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To Each According to His Need? Variability in the Responses to Inequity in Nonhuman Primates

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To each according to his need? Variability in the responses to inequity in nonhuman primates

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Abstract

While it is well established that humans respond to inequity, it remains unclear the extent to which this behavior occurs in our nonhuman primate relatives. By comparing a variety of species, spanning from New World and Old World monkeys to great apes, scientists can begin to answer questions about how the response to inequity evolved, what the function of this response is, and why and how different contexts shape it. In particular, research across nonhuman primate species suggests that the response is quite variable across species, contexts and individuals. In this paper, we aim to review these differences in an attempt to identify and better understand the patterns that emerge from the existing data with the goal of developing directions for future research. To begin, we address the importance of considering socio-ecological factors in nonhuman primates in order to better understand and predict expected patterns of cooperation and aversion to inequity in different species, following which we provide a detailed analysis of the patterns uncovered by these comparisons. Ultimately, we use this synthesis to propose new ideas for research to better understand this response and, hence, the evolution of our own responses to inequity.

KEY WORDS: inequity response; fairness; inequity aversion; nonhuman primates; species comparison

The concept of fairness is highly developed in humans and pervasive in many aspects of our culture. Children complain to mothers over sibling rivalry, employees compare salaries and search for justifications over disparities, and more recently, people living in major cities in the USA have been protesting Wall Street in order to combat economic inequality. How is it that such a strong sentiment can unite thousands of people in support for a cause, risking immediate costs, such as arrest, for a more long-term yet distant goal? Moreover, how do humans decide what is fair or not? How can the Occupy Wall Street protesters and the Wall Street businessmen both think that their position represents a fair solution? By studying the responses to inequity in nonhuman primates, we can begin to answer these questions about the evolutionary roots of fairness. Moreover, by understanding these evolutionary roots, we can begin to consider the complexity of fairness in humans, what factors drive such different opinions about what is fair, and how language and culture might contribute to this.

Specifically, research on responses to inequity with nonhuman primates can help us understand why the sense of fairness evolved, and how it affects individuals within different social contexts. A variety of social contexts, depending on each individual's sex, age, or rank, can be investigated in nonhuman primate species to shed light on how human social relationships may shape responses to inequity based on each individual's expectations. By comparing a variety of species, spanning from New World and Old World monkeys to great apes, scientists have used a behavioral phylogeny approach to investigate the likelihood of common descent for the response to inequity. This technique can help answer questions about how this response evolved, what the function of this response is, and why and how different contexts shape it. Specifically, it can help clarify whether the response represents a homology, meaning it shares a common evolutionary origin, or whether it converged in several species due to similar selective pressures, absent shared descent.

Several theories have been put forth to help explain negative reactions to inequity. For instance, it may be that a negative response to inequity evolved within a social context in order to recognize and avoid future inequity. This process may have occurred through steps that each increased fitness for individuals (Brosnan, 2006). First, individuals may recognize that another individual obtains rewards that are different from one's own, and then feel strongly enough to react to this discrepancy, which, if it caused the individual to sample the environment and explore other potential partners, could lead to increased fitness. Ultimately, this may lead to responses such as sacrificing a positive (but lower value) reward in order to restore equity or to punish the other individual, something humans are known to do (see Raihani & McAuliffe, 2012, this issue). Alternately, inequity may have evolved from non-social, more generalized reward mechanisms that exist in multiple contexts, such as loss aversion (Chen & Santos, 2006; Raihani & McAuliffe, 2012, this issue). In this case, individuals form expectations about rewards within different contexts, and compare these rewards to the initial expectation rather than a social reference point. Consequently, a negative response occurs when these expectations are violated in a way that does not benefit the individual.

But whether or not the origins are social, what is the benefit of this response? One hypothesis is that this negative response to inequity evolved in tandem with cooperation. Humans with a sense of fairness are proposed to be more likely to succeed in cooperative interactions (Fehr & Schmidt, 1999), due to their greater ability to avoid cooperative interactions which are not in their best interests. Many social nonhuman primate species (and those in other taxa) also demonstrate cooperation in the wild, and also succeed in laboratory experiments on cooperation (Table 1). Joint tasks require effort from multiple individuals and demand an assessment of payoffs and contributions to determine whether it will provide some advantage to participants. In order to evolve, both individuals must receive some benefit from cooperating. Therefore, if one individual gets more than a partner, it benefits the partner to be able to recognize this inconsistency (whether or not consciously) and determine whether to continue cooperating or to find a better option. The short-term cost of losing the immediate rewards is worth the long-term gains of finding a new partner that will "play fair" and maximize both individuals' payoffs. In addition, the overt response to inequity may function as a way to establish commitment (Frank, 1988, 2001; Yamagishi et al., 2009), signaling to one's partner one's expectations; you are interested in equity and you expect the same from him. Therefore, by responding in a way to resolve an iniquitous situation, you are advertising your commitment to and expectations for equity.

However, the response is quite variable across contexts and individuals. In fact, responses amongst primates are not always consistent, even within the same study (e.g., Brosnan et al., 2005; Brosnan et al., 2010b). This makes finding underlying causes and mechanisms more challenging, as they presumably interact with other features of the individual, the relationship, and the context. In this paper, we aim to review these differences across species and contexts in an attempt to identify and better clarify the patterns that emerge from the existing data. To begin, we provide a brief overview of how understanding socio-ecological factors in nonhuman primates can help predict expected patterns of cooperation and aversion to inequity in different species (specific ecological factors, social factors, and evidence from both the wild and captivity are summarized in Table 1 and are described in more detail in the Appendix). We follow this with a detailed analysis of the patterns uncovered by these comparisons. Our ultimate goal is to propose new ideas for how to pursue an understanding of the large degree of variability and make specific predictions for future research.

1. INEQUITY IN NON-HUMAN PRIMATES

We begin with a few important operational definitions. In humans, we speak of fairness, justice, and so forth, but these terms describe phenomena that are not currently appropriate for discussion with other species (see Brosnan; Pierce & Bekoff; Horowitz, 2012, this issue, Bräuer & Hanus, 2012, next issue). All of these terms imply a motivation that has not been tested in other species, that the interest in equity is based on an impulse for equity that is relatively permanent across contexts. That is, my interest in fairness for myself should be based upon an interest in the ideal of fairness or equity, rather than on my own urge to maximize my own rewards, and moreover my interest in your outcomes should not differ (much) from my interest in my own. This differs substantially from what is tested in animals. While we can study primates' and other species' interests in their outcomes relative to their partners', what no one has yet done is determine whether these other species have an ideal of fairness that they strive to match, as humans appear to. Thus in this paper, as with the others in these issues, we focus on *aspects* of fairness in other species, including how individuals respond to inequitable outcomes or inequitable levels of effort, but do not discuss fairness *per se*.

