

## **At a Crossroads of Disciplines**

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Studies on fairness are at an exciting juncture. There is interest in these topics across a wide range of disciplines and new technology gives the potential for further avenues of research. Perhaps the most recent area of interest addresses the ways in which reactions to inequity in nonhuman species are similar to or different from humans' reactions. With this knowledge in hand, we can better understand ourselves, other animals, and the evolution of this behavior. A cross-disciplinary approach uniting theory and techniques from disciplines as diverse as economics, social psychology, and animal behavior allows us to best address these questions. Through such studies, we will hopefully better understand the breadth of inequity responses as they relate to a variety of different behaviors and situations. A cohesive theory of the evolutionary trajectory of this behavior will also help us gain a better understanding of the function of the behavior.

These commentaries address just these issues. Researchers from diverse fields (representing social and cognitive psychology, neuroscience, economics, and primate behavior) attempt to meld the information on nonhuman reactions to inequity into their field of study and provide a good framework for how such work must be approached in the future. Many of these ideas represent directions that are already being taken. Here, I respond to and re-emphasize some of the ideas presented.

### **ORIGINS OF THE RESPONSE: SOCIAL OR NONSOCIAL?**

In the target article, I proposed that the origins of the inequity response were rooted in social behavior (Brosnan, 2006). In this reply to my

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commentators, I believe that the first necessary step was the recognition that rewards differ between individuals, which I argue could have derived from their abilities at social learning; after all, one of the necessary elements of social learning is recognizing that another individual has a better outcome than oneself. Thus, no matter what mechanism individuals use to socially learn (stimulus enhancement, emulation, imitation, etc.), an individual must initially notice that the other individual is obtaining some benefit they cannot themselves. Later, after understanding that rewards vary between conspecifics, individuals may be motivated to obtain these better rewards as well.

A crucial next step is that animals were selected to respond negatively to discrepancies against the self. In fact, this may not always lead to an absolutely better outcome for the individual, but instead to alternate behaviors which might, in the long run, minimize both inequity and the cost of achieving equity. The best example of this thinking is the work on commitment problems by Robert Frank (1988, 2001). He argues that individuals may make short-term sacrifices that lead to long-term benefit. For example, an individual who takes on great cost to sue those who take advantage of him (cost above and beyond the value of the lost benefit) will not likely be treated badly by others in the future, out of fear that he will continue to follow this strategy and sue them (causing them a loss of time and resources). Thus, the willingness to irrationally punish becomes a signal of one's commitment to good treatment and leads to future positive interactions with others without further cost accrued. Back to the evolution of inequity, reacting negatively to a conspecific who does not behave equitably in their treatment of oneself may lead to finding new cooperation partners who will presumably show more equitable treatment.

The last step to evolve, I propose, was costly punishment, in which individuals are willing to sacrifice their own gains to rectify inequity. This presumably leads to further cooperation (and more equity) as punished individuals toe the line in the future (Fehr and Gächter, 2002). In humans, it is also known that individuals respond negatively to advantageous inequity, or inequity that is detrimental to another (Fehr and Schmidt, 1999; Hatfield *et al.*, 1978; Loewenstein *et al.*, 1989). Either through attempts to rectify the situation or psychological leveling mechanisms, individuals work to bring equity to these situations as well. Thus, we find the inequity averse behavior present in humans.

Chen and Santos do not disagree with the basic trajectory I propose, but make an argument that the origins of inequity aversion are rooted not in the social interactions in which the behavior occurs, but in reference-point evaluation, or the ability to detect violations in expectations, as used in foraging and other nonsocial endeavors. Clearly monkeys and apes have this ability. Tinklepaugh (1928) initially examined this in monkeys, who responded negatively when they did not receive the reward they had seen

hidden previously, and presumably expected. Work by Santos *et al.* (2002) has further demonstrated this ability. In fact, it is clear that the main difference between violation of expectation (as, for instance, in Tinklepaugh's experiments) and inequity aversion is that the source of the expectation is based on personal experience in the case of the first (the monkey saw a nice tidbit of food hidden for their later consumption), while in the second case expectation is based on what *another* individual received. Thus, the two behaviors are not so different, only the antecedent which leads to the negative reaction. The question then becomes one of which came first. Did individuals first react to situations in which they didn't get what they expected, or to situations in which they didn't get what a conspecific did?

Nonhuman primates spend most of their lives in the social realm. The dominance hierarchy and other conspecifics interact both positively (warning of danger, grooming, etc.) and negatively (monopolizing food or mates, aggression, etc.) in almost every aspect of their lives. In fact, by focusing on experimental situations, Chen and Santos may have overlooked the fact that reference point evaluation can be a highly social activity in primates. One of the situations that Chen and Santos use in support of reference-point evaluation hypothesis I think more accurately represents a social situation. An individual who observes a conspecific foraging more successfully, then alters her foraging strategy to increase her gains is making this judgment based on the *social* information, as to her, this resource was made more salient by the presence of a conspecific, even though the resource itself is unchanged. This is a social determination of value.

