7, 15–18.
- Russell, Y.I., Call, J., Dunbar, R.I.M., 2008. Image scoring in great apes. *Behavioural Processes* 78, 108–111.
- Schino, G., Aureli, F., 2008. Grooming reciprocation among female primates: a meta-analysis. *Biology Letters* 4, 9–11.
- Silk, J.B., 2007. Empathy, sympathy, and prosocial preferences in primates. In: Dunbar, R.I.M., Barrett, L. (Eds.), *Oxford Handbook of Evolutionary Psychology*. New York, Oxford University Press.
- Silk, J.B., Brosnan, S.F., Vonk, J., Henrich, J., Povinelli, D.J., Richardson, A.S., Lambeth, S.P., Mascaró, J., Schapiro, S.J., 2005. Chimpanzees are indifferent to the welfare of unrelated group members. *Nature* 437, 1357–1359.
- Skitka, L.J., 2012. Cross-disciplinary conversations: A social psychological perspective on justice research with non-human animals. *Social Justice Research* 25 (3), 327–335.
- Sloan, S., Baillargeon, R., Premack, D., 2012. Do infants have a sense of fairness? *Psychological Science* 23, 196–204.

- Smith, P., Silberberg, A., 2010. Rational maximizing by humans (*Homo sapiens*) in an ultimatum game. *Animal Cognition* 13, 671–677.
- Stevens, J.R., 2010. Donor payoffs and other-regarding preferences in cotton-top tamarins (*Saguinus oedipus*). *Animal Cognition* 13, 663–670.
- Subiaul, F., Vonk, J., Okamoto-Barth, S., Barth, J., 2008. Do chimpanzees learn reputation by observation? Evidence from direct and indirect experience with generous and selfish strangers. *Animal Cognition* 11, 611–623.
- Takimoto, A., Kuroshima, H., Fujita, K., 2010. Capuchin monkeys (*Cebus apella*) are sensitive to others' reward: an experimental analysis of food-choice for conspecifics. *Animal Cognition* 13, 249–261.
- Talbot, C., Freeman, H.D., Williams, L.E., Brosnan, S.F., 2011. Squirrel monkeys' response to inequitable outcomes indicates evolutionary convergence within the primates. *Biology Letters*, <http://dx.doi.org/10.1098/rsbl.2011.0211>.
- Van Schaik, C.P., Burkart, J., 2010. Mind the gap: cooperative breeding and the evolution of our unique features. In: Kappeler, P.M., Silk, J.B. (Eds.), *Mind the Gap: Tracing the Origins of Human Universals*. Springer, Heidelberg, Germany, pp. 477–497.
- Van Wolkenten, M., Brosnan, S.F., de Waal, F.B.M., 2007. Inequity responses in monkeys modified by effort. *Proceedings of the National Academy of Sciences* 104, 18854–18859.
- Vonk, J., Brosnan, S.F., Silk, J.B., Henrich, J., Richardson, A.S., Lambeth, S.P., Schapiro, S.J., Povinelli, D.J., 2008. Chimpanzees do not take advantage of very low cost opportunities to deliver food to unrelated group members. *Animal Behaviour* 75, 1757–1770.
- Warneken, F., Hare, B., Melis, A.P., Hanus, D., Tomasello, M., 2007. Spontaneous altruism by chimpanzees and young children. *PLoS Biology* 5, e184.
- Warneken, F., Tomasello, M., 2006. Altruistic helping in human infants and young chimpanzees. *Science* 311, 1301–1303.
- Yamagishi, T., Horita, Y., Takagishi, H., Shinada, M., Tanida, S., Cook, K.S., 2009. The private rejection of unfair offers and emotional commitment. *Proceedings of the National Academy of Sciences* 106, 11520–11523.
- Yamamoto, S., Humle, T., Tanaka, M., 2012. Chimpanzees' flexible targeted helping based on an understanding of conspecifics' goals. *Proceedings of the National Academy of Sciences* 109, 3588–3592.