Inequity comes in different forms (Fehr & Schmidt, 1999). Most inequity studies in nonhuman primate species focus on disadvantageous inequity (when another individual receives more than you), but advantageous inequity (when you receive more than another individual) is a second form of inequity studied in humans and, to a much lesser degree, non-humans. Another important consideration in terms of the response to variable rewards is the difference between social and individual expectations. The behavioral response may be influenced by violations of social expectations, based on what a partner receives compared to what the subject receives, or individual expectations, where an outcome differs from what is anticipated based on one's own previous experiences. This contrast effect, in which an animal responds to the difference in what is currently available (generally a food item) versus what was received in a previous testing experience, may result in the same types of negative behavior as seen in social responses, or inequity. In fact, these contrast effects may even be part of the underlying mechanisms that produce behavioral responses to inequity. Thus, it is important to consider methodologies that distinguish social and non-social contexts.

In human studies, we can ask individuals how they feel to assess their responses to situations of inequity. In nonhuman primates, we can only measure overt behavioral responses. It is impossible to question them about their feelings in a certain context, and so scientists rely on how they react to assess an aversion to inequity. One common experimental testing procedure involves having animals complete a task with a human experimenter for a food reward. Two participants, one acting as a subject and the other as a partner, sit adjacent to one another in front of the experimenter and alternate participation. This allows them to observe what tasks the other completes and what reward the other receives (c.f. Brosnan & de Waal, 2003). Thus, experimenters can vary the effort required for the task or the reward received in order to examine how subjects' reactions change. Generally, their response when the partner receives a better food reward is compared to the response in a baseline condition in which both individuals receive a lower-value food reward. In order to distinguish violations of social expectations (the inequity test) from violations of individual expectations, a control test can also be conducted to examine how subjects react when a high-value reward is explicitly offered, but neither individual receives it (e.g., Brosnan et al, 2010). Because we can only measure overt behaviors, a negative response to inequity is inferred through the frequency of refusals to exchange or refusing to consume the food reward.

Our goal is to understand the evolution of this response by examining this reaction across numerous primate species (and, ideally, non-primate species as well; see contributions in this volume by Range et al.; Horowitz; Raihani & McAuliffe; Pierce & Bekoff, 2012, this issue). Such analyses can help to inform us about why this behavior might exist. Similar responses across primate (or other) species may be explained either by homology or by convergence. Other possibilities may be that the response to inequity was an emergent property, representing a byproduct of sociality and cognition, or evolving with cooperative tendencies. By comparing the patterning of these responses across multiple species, we can begin to understand the factors which led to its origin.

2. SOCIO-ECOLOGY AND INEQUITY RESPONSES

Although these behaviors must be studied across all species, the Primate Order represents a particularly good start. An investigation into the Primate Order provides insights into the evolution of human physiology, anatomy, and behavior, and also allows for comparison due to the diverse array of behaviors, social systems, and ecological adaptations across primate species. In fact, if there is a key shared feature amongst the primates, perhaps the best candidate is their cognitive and behavioral flexibility (Harlow, 1949). There are a few hundred species of primates in the world today (the exact number is debated; Cowlishaw & Dunbar, 2000), geographically encompassing a wide range of regions and adapted to different types of habitats. Primates have the biology and physical structure to flourish in changing environments, including large, elaborate and highly-developed brains that help them adapt their behavior to suit their specific needs (Campbell et al., 2010). Moreover, the impressive cognitive abilities of these primate species make them ideal to study the evolution of cognition and intelligence (Byrne & Bates, 2010; Reader et al., 2011; Rosati et al., 2010; Roth & Dicke, 2012; Tomasello & Call, 1997).

While the diversity within this Order makes for a fascinating taxonomic group to study, it also provides a challenge for analyzing the evolution of characteristics and traits. Unlike physical characteristics, behavioral traits cannot be traced through fossil records. However, scientists can map out the origin and evolution of a behavior by looking at a phylogenetic tree within the Primate Order. This process involves comparing living species and determining phylogenetic relationships based on similarities or differences in traits; depending on which species share the trait, we can better determine whether the trait is shared through common descent (homology) or derived due to shared selective pressures (convergence; see Brosnan, 2012, this issue). In taking a phylogenetic approach to behavior, we must consider several factors unique to each species, such as ecology and social systems, before making a generalized comparison across species. For example, we may prematurely attribute a cognitive ability to being a byproduct of the high level of sociality observed in the species tested, until evidence of the same cognitive ability arises in one of the species that are less gregarious. This creates a challenge to researchers, as theories are constantly changing when confronted with emerging evidence from new research.

This variability in behavior, sociality, and ecology across species also presents a challenge in a review, as critical characteristics may not be noted without a sufficient understanding of the species' social and ecological environments. Several factors within the socio-ecology of a species can provide clues as to the ecological importance of inequity and cooperation for each species. As cooperation requires the contribution of another individual, we should expect that larger social groups would provide more opportunities for individuals to cooperate; thus, increased sociality presumably requires a greater need to pay attention to the outcomes of other individuals in comparison to one's own outcomes and keep track of these outcomes through repeated social interactions. Within social groups, the proportion of related and unrelated individuals may drive cooperation and aversion to inequity, since it is more adaptive for unrelated individuals to keep track of the behavior of a partner; unrelated individuals must determine whether to continue a cooperative relationship or find a different, more equitable partner in the face of inequity, while related individuals may be able to better tolerate disproportionate outcomes now and then due to potential benefits gained from inclusive fitness. Hierarchy may also have a large influence; the ranks of those individuals involved in a cooperative context may determine their expectations for outcomes in an inequitable situation. Moreover, there may be different hierarchies between the sexes. In addition to social factors, ecology may influence how prominent cooperation occurs in the wild. For example, certain types of prey require a group effort for hunting, and predation pressure may influence group defense mechanisms. The abundance or scarcity of resources affects food sharing, and other services may be exchanged in social settings, often requiring individuals to keep track of costs and benefits.

On the other hand, a summary of the relevant features of the primates is a book's worth of information in and of itself (see Campbell et al, 2010). Thus, we limit ourselves to a few critical comments, rather than a comprehensive survey of each species or each relevant feature within the species we discuss. Table 1 and the Appendix provide a summary of the social systems and ecologies of each of the species we discuss, as well as evidence in the field and in captivity of behaviors and complex cognitive abilities that relate to theories surrounding the inequity response, such as sharing tendencies and cooperative behavior. Table 2 provides data as known for each species' responses to inequity in experimental tests. Given the format, this summary is necessarily brief, and given the relative recency with which this topic has been addressed, we have surely left out species for which data will shortly become available. Nonetheless, we hope that this is useful in placing even studies as yet unpublished into this context.

3. HOW CONTEXT AFFECTS RESPONSES TO INEQUITY

The response to inequity involves and is affected by many different factors beyond each species' ecology and social system, in particular the specific context of the situation. This may include social factors, such as rank, social closeness, and group structure as well as individual factors like personality, sex, age, and history. Additionally, the methods used by experimenters to create an iniquitous situation may also shape expectations and resulting behavior. Therefore, within each inequity study, the specific context must be carefully considered in the interpretation of results.