To give an example, a female who sees an excellent cache of fruit, but cannot easily obtain it, may assume that the food is unreachable and therefore, fail to go after the fruit. However, if she sees another female successfully obtain it, she may re-orient and pursue the food more vigorously, even in the absence of any sort of social learning (the first female does not learn *how* to get the fruit from watching the conspecifics, just that it is apparently obtainable). Although the activity of obtaining the food is non-social (i.e., completed individually or even alone), the comparison that made her decide to pursue the food is clearly social. Thus, it is difficult to separate an apparently nonsocial activity from its social roots, and may well mean that all sorts of comparisons in nonhuman primates initially derive from assessments made in their highly social environment. Arguably, even reference-point evaluation may have roots in social learning and other activities that draw attention to social partners and their activities or rewards.

Furthermore, Chen and Santos discuss reference-dependent behavior in the context of foraging, but in these social species, it may occur in many other nontangible realms, such as grooming or support. These interactions are inherently social and a comparison can only be made in reference to what another individual received. This is more evidence for the hypothesis

that social referencing could have evolved first, and then eventually moved outside of the social realm to the nonsocial reference-point behavior that Chen and Santos find in their experiments.

Ideally, of course, we would test this to gain a better understanding of the circumstances under which the various behaviors occur. While it is not possible to explicitly test evolutionary hypotheses, particularly with regard to behavior, which leaves few traces, empirical investigation does lead to more refined theorizing. I have previously stated that I believe this reaction is much more common in species with a more tolerant dominance structure (see target article). This does not mean species without a dominance hierarchy, but those in which the dominants are not exceedingly despotic. In both capuchin monkeys and chimpanzees, while dominants do tend to get first access to rewards (be they food, females, support, or grooming), and get the best bits of those rewards, subordinates have a reasonable expectation of receiving some as well. Subordinate individuals do get good foods and can expect to hold on to these rewards once they have possession of them. As a result, primates of these species have some basic expectations about what they will receive, and hence, some comparison point against which to judge inequity. In a particularly despotic species, such as rhesus macaques, I would not expect the individuals, especially more subordinate ones, to show much response. Subordinates never have any expectation of holding on to particularly nice foods, and dominants have little experience with receiving second best. Thus, I propose that the inequity response would be much more pronounced in species (both primate and nonprimate) with relative tolerance than in those species with quite despotic dominance structures.

Chen and Santos, on the other hand, predict that if the reference-point evaluation hypothesis is correct, we will see much more evidence of inequity aversion in species with quite variable environments. These are the environments with the least stability and hence those in which the best strategy is most variable. They suggest that this could be tested by looking at the variation in the inequity response in species with different environmental stability.

In fact, I recommend an expansion of this, comparing individuals across at least four different categories. First, we need to be species representing relatively tolerant versus relatively despotic species. Second, these dominance styles must be distributed between species with life-history patterns reflecting high environmental stability and species with life-history patterns reflecting low environmental stability. Such environmental stability should be a characteristic of the species rather than one particular group of individuals within a species. Otherwise, one runs the risk of simply finding that the behavioral response is plastic rather than that the life history of the species has affected the evolution of inequity responses. The predictions that follow for the social hypothesis I put forth is that the relatively tolerant

species will show evidence of an inequity response in situations regardless of the environmental stability in their life history. The predictions from Chen and Santos' reference-dependence hypothesis is that species with a life history of low environmental stability should show more evidence of an inequity response, regardless of whether they are a tolerant or despotic species.

Clearly, there are problems with even such a study. For instance, by comparing different species (which is necessary to get at the development of the behavior across a history of environmental stability or variability rather than behavioral flexibility), we introduce other uncontrolled variables which may also affect the results. Not to mention the fact that by testing only a single prediction of each hypothesis, we leave out many other possibilities. However, quantitative studies like these, while they cannot conclusively settle questions of evolutionary origins, go far towards helping us find the best solution.

## **CROSS-DISCIPLINARY APPROACHES TO COMPLEX SOCIAL QUESTIONS**

### **Neuroscience and Animal Behavior**

Oftentimes the best answers to complex questions arise through cross-disciplinary conversation. In their reply, Watson and Platt point to the numerous areas of the brain that neuroscientists have located in both human and nonhuman primates for behaviors that may be related to inequity. I believe neural evidence will play a great role in these discussions, perhaps primarily in two areas.

