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J.B. Wight and E.L. Khalil, Emotions, natural selection, and rationality	1																				
D. Haig, Sympathy with Adam Smith and reflexions on self	4																				
E. Schliesser, Reading Adam Smith after Darwin: On the evolution of propensities, institutions, and sentiments	14																				
S.F. Brosnan, An evolutionary perspective on morality	23																				
D. Chavanne, K. McCabe and M.P. Paganelli, Whose money is it anyway? Ingroups and distributive behavior	31																				
D.M. Levy, K. Padgitt, S.J. Peart, D. Houser and E. Xiao, Leadership, cheap talk and really cheap talk	40																				
P.J. Zak, The physiology of moral sentiments	53																				
L. Fogassi, The mirror neuron system: How cognitive functions emerge from motor organization	66																				
I. Molnar-Szakacs, From actions to empathy and morality – A neural perspective	76																				
E.L. Khalil, The mirror neuron paradox: How far is <i>understanding</i> from <i>mimicking</i> ?	86																				

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An evolutionary perspective on morality

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ABSTRACT

Moral behavior and concern for others are sometimes argued to set humans apart from other species. However, there is some evidence that humans are not the only animal species to possess these characteristics. Work from behavioral biology and neuroscience has indicated that some of these traits are present in other species, including other primates. Studying these behaviors in other species can inform us about the evolutionary trajectory of morality, helping us to understand how the behaviors evolved and which environmental characteristics were critical for their emergence. A brief historical look indicates that, while this evolutionary approach to human behavior is not always well received, this line of inquiry is not new. For instance Adam Smith, better known for his economics than his natural history, was clearly sympathetic with the view that moral behaviors are present in species other than humans. This paper focuses on how individuals respond to inequity, which is related to moral behavior. Recent evidence shows that non-human primates distinguish between inequitable and equitable outcomes. However, this is primarily in situations in which inequity hurts the self (e.g. disadvantageous inequity) rather than another (e.g. advantageous inequity). Studying such responses can help us understand the evolutionary basis of moral behavior, which increases our understanding of how our own morality emerged.

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1. Introduction

Do moral behaviors mark humans as unique? While our system of morality presents as much more highly developed and extensive than other species', it is not without precedent. A close look at individual moral behaviors indicates that, in many cases, antecedent or related behaviors and mechanisms can be found in other species, including conflict resolution, reciprocity, empathy, sympathy, and community concern (Flack and de Waal, 2000). While this does not mean that a fully human moral system is present in any other species, studying other species can teach us something about the evolution of these behaviors.

Studying moral behaviors in other species has several benefits. First, these behaviors give scientists the opportunity to determine how and under what conditions our own moral behaviors might have evolved. In the comparative approach, behaviors from different species with known phylogenetic relationships are compared. By linking the observed behavior to the known relationships, a picture of the evolution of the behavior emerges. If two closely related species share a behavior, this is likely the result of a common ancestor which had the behavior, termed homology.¹ On the other hand, if two species which are distantly related, but inhabit similar environmental niches, and share a behavior, it is likely the result of convergence due

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¹ It is important to note that there are two evolutionary mechanisms which could have led to similar moral behaviors in humans and other species. First is homology, in which behaviors are shared by two species through common descent. In other words, the behavior existed in an ancestor of the two species

to shared environmental constraints (of course, convergence may also occur between closely related species; see Brosnan et al., 2009b). Care must be taken when making these assessments, but this approach allows for a determination of which behaviors existed in a common ancestor and which environmental or social factors may have been critical to the emergence of the behavior(s) (Boehm, 1999). Having this information may help us to understand situations in which humans do or do not appear to deploy