3.1 Effort

Amongst humans, effort is important in how people perceive fairness. More effort expended is typically assumed to require more reward at the other end (Lawrence & Festinger, 1962); if I work just as hard as you, but get less reward, I am likely to be dissatisfied. However, it is unclear whether this is also the case in other species. Most studies find that changing the levels of effort do not change subjects' responses (Brosnan et al., 2010b; Fontenot et al., 2007). At most, they have amplified the effects of inequity, causing stronger reactions when both rewards and effort were unequal (van Wolkenten et al., 2007). One recent study, however, indicates that effort, too, can be important. In capuchins, a subject operating a pull-drawer device was significantly more likely to provide a high-value reward to a conspecific recipient, regardless of social rank, when that recipient helped the subject operate the device (in essence providing equal labor). However, when the subject had to do all of the work (unequal labor), food sharing was not influenced by the presence or rank of the recipient (Takimoto & Fujita, 2011).

A second question is whether effort, as defined as the presence of a task, is *necessary* to elicit a response. Initial studies all included a task (e.g., Brosnan & de Waal, 2003), but subsequent studies often eliminated the task and just compared subjects' responses when final outcomes varied (e.g., food rewards were handed out for free; Bräuer et al., 2006; Dindo & de Waal, 2007; Roma et al., 2006; see also Bräuer & Hanus, 2012, next issue). In none of these studies did subjects show any response to different rewards, and circumstantial evidence began to accrue that a task was essential. For instance, in the same group of capuchin monkeys, the monkeys responded negatively in two different studies involving a task (Brosnan & de Waal, 2003; van Wolkenten et al., 2007), yet between these studies, showed no response to a situation that did not include a task (Dindo & de Waal, 2007). However, the tasks and foods varied between these studies, and they were run by different researchers at different times, making direct comparisons impossible. Since then, several studies have more rigorously tested this proposition. Neiworth et al. (2009) tested tamarins on a between subjects design, but kept all other aspects of the study the same between the different groups. Although neither group responded negatively to inequity, they found that subjects in the exchange condition overall refused food items more often than those who were not. Brosnan and colleagues have used a within-subjects design in several species. When effort and no-effort conditions involving the same outcomes were randomized, chimpanzees responded negatively to conditions with a task, but not to a no-effort "gift" condition (Brosnan et al., 2010b). Moreover, as with Neiworth et al.'s findings, even in species that do not respond to inequity, there is typically a greater frequency of refusals in exchange conditions than in the "gift" conditions without a task (squirrel monkeys: Talbot et al., 2011; marmosets; Freeman et al., in review; orangutans, Brosnan et al., 2011a).

It is not clear why this is the case. As a first possibility, studies testing the negative response to inequity involve captive animals, who regularly receive food provisioned by human caretakers. Food is often distributed unequally, based on need or rank, and some individuals may be accustomed to getting more (or less). Captive animals may come to learn that there is no point in protesting food being handed out for "free." Second, it may be that the presence of a task is what cues the subject to a context in which sensitivity to inequity is important (Brosnan et al, 2010; Brosnan, 2011). That is, if one purpose of inequity aversion is to help individuals recognize and avoid those situations in which a partner is receiving a greater benefit for a joint interaction (e.g., cooperation), then inequity aversion is far more important in contexts in which there has been joint interaction than those in which there has not. Although the procedure itself is not joint, in the sense that the two individuals' outcomes do not rely on each other, it may be that the presence of two actions completed in such close succession indicates to the animals a joint task. This may cause individuals to respond differently in trials with a task than in those "gift reward" situations in which no task is present. Further work is needed to fully understand how effort and reward are interrelated in subjects' perception of inequity.

3.2 Social factors

Social factors, such as sex and rank, have shown quite varied effects. This is rather surprising, as presumably individuals who are more used to getting the best rewards (that is, dominants, who also are, in most primate species, males), would be more sensitive to the inequities generated by these studies, given that they typically get the most and the best of everything. That being said, both rank (Bräuer, et al., 2006; Brosnan, et al., 2010b) and sex

(Brosnan et al, 2010b) effects have been found in chimpanzees, with both dominants and males being more likely to respond to inequity. In the capuchin study discussed earlier, in which capuchins could pull in a drawer to bring each other food, inequity in the reward distribution depended on an interplay of rank and the presence or absence of visual contact (Takimoto et al., 2010). Finally, dominant long-tailed macaques, but not subordinates, react to inequity (Massen et al., 2011b).

Although social influences are emerging, the nature of the test may mask these to some degree. For instance, responses may be directed at the experimenter (who caused the inequity) rather than the partner. In most studies, the experimenter causes the inequity, but in one study in which individuals had to work out their rewards amongst themselves, capuchins were more sensitive to their partners' behavior than to the reward distribution (Brosnan et al., 2006). A more direct relationship between task completion and reward payoff may uncover more consistent social effects. Additionally, new studies which remove or lessen the presence of the experimenter may help unravel this question.

Moreover, it may be that we are investigating the wrong social factors. Studies of collaboration find that what really seems to matter is the relationship between the individuals involved (Melis et al., 2006). With respect to inequity, Brosnan et al. (2005) found differences between chimpanzee groups, such that individuals in a long-term, well-established social group showed less of a response to inequity, while individuals in a short-term group showed a stronger reaction, suggesting that social closeness and tolerance may influence the reaction to inequity. These results fit the broader perspective of group behavior; long-term social groups have demonstrated high levels of reciprocity in terms of sharing food and grooming (de Waal, 1997a), and show reconciliation after fights (Preuschoft et al., 2002) while avoiding confrontation (Hare et al., 2000). Thus, it makes sense that inequity responses would be stronger in situations in which groups were unstable or relationships were forming, as individuals presumably have more of a need to assess their partners' trustworthiness. Future studies including tolerance (acceptance of strains and imbalances in a relationship) may provide some answers, at the levels of the individual (e.g. individuals with an overall more tolerant personality), relationship (e.g., increased male tolerance towards a female with a swollen sexual swelling that is more attractive) and group (e.g., groups with more tolerant, stable interactions).

3.3 Methodology

Methodology may play a large role in the variability of the response to inequity both between and within species. First, there are inevitably limitations regarding the set-up in social arrangement of nonhuman primate subjects in a captive research setting. Researchers must work around the infrastructure of the facilities, which vary in terms of the size of shared space for a group of animals, the number of available cages for individual separation, the number of access points to other areas, and so forth. In addition, the overall behavior of a species may influence social arrangement; whereas chimpanzees can be trained to calmly sit next to one another, other species are naturally much more frenetic and may require separation to facilitate a more controlled methodology and to prevent stealing of rewards or tokens between subjects. Within a species, there are social concerns and limitations. Some individuals may not get along as well with others, and this must be taken into consideration, limiting available pairings, and restricting data to only those individuals who have more tolerant relationships (see above). There are really two separate issues here. The first is the degree to which different results are explicable by different methodological practices. The second is the degree to which these behaviors may be influenced by the very fact of captivity.

Regarding methodological practices, small differences in experimental protocols, such as how the subjects are seated with respect to one another, may make big differences in response. Takimoto et al. (2010) found behavioral differences in capuchins based on visual contact, which suggests that any sense of separation, either visually or physically, affects behavior. Additionally, whether individuals are seated next to one another in a shared enclosure (Brosnan et al., 2005; 2010b) or across from one another in separate enclosures (Bräuer et al., 2006; 2009) may play a role. In humans, the orientation of the subjects has proven important (Sommer, 1967). However, this is something that is often beyond the control of researchers, particularly with large species such as the great apes, who cannot easily be moved in to different arrangements (and may not always affect behavior; Silk et al., 2005).

Regarding the impact of captivity, psychology is constantly concerned with how experiments are affected by the very artificiality of the procedures. Do individuals respond as they perceive the experimenters desire? Are their behaviors influenced by the set-up in ways that human experimenters may not recognize? If, for instance, subjects are separated into individual enclosures and can only interact through mesh or a barrier, more natural behavior that may be important to social interactions, such as grooming or begging, may be prevented. Additionally, unwanted behavior, such as stealing of rewards, is prevented (in fact, the barrier may have been implemented to prevent just that!). Also, artifacts of daily husbandry practice may affect behavior in these studies, as discussed above with respect to food distribution. Finally, experiments vary in their degree of control, and experimenters should take care to balance highly controlled but potentially more artificial studies with those that are less controlled, but potentially more natural. In this way we get the best of both worlds; sufficient control to tease apart mechanisms and causality, but a “reality check” to verify the appropriateness of the results to the species. Of course, this is not to say that any of these studies are irrelevant, any more than it would be appropriate to say studies on humans are irrelevant for their reliance on artificial procedures or foci on limited subsets of the human population. Often, the only way to conduct a study that is sufficiently controlled to enable the dissection of causality and underlying mechanisms is to use a very controlled experiment in the laboratory. Nonetheless, researchers should pay careful attention to differences in housing and husbandry to consider whether these methodological concerns may be affecting responses in experimental tests.

3.4 Delay of gratification

Of course, cognitive factors that vary between species may also influence mechanisms. While a discussion of all of these possible cognitive factors is beyond the scope of this paper (see Raihani & McAuliffe, 2012, this issue and Yamamoto & Takimoto, 2012 in the subsequent issue for further discussion of some relevant cognitive factors), we do discuss one that we think is quite important, and understudied, in relation to inequity. In order for an animal to refuse a reward as a means of displaying displeasure, they must be able to control impulses, or delay gratification. Animals vary in their ability to do so. While many animals prefer immediacy of reward (Abeyesinghe et al., 2005; Mazur, 1987; Richards et al., 1997), several of the primate species are able to delay gratification for very long periods of time. Many of the species we discuss can do so, including chimpanzees, capuchins, and rhesus and long-tailed macaques (Beran & Evans, 2006; Dufour et al., 2007; Evans & Westergaard, 2006; Evans & Beran, 2007a, 2007b; Szalda-Petree et al., 2004; Tobin et al., 1996). Chimpanzees can delay for up to 11 minutes, and use self-distraction to facilitate this delay (Beran & Evans, 2006; Evans & Beran, 2007b). Tamarins and marmosets are also able to delay in specific contexts that are related to their species-specific ecologies (Stevens et al., 2005). Such ecological specificity may indicate specificity in other areas, too, such as in social contexts related to cooperation and inequity.

Considering this, then, it may not be surprising that the list of species with noted delay of gratification abilities are also the species that show behavioral responses to inequity (although we hasten to point out that not all of the species tested for inequity have been tested for delay of gratification, and some species that can delay gratification do not show behavioral responses to inequity). Turning down an immediate food reward is clearly challenging for most species, and not something that they will easily do even for a potentially greater payoff in the future. However, if the hypothesis that individuals' tendency to do so is related to cooperation is correct, then a negative response to inequity may involve expectations about what an individual will, should, or could receive in the near future. That is, it is possible that animals reject the immediate food based on the possibility of increased payoffs in the future. This is similar to delay of gratification, albeit with a far less certain future outcome, thus the act of refusing may be scaffolded by the individual's ability to delay gratification. Note of course that this does not mean that the animals must understand this chain of logic, but that the ability to delay gratification may open up opportunities for refusing that would not exist otherwise, thus providing selective pressures which increase species' abilities in this area. We also note one very speculative possibility, which is that one reason subjects may be better able to refuse in the context of a task than when simply handed foods could be the presence of an object (e.g., a token) with which to play. This may help individuals to distract themselves from the temptation of returning the reward (e.g., Evans & Beran, 2007a). It will be interesting to see how various cognitive mechanisms influence individuals' ability to respond to inequity.

5. THE EVOLUTION OF INEQUITY

Primate species vary widely in their responses to inequity, which seems to eliminate the possibility that the inequity response is a homology shared amongst the primates (see Table 2). Moreover, the variability does not even suggest homology within smaller clusters, such as the great apes. For instance, amongst the great apes, there is evidence for a negative response to inequity in humans and chimpanzees, and possibly in bonobos, but not in orangutans (gorillas have not yet been tested using a similar protocol). Amongst the New World monkeys, in the Family Cebidae, capuchin monkeys respond negatively to inequity, but not the very closely related squirrel monkey. Thus, based on these data, the inequity response is almost certainly a convergent trait. But, which traits are those which led to the emergence of inequity aversion? Although the data are messy, some patterns are beginning to emerge. Below we discuss several traits that seem likely candidates, and consider whether or not they deserve additional attention as possible links to the evolution of inequity.

One possibility that we seem to be able to rule out is that the response to inequity varies as a function of cognitive abilities or brain size within the primates. Presumably this comparison requires some basic cognitive abilities (e.g., those necessary to compare one's outcome with another conspecific's), but the data indicate that within the primates, neither absolute brain size (Deaner et al., 2007) nor brain-to-body ratio (Jerison, 1973; Martin, 1984), correlate with inequity responses. Within the great apes, which have comparatively similar brain sizes, orangutans do not respond to inequity (Bräuer et al., 2009; Brosnan et al., 2011a), thus a large brain is not sufficient to respond to inequity. Additionally, while both capuchins and macaques show negative responses to inequity, capuchins are highly encephalized, but macaques are not (Martin, 1984). This latter point rules out the possibility that a large brain-to-body ratio is necessary (although absolute brain size may play a role). Future testing in species that share other important traits in common with primates (e.g., cooperation; see Raihani et al., 2012, this volume) but lack the high degree of encephalization will be essential to distinguish these possibilities.

Another very reasonable assumption, particularly if the response to inequity is considered to have a social origin and requires paying attention to what another receives, is that it should relate to social living, and thus be more prevalent in gregarious species. That is, individuals in social groups with strong bonds should be more inclined to be aware of and react to the behavior and outcomes of others as compared to their own. However, while the data thus far support the prediction that only species that are habitually socially living show the response, social living in itself is not sufficient to predict the response. Squirrel monkeys, a socially living species that shares a phylogenetic family with capuchins, and are even sympatric with them (e.g., live in the same habitat), do not respond to inequity, nor do species that exhibit bi-parental care, which live in close-knit family groups and for whom the mated pair show a high degree of interdependence. We also note that this cannot be explained by sociality combined with tolerance. Not only do results suggest that species with bi-parental care and squirrel monkeys fail to respond to inequity, but macaques, which live in a society that is not as tolerant and involves a very strict hierarchy, do respond negatively to inequity.

Thus far, the existing evidence best supports the hypothesis that an aversion to inequity emerged in concert with cooperative behavior between unrelated individuals. They may be directly linked, in which case attending to and responding to inequity may function to increase the success of long-term cooperative relationships (Fehr & Schmidt, 1999; Brosnan, 2006; 2011). Considering the apes, orangutans show the lowest frequency of cooperation in the wild (although they do cooperate in lab-based studies), while chimpanzees are highly cooperative both in the wild and in captivity (see Table 1 for references). This hypothesis is further supported in the New World monkeys; squirrel monkeys are much less cooperative than capuchins and also do not respond negatively to inequity. Finally, the macaques, which are socially cooperative, also show a response to inequity.

Moreover, studies that have looked at inequity in the context of a cooperative interaction support this hypothesis. For instance, pairs of capuchin monkeys were much more successful in a cooperative task when they alternated which individual received the better reward (Brosnan et al., 2006; Hattori et al., 2005). This inclination to accept short-term costs (not receiving a good reward for a trial) for long-term gains (a balanced strategy to maximize benefits to both individuals) may aid in establishing cooperative relationships in the future. This may be essential for the development of cooperation, as typically rewards are not perfectly equitably distributed on each trial (or interaction), but only over the course of the pairs' interactions. These data also may indicate that in non-human species, the inequity response could serve as a commitment device, in which individuals accept short-term losses in order to establish more beneficial long-term relationships (e.g., Frank, 1988). Moreover, the negative response to inequity may be especially important in unrelated individuals compared to related individuals; inclusive fitness and increased tolerance in individuals that are related may promote cooperation and thus, lead to a decreased sensitivity to inequity. Therefore, it may not be adaptive for related individuals to keep track of and respond to inequities, since commitment to cooperation is already present in the inclusive fitness benefits.

We also note one additional piece of the puzzle. An inconsistency is observed in the cooperative breeders, in which both males and females, often with adult offspring, care for infants. This social system leads to fitness interdependence between the males and females.

According to the cooperative breeding hypothesis (Burkart et al., 2009; Hrdy, 2009), this unique social system, characterized by extreme social tolerance and cooperation, ranging from food sharing to caring for infants, has led to the evolution of enhanced prosocial behavior as compared to other primates. It is possible that this interdependence may also lead to a changed inequity response. That is, despite strongly cooperative behavior, males and females rely on each other for reproductive fitness. Thus, minor breaches in equity may be tolerated since the costs of finding a new partner would outweigh the costs of the inequitable interaction. This hypothesis deserves further testing, both among cooperative breeders and among monogamous species with shared parental duties (e.g., owl monkeys; Fernandez-Duque et al., 2001), for whom breeding adults may share similar selective pressures as do cooperative breeders (Brosnan, 2011; Freeman et al, in review).

7. Future directions

The studies discussed have made great contributions to understanding the evolution of the response to inequity, at least amongst primates (for a phylogenetically broader view, see Pierce & Bekoff; Raihani & McAuliffe; Horowitz; Range et al., all 2012, this issue). Based on the amount of variability between and within different species, more research will be required to confirm and expand on past results. Changes in methodology can provide a new perspective, and different contexts should continue to be explored, especially due to the scarcity of data on the effect of social factors.

For instance, how important are tangible food rewards in eliciting a response? Do these responses translate to other types of rewards? There is evidence of attention to inequity during play behavior in gorillas (van Leeuwen et al., 2011), but other more experimental studies up to this point have only used food as a reward. However, an abstract representation of food (e.g., tokens) could replace actual food rewards to determine the influence of visible and tangible food rewards on the response to inequity. Primates are certainly capable of using tokens to represent foods for these sorts of tasks (Addessi et al., 2007; Addessi & Rossi, 2011; Brosnan & de Waal, 2004a; Brosnan & de Waal, 2004b; Sousa & Matsuzawa, 2001). We predict diminished negative responses with tokens as compared to tasks with tangible foods, but also that individuals that have had greater experience with token tasks should show stronger responses to inequity, due to their increased experience (e.g., Brosnan et al., 2011b). In addition, it would be interesting to explore other types of biologically relevant rewards (e.g., other than foods or tokens representing foods) that might elicit the negative response to inequity.

It will also be intriguing to explore how new methodologies that minimize the interaction between the subjects and the experimenter might affect responses towards a social partner. For example, using an automatic token or food dispenser would diminish human interaction and might make the behavior of the conspecific more salient, while also removing the “free gift” association with rewards that often arises in captivity with food provisioning and training (Price and Brosnan, in prep). Future research should also take in to account social factors that have not yet been studied. For instance, it would be interesting to consider fluctuating social influences, such as the reproductive state of the females. Male chimpanzees may show a preference for females that are in estrus, through grooming (Hemelrijk et al., 1992), which peaks during the onset of swelling (Wallis, 1992). Therefore, males might be more tolerant of a female benefiting from a better reward (and thus, will be less likely to show a response to inequity) when she is maximally swollen or otherwise reflects being in a state of estrus. Related to this, what are the impacts of an observer on inequity aversion? Eavesdropping affects behavior in many species (e.g. Marshall-Pescini et al., 2011), and might do so in the context of inequity as well. Finally, other factors such as practice or experience may play a role in affecting these responses.

Finally, our exploration of these topics needs to extend further. First, without studies that examine these responses in the animals' natural lives to supplement what can be inferred by studies in captivity, we will not fully understand how they impact behavior (Janson & Brosnan, in press). Second, without a broader phylogenetic perspective, we will not fully understand the evolution of this response. Regarding the first, there is very little data on how individuals respond to inequity in their typical interactions (see Bekoff, 2004, for an exception). How do inequity responses impact animals' daily decision-making and behavior? These sorts of issues are difficult to address in field settings, as behavior now may be impacted by events that occurred months or even years in the past, but the data may be available at long-term field sites or other situations with extensive data collection. Regarding the need for a broader phylogenetic perspective, there has been the welcome addition of data from other phylogenetic taxa (see Pierce & Bekoff; Raihani & McAuliffe; Horowitz; Range et al., all 2012, this issue), and these data will help us tease apart how the factors we discuss are important outside of the primates. Without studying species that vary in social structure, cognitive ability, and cooperation, as well as other behaviors, it is impossible to answer questions about the relative importance of each of these factors in the origins of this response.

8. CONCLUSION

The comparative study of the response to inequity can help us understand the evolution of this behavior. Thus far, data suggest that this is a convergent trait that most likely co-evolved with cooperative behavior. How do these results in other species, particularly the non-human primates, inform us about human fairness and justice (see Chen & Houser; Skitka; Christen &

Glock; Olson; Brosnan & de Waal, 2012, next issue)? In some ways, this still seems to be quite a challenge. The concept of "fairness" in humans is much more complex than what we have seen thus far in non-humans, incorporating advantageous inequity and disadvantageous inequity as well as cultural norms that impact how humans respond to each other. In human society, fairness is treated as a norm (albeit one that varies across cultures), and there are certain standards that are understood by all within a group as those by which all actions are to be judged. Responses in non-humans appear thus far to be focused on the individual's outcome as compared to a partner, not as compared to some standard of fairness, indicating differences between humans and other species, and potentially limiting the value of such comparisons.

On the other hand, there are clearly commonalities. Both humans and other species are more sensitive to inequities against themselves (e.g., disadvantageous inequity aversion) than those in other contexts. Moreover, there are other features in common, such as the impact of social factors on such reactions. Finally, at the practical level, far less is known about other species than is known about humans. There have been far fewer studies, and frequently procedures are not comparable across species, particularly between humans and non-humans, making such comparisons challenging. Thus it is unknown the degree to which this difference may hold, and future research is needed to more carefully pin down the similarities and differences. Of course, at the broadest level, the roots of this human behavior are seen in other species. A better understanding of these evolutionary roots, including the ways in which humans do or do not differ from other species, can inform our understanding of human fairness, and provide a greater understanding of how this important trait affects a wide variety of human endeavors.

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Table 1: *An overview of the primate species and their defining socio-ecological features. Geography includes geographical locations and types of habitat. Social organization includes composition of social units. Group size includes size of immediate social unit and communities, and stability of these units. Despotism describes a social organization with a strict dominance hierarchy. Foraging style describes the type of diet; omnivores eat plants and animals, folivores primarily eat plants, and frugivores primarily eat fruit. The presence of meat in the diet is indicated, which may also involve hunting behavior. Sharing food refers to active sharing between two or more individuals, both naturally in the wild based on observations as well as in experimental setups in the laboratory. Cooperation refers to two or more individuals working together, both naturally in the wild based on observations as well as in experimental setups in the laboratory. EQ (encephalization quotient) is a measurement of relative brain size (ratio between actual brain mass and predicted brain mass depending on the size of the animal), and is often used as an estimate of intelligence.*

Species	Geography	Social organization	Group size	Despotism?	Foraging style	Eat meat?	Share food in wild?	Share food in lab?	Cooperate in wild?
Chimpanzee	forests and savannah woodlands of West and Central Africa	Multi-male, multi-female[1]	Small subgroups within larger communities; fission-fusion[1]	No	Omnivore[1]	Yes[1]	Yes[1]	Yes[2]	Yes[3]
Bonobo	Humid forests in DRC	Multi-male, multi-female; female-dominant[5]	Small subgroups within larger communities; fission-fusion	No	Omnivore[6]	Yes[6]	Yes[6]	Yes[7]	Yes[8]
Gorilla	Forests of Central Africa; lowlands to mountains	One-male units[10]	Ranges from 2- 20 individuals	No	Folivore[11]	No[11]	Rare[12]	Yes[13]	Yes[14]
Orangutan	Tropical rainforests of Asia (Borneo, Sumatra)	One-male range overlaps with smaller female ranges[15]	Mostly solitary[15]	No	Frugivore[16]	Yes[16]	Rare[17]	Rare	No[18]
Macaque	Wide range of environments; South, Central, Southeast Asia	Multi-male, multi-female; female-bonded and matrilinear[20]	Varies[20]	Yes (rhesus macaques)[22]	Omnivore[20]	Yes[20]	No	No	Yes[21]
Capuchin	Forests of Central and South America	Multi-male, multi-female[24]	Varies[24]	No	Omnivore[24]	Yes[24]	Yes[25]	Yes[26]	Yes[27]

Squirrel monkey	Tropical forests of South and Central America	Multi-male, multi-female[29]	Varies[29]	No	Omnivore[29]	Yes[29]	Rare[30]	Rare[30]	Yes[29]
Tamarin	Forests from southern Central America – central South America	Multi-male, multi-female[31]	Varies (monogamous and polyandrous); small family units[31]	No	Omnivore[32]	Yes[32]	Yes[33]	Yes[35]	Yes[34]
Marmoset	Tropical rainforests of South America	Multi-male, multi-female[31]	Varies (monogamous and polyandrous); small family units[31]	No	Omnivore[37]	Yes[37]	Yes[38]	Yes[39]	Yes[40]
Owl monkey	Tropical rainforests of Central and South America	Monogamous pair and young, but can be more flexible[42]	One male, one female, and their young (and sometimes other adults)[42]	No	Omnivore[43]	Yes[43]	Yes[44]	Yes[45]	Yes[46]

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Table 2: *Summary of inequity studies by species. An indication of whether inequity has been found in that species is provided. If inequity has been found in a species, the specific methods used are indicated; exchange task refers to procedures described in section 1, other task refers to a task that does not involve an exchange, and no task refers to the absence of any physical task that needs to be performed. Evidence of different effects on the response to inequity are indicated; effort refers to differences in the effort required to solve a task, and social context refers to social features such as sex, rank, or relationships.*

	Has response to inequity been seen?	**Task used/results**			**Effects of…**	
		Exchange	Other Task	No task	Effort?	Social context?
Chimpanzee	Yes	Yes[1-3]	---	No[4]	No[2]	Social closeness[1] Sex[2] Rank[2,4]
Bonobo	Possibly	Trend	---	No[4]	---	---

		towards yes[3]				
Gorilla	Yes	---	---	Yes[5] No[4]	---	---
Orangutan	No	No[3,6]	---	No[4]	---	---
Macaque	Yes	Yes[21]	Yes[7]	---	Yes[7]	Rank[7] Social relationship[7]
Capuchin	Yes	Yes[8,9,12] No [16,17]	Yes[10,11]	No[4,18,19]	Yes[8, 20] No[12, 16]	Rank[11]
Squirrel monkey	No	No[13]	---	---	---	---
Tamarin	No	No[14]	---	---	Yes[14]	---
Marmoset	No	No[15]	---	---	---	---
Owl monkey	No	No[15]	---	---	---	---

[1] Brosnan et al., 2005. [2] Brosnan et al., 2010b [3] Bräuer et al., 2009. [4] Bräuer et al., 2006 [5] van Leeuwen et al., 2011 [6] Brosnan et al., 2011a [7] Massen et al., 2011b [8] Brosnan & de Waal, 2003 [9] Brosnan et al., 2010a [10] Fletcher, 2008[11] Takimoto et al., 2010 [12] van Wolkenten et al., 2007 [13] Talbot et al., 2011 [14] Neiworth et al., 2009 [15] Freeman et al., in review. [16] Fontenot et al., 2007 [17] Silberberg et al., 2009 [18] Dindo & de Waal, 2007 [19] Roma et al., 2006 [20] Takimoto & Fujita, 2011 [21] Hopper et al., in review

APPENDIX

1. Chimpanzees

Chimpanzees (*Pan troglodytes*) are great apes, and one of our two closest living relatives (along with bonobos, *Pan paniscus*). Chimpanzees are highly social, living in large fission-fusion groups with complex social relationships and strong dominance hierarchies (de Waal, 1989; Harcourt & Waal, 1992). Males are philopatric and remain in their natal social communities, forming strong social bonds, while females emigrate when they reach adolescence. Chimpanzees also cooperate, for instance in territorial patrols (Boesch & Boesch-Achermann, 2000) or when hunting in groups (Boesch, 1994; Mitani & Watts, 2001). Although food sharing is in general rare outside of mothers and offspring (Goodall, 1986; Silk, 1978; although see Preutz & Lindshield, 2011), meat sharing occurs (Goodall, 1986; Nishida et al., 1992), often in return for agonistic support (Mitani & Watts, 2001) or mating opportunities (Gomes & Boesch, 2009). Males may also share hard-to-get cultivated fruits with females (Hockings et al., 2007).

The wide range of tolerant, cooperative behavior in the wild suggests that chimpanzees are aware of each other's behaviors and the distribution of payoffs received through these interactions.

Chimpanzees also show a number of behaviors indicative that they pay attention to the equity of distributions. For instance, in laboratory cooperation studies, in which individuals must work together to acquire rewards, chimpanzees who were working for a single reward that must be shared were far more likely to succeed with a partner with whom they otherwise tolerantly share food (Melis et al, 2006b), and actively recruited the more tolerant partner (Melis et al., 2006a). Chimpanzees also were able to coordinate their responses in a Stag Hunt game such that both individuals achieved the highest reward, although this ability seemed to interact with experience, with chimpanzees with a more extensive history of testing outperforming those with less such experience (Brosnan et al., 2011b).

Chimpanzees also respond to inequity in experimental studies (following the exchange procedure described in the main body of the text), although responses vary widely, based on factors that are not yet well understood. For instance, chimpanzees' responses have varied between facilities, even when an identical protocol was used (Brosnan et al., 2005; 2010b). Within the same facility, responses have varied based on the quality of individuals' relationships (Brosnan et al., 2005), sex, and rank (Brosnan, et al., 2010b), with male and dominant chimpanzees responding more negatively to inequity than females and subordinates (when tested in same-sex pairs). These results seem to fit chimpanzee socioecology; males form much closer bonds, through coalitions and alliances often associated with hunting and patrolling, and therefore may be more sensitive to differing outcomes, while females spend most of their time foraging alone or with offspring, and so may be more focused on individual expectations. Additionally, high-ranking individuals may be more accustomed to receiving a better share of a distribution or a better quality food resource. However, what is important to remember is that this is not always consistent across sites and protocols; sometimes sex and rank differences are seen, but other times they are not (Brosnan et al., 2010b; Brosnan et al., 2005; Bräuer et al., 2006; Bräuer et al., 2009). Additionally, even the orientation of the subjects to each other in the experimental set-up appears to make a difference in their responses (Brosnan et al, 2010b). Thus, future work is needed to understand how this variation affects responses, and what this tells us about the evolution of inequity responses.

2. Bonobos

Bonobos (*Pan paniscus*) differ from chimpanzees in their social structure. Bonobo society is more female-centered, female-dominant, and egalitarian (de Waal, 1995). Males are philopatric and remain in their natal group, while females migrate around adolescence (Idani, 1991; Kano, 1982). Female bonobos have much stronger bonds compared to males, and bonobo females can cooperatively dominate males (Kano, 1992; Parish, 1994, 1996). Bonobos have been observed in the wild and captivity sharing both plants and meat (de Waal, 1992; Hohmann & Fruth, 1993; White, 1994), and may exchange food for mating access (Kuroda, 1984), although recent evidence indicates that chimpanzees may actually be more tolerant sharers (Jaeggi et al., 2010). Bonobos have also cooperated in captive experiments, and in such studies were more successful than chimpanzees when food sources were monopolizable (Hare et al., 2007). Only one study has tested the inequity response in bonobos, and although individuals refused rewards twice as often when their partner got a better reward than when they got the same, lower-value reward, the result was not statistically significant, possibly due to the small sample size (Bräuer, et al., 2009).

3. Gorillas

Gorillas (genus *Gorilla*) live in harems comprised of one adult male (silverback), multiple adult females with their offspring, and sometimes other males (Harcourt, 1978; Robbins, 1995). The silverback has strong bonds with his females (Harcourt, 1979a) but bonds between females vary, ranging from friendly to aggressive interactions (Harcourt, 1979b). In the wild, female gorillas have been observed cooperating and forming alliances in competition over food resources and to protect relatives from harm (Harcourt & Stewart, 2007; Watts, 1997). Although food sharing is rarely reported in the wild, gorillas have demonstrated food sharing in captivity (Maestripieri et al., 2002; Schaller, 1963). Unfortunately, there is as yet very little captive research on social cognition in gorillas, although one recent study investigating responses to inequities during play fighting (Van Leeuwen et al., 2011) found that individuals worked to maintain inequities in their favor (e.g., running away after hitting, apparently so that the competitive advantage could be maintained). Future work on gorillas is needed to complete our understanding of the great apes.

4. Orangutans

Orangutans (Genus *Pongo*) are great apes that, in the wild, have a more solitary lifestyle compared to the other great apes. Although home ranges overlap (Galdikas, 1988), orangutans other than mother-offspring dyads spend most of their time alone (MacKinnon, 1974). Nonetheless, groups of orangutans may travel together, or feed together when fruit is abundant, and in captivity, orangutans show increased social behavior (Edwards & Snowdon, 1980). Based on research in the wild, food sharing among orangutans is rare (Bard, 1992; Jaeggi et al., 2008; van Noordwijk & van Schaik, 2009). Also, unlike other apes in the wild, orangutans form coalitions and alliances to a lesser degree (van Schaik, 2004). However, the lack of cooperative behavior may again be due to limited opportunities, not limited abilities. In captivity, orangutans have both solved cooperative tasks to achieve food (Chalmeau et al., 1997) and traded tokens reciprocally to receive mutual benefits (Dufour et al., 2009). Despite this, however, orangutans did not show negative responses to inequity (Bräuer, et al., 2009; Brosnan, et al., 2011a).

5. Macaques

Macaques (genus *Macaca*) are Old World monkeys, and include two species that have received attention in inequity studies, rhesus macaques (*Macaca mulatta*) and long-tailed macaques (*Macaca fascicularis*). Macaques are social, living in large, multi-male, multi-female groups, but tend to be despotic, with low social tolerance, and frequently use aggression to establish and reinforce social position in the asymmetrical dominance hierarchy (Smuts et al., 1987; Thierry, 2000). Although macaques are not known to cooperatively share food, or to successfully cooperate in experimental studies (Petit et al., 1992), they demonstrate other forms of cooperative behavior in the wild. Long-tailed macaques form alliances in aggressive contexts (de Waal, 1977; van Noordwijk & van Schaik, 1985), reciprocate grooming to decrease aggression (Gumert & Ho, 2008), and exchange grooming for access to sexually active females, infant handling, and support (Gumert, 2007a, 2007b; Massen, 2010). Female rhesus macaques show cooperative behavior (grooming and agonistic aid) towards kin (Widdig et al., 2001). Possibly connected to this, long-tailed macaques have shown prosocial behavior in the laboratory, choosing options that bring food to their partners (Massen et al., 2010). However, in most cases prosocial behavior was limited to female kin pairs or the dominant member of the pair, the latter of which may have been an attempt to curry favor with the subordinate. In fact, rank predicted prosocial sharing better than did relationship quality (Massen, et al., 2011a). Related to this, dominant long-tailed macaques showed responses to inequity when the level of effort required was small (Massen et al, 2011b). As with long –tailed macaques, rhesus monkeys coordinated in a Stag Hunt game (Brosnan et al., 2011c), and also have responded negatively to inequity, although only once they have reached approximately two years of age (Hopper et al., in review).

6. Capuchin monkeys

Brown capuchins (genus *Cebus*) are New World monkeys that live in small groups comprised of related females with offspring and several males. Capuchin society is rather tolerant (Fragaszy et al., 2004); capuchins both share food (Perry & Rose, 1994) and cooperate, including cooperative hunting (Rose, 1997), defense against predators (Boinski, 1988; Rose, 1994), and coalitions against neighboring groups (Gros-Louis et al., 2003). These coalitions are especially interesting because, unlike chimpanzee males, who form strong bonds and who often form coalitions for aggressive purposes, capuchin males are not philopatric and do not form close affiliative bonds (Perry, 1998).

Capuchins have been widely used in cooperative studies, which have confirmed that they are aware of the contingencies of cooperation, including the role of a partner, the effort required, and the distribution of outcomes (see Brosnan, 2010 for review). Capuchins have also shared food (de Waal, 1997), and after successful cooperative trials, the amount of food shared increased (de Waal & Berger, 2000). On the other hand, in the Stag Hunt game, capuchins showed the least structured coordination behavior compared to humans, rhesus and chimpanzees, and apparently require cues in order to be able to coordinate (Brosnan, et al., 2011b; Brosnan, et al., 2011c). Capuchins have also demonstrated prosocial preferences, which seem to be affected by dominance rank or social closeness with the partner, whether or not they can see the partner, and reward distribution (de Waal et al., 2008; Takimoto et al., 2010). They have even brought their partner more food than they received (Brosnan et al., 2010a; Lakshminarayanan & Santos, 2008).

Several studies have confirmed a negative response by an individual when unequal distributions resulted in a partner receiving a better reward (Brosnan & de Waal, 2003; Brosnan, et al., 2010a; Fletcher, 2008; Takimoto, et al., 2010; Van Wolkenten et al., 2007).They have also been sensitive to the effort required to perform the task, at least in some contexts (Hattori et al., 2005, but see Fontenot et al., 2007; van Wolkenten et al., 2007). Finally, individuals who were working together for rewards were more sensitive to their partners' behavior than to their outcomes, continuing to cooperate as long as both partners received the superior reward sometimes (Brosnan et al., 2006). This latter study demonstrated that they could extrapolate rewards across multiple trials, presumably an essential ability given that cooperative encounters do not result in equal outcomes on every trial.

7. Squirrel monkeys

Squirrel monkeys (genus *Saimiri*) share both a phylogenetic Family and a similar ecology with capuchins, but differ in their social structure and behavior (Boinski, 1999). Most importantly for this discussion, they demonstrate only limited cooperative behavior in the wild. Adult females with neonates will cooperate in anti-predator vigilance and defense (Boinski, 1987), and males form coalitions in order to immigrate into a new group (Boinski, 1999; Mitchell, 1994). Squirrel monkeys have not been tested experimentally for cooperative behavior, but did show reduced food sharing behavior, except when harassed by a partner (Stevens, 2004). Squirrel monkeys also did not respond negatively to inequity (Talbot et al., 2011).

8. Tamarins

Tamarins (genus *Saguinus*) are cooperatively breeding New World monkeys that live in groups in which, typically, only a single female is reproductively active (Sussman & Garber, 1987). Cooperation is vital in tamarin societies; data from the field and captivity have demonstrated that infant survival is directly related to number of caretakers present (Garber et al., 1984; Savage et al., 1996; Snowdon, 1996). Food sharing is also common. Field studies show that food sharing is used to help the young locate and obtain prey that may be hard to acquire, and this food sharing decreases as the young become more competent (Rapaport & Ruiz-Miranda, 2002; Rapaport, 2006). Studies in captivity reinforce tamarins' tendencies to share food (Cronin et al., 2005; Cronin & Snowdon, 2008; Feistner & Price, 1999, 2000; Price & Feistner, 2001; Rapaport, 1999). Data conflict on whether tamarins are prosocial (Cronin et al., 2009; Cronin et al., 2010; Stevens, 2010). Tamarins showed little evidence of an inequity response, although they were more likely to respond negatively to a lower-value reward when any effort was involved (Neiworth et al., 2009).

9. Marmosets

Marmosets (genus *Callithrix*) are also New World monkeys that are in many ways similar to tamarins (they share a phylogenetic Family and are also cooperative breeders; Koenig, 1995; Sussman & Garber, 1987). Marmosets tend to share food in the wild (Brown et al., 2004; Goldizen, 1987) and in captivity (Brown et al., 2005). Group territorial defense is also common (Lazaro-Perea, 2001). In experimental studies, marmosets demonstrated cooperative behavior that depended on the distribution of roles in a cooperative task as well as the tolerance of high-ranking individuals (Werdenich & Huber, 2002) and prosocial behavior (Burkart et al., 2007). However, marmosets were not sensitive to situations in which a partner received a better reward (Freeman et al., in review).

10. Owl Monkeys

Owl monkeys (genus *Aotus)* are also New World monkeys that, while not considered cooperative breeders, are monogamous and rely on dual-parental care for the survival of offspring (Fernandez-Duque et al., 2001; Wright, 1994). Food sharing has been observed in the wild (Wolovich et al., 2008b) and captivity (Wolovich et al., 2006; Wolovich et al., 2008a). They also exhibit biparental care, a form of cooperation in which males help to transport and groom infants (Rotundo et al., 2002; Rotundo et al., 2005; Wright, 1984). However, as with the cooperative breeders, owl monkeys did not respond negatively to inequity in an experimental context (Freeman et al, in review).