First, neural evidence can be used to correlate behaviors to areas of brain activation, which may help us to determine how behaviors are related to each other. To use an example from the previous section of this reply (and mentioned by Watson and Platt), it would be possible to correlate brain activity from both social and nonsocial instances of social comparison for a rough comparison of inequity aversion and reference-point decisions. Such evidence alone would not be conclusive, but could be used to guide further research in many fields.

Second, neural evidence can be used to understand how behaviors which appear similar in human and nonhuman primates (and other animals) are related at the level of the brain. Although the structure of different species' brains is not identical, related areas can be compared for a general understanding of the evolutionary history of different areas of the brain or behaviors. Given that we cannot ask animals about their thoughts and feelings (and that humans may not report accurately), it is useful to have a tool to address this with some objectivity.

However, as exciting as recent advances in neuroscience are, it is important to bear in mind the purpose of these tools. Knowing which areas of the brain are active during different activities has little meaning unless these responses are correlated across behaviors and species. Without this information, the data is interesting but does not broaden our understanding to a great degree. As we get a larger set of tools for neuroimaging and a greater understanding of the workings of the brain, it will become even more important to actively extrapolate this information in meaningful ways. This is an area of potential fruitful collaboration between scientists who study different species or behaviors, or those studying different disciplines, such as neuroscience and behavior.

### **Social Psychology and Animal Behavior**

Reviews from both Bierhoff and Rohmann and Keltner *et al.* point to the important role of social psychology in this conversation. There is a long history of studying inequity aversion in humans in the field of social psychology. This can inform and be informed by new programs of study involving nonhuman animals.

Bierhoff and Rohmann went into the most detail regarding the bridging between animal studies and social psychology. This seems like an obvious connection, but is more difficult than it seems due to differences in training, and because the scientists involved tend to read different journals and work in different departments. Bierhoff and Rohmann generally focus on how studies on animals can inform social psychology, but of course the opposite is true as well. In fact, they provide examples of well-known social psychology models that may be applicable to animal studies. For instance, investment theory postulates that people stay in groups for reasons above and beyond their satisfaction, including their investments in the group and the availability of alternatives. I explicitly argue (as Bierhoff and Rohmann discuss) that the social structure of an animal's group has a large impact on the relative level of equity within a group. Individuals with few alternatives are more likely to live in despotic groups where equity is rare. Bierhoff and Rohmann suggestion to apply investment theory to primate groups (or other species) is very well taken, although it may be difficult to do this as explicitly as Bierhoff and Rohmann recommend.

Some measures are easier to take in nonverbal species than others. For instance, it is fairly easy to get a handle on a group-living nonhuman's alternative options. One can assess predation risk, potential for finding and processing food independently, risk from conspecific groups, chances of joining another group, chances of reproducing independently and so forth, which leads to a reasonably good understanding of the animal's alternatives.

However, it is very difficult to get at nonmeasurable quantities or feelings like “satisfaction” in a species that cannot self-report. There are some measures, of course, but these are all behavioral correlates such as access to food or mates, degree of harassment, and so forth. None involve any sense of subjective wellbeing. Thus, it will be hard to compare human social psychology research with animal research until there are good definitions of such things based solely on behavioral outcomes, rather than on reported emotions or feelings.

Thus, we should continue the effort to bridge the gap. Social psychologists can strive for measurable behavioral correlates of activities or actions of interest, to be more easily compared cross-species, in addition to collection of self-report or other data that is more difficult to compare cross-species. On the other hand, those of us studying nonhuman species can more actively engage social psychologists and attempt to correlate behaviors across these species. There are a great many behaviors shared across species that could be used for such comparisons, rather than focusing exclusively on behaviors that nonhumans do not perform (such as verbal behaviors).

Best yet, of course, is for individuals to attempt to bridge the gap themselves, and apply social psychology to animal populations. Perhaps the best example of this is the recent work addressing personality in different species (Gosling, 2001). Researchers studying chimpanzees have used the Big 5 personality trait model from social psychology as a basis for constructing a personality model of chimpanzees. This has led to a 6 factor rather than 5 factor model (representing the Big 5 in humans plus a dominance factor (King and Figueredo, 1997)), but because they are using the language of social psychology, direct comparisons are possible.

Related to this topic, a key contribution of Keltner *et al.*'s commentary is the insight that scientists studying humans should look in more detail at the mundane details of everyday life. They argue that many of the reactions that students of animal behavior study represent just such things—grooming, food sharing, and so forth. Not only is this good advice for social psychologists, but will allow for more comparisons across species, as such behaviors are more commonly shared with nonhumans. Moreover, by focusing on everyday activities, we may gain a better understanding of the building blocks of the sense of fairness in humans. A bottom-up approach, which breaks down the big picture into its constituent details and mechanisms, to be studied individually, will advance our understanding of how the sense of fairness functions in humans.

### Social Emotions

Keltner *et al.* elaborate quite extensively on my proposal that social emotions may underlie the reactions inequity in nonhuman primates, as they

do in humans. This was based mostly on my assumption, in my previous exchange studies, that it seems unlikely that the response involves cognitive calculation. These monkeys failed to accept a perfectly good cucumber, which was the logical action, particularly after it became clear that the better reward would not be made available. Instead, they refused to participate or threw the reward out, which did not increase their rewards, nor decrease their partner's rewards. This seems irrational, and hence not a likely candidate for a cognitive decision. Humans have been proposed to use emotions as "rules of thumb" to make decisions more rapidly and easily, and it seems possible that nonhumans, too, have evolved to use social emotions to rapidly make certain decisions.

In fact, a study we recently completed examining the role of choice in capuchin monkeys' reactions to inequity provides more tangential support for the idea that social emotions may play a role (Brosnan *et al.*, in press). In the original exchange experiments, the monkeys were allocated a reward by the experimenter, which differed from that of their partner, but was not controlled by their partner. This did not allow us to examine how they would choose to behave in a situation in which they (or their partner) can control the situation with their choices. To address this issue of choice, we completed a study in a situation in which no human experimenter made decisions, but the monkeys were able to decide whether or not to cooperate for an unequal reward and, if they did cooperate, they chose which monkey received which reward. If they failed to cooperate, no one got anything, so in this situation either monkey could affect the other's outcome by refusing to participate.

This was done using a mutualistic barpull task, which had extensively been used previously to test cooperation and altruism in capuchin monkeys (Brosnan and de Waal, 2002; de Waal and Berger, 2000; de Waal and Davis, 2002; Mendres and de Waal, 2000). In this study, a tray was weighted such that no capuchin could pull it in alone, but by working together two individuals could bring it in. On the tray were rewards for the pullers, one on each side. We know from previous studies that the monkey will receive the food that is in front of the bar they are pulling (de Waal and Davis, 2002). Thus, we could manipulate rewards such that the monkeys were pulling for the same or different rewards.

In this case, the tray was baited with either two low-value (apple) rewards, two high value (grape) rewards, or an inequitable distribution of one low- and one high-value food. We found that individuals did not vary their pulling based on the distribution of the reward; they were equally likely (or unlikely) to pull in all three conditions. However, we did notice an interesting discrepancy. Some pairs were very good about dividing the reward in the unequal situation. In these cases, both individuals received the

better grape in about half of the trials, indicating that there was some sharing or reciprocity across trials. These pairs, which we dubbed “equitable pairs”, were very successful with the barpull, regardless of condition. The other pairs tended to have one individual dominate the better grape in the successful unequal trials—about 80% of the time. In these pairs, which we dubbed “inequitable pairs”, the success rate was quite low (less than half of the equitable pairs) in all conditions.

There are two major implications of these results. First, it appears that when the individuals interact, it is not the reward distribution but the behavior of the partner that is important in determining “fairness.” This may have profound implications for group activities, such as cooperative hunts, in which many individuals participate but the reward is not readily divisible. Second, this may shed light on the mechanism these monkeys are using to make such decisions. It is enlightening that in the inequitable pairs, success rate was low across all conditions—including those in which there was no possibility for inequity (e.g., the rewards were the same for each monkey). This may imply that the decision to cooperate is based on an emotional response to the partner rather than a calculated determination of one’s potential rewards. In the latter case, we would expect individuals to participate regardless of their partner’s behavior in the two conditions in which the rewards are identical, and only refrain from cooperating when the partner will claim more. This is another area where cross-disciplinary research in neuroscience allowing us to determine what brain areas are active may be very informative as to the mechanism the monkeys are using.

## FUTURE DIRECTIONS

I concluded the original paper with a discussion of what I saw as the future directions of the field, and little needs to be added here. As more research is done, I suspect the lines between disciplines will continue to blur. It is also important to look broadly at studies that are not explicitly billed as studies on inequity. As an example, colleagues and I recently addressed the issue of prosocial behavior in chimpanzees in a way that speaks to their sense of advantageous inequity aversion (Silk *et al.*, 2005). Consistent with my previous results, we found that chimpanzees did not provide a reward to a conspecific at no cost to themselves. Thus, in multiple situations in multiple groups we find consistency of response, which strengthens our understanding of these phenomena. As we continue to think about such behaviors, and continue to weigh different theories, we will better understand the links between ourselves and other species, as well as gaining a better understanding of ourselves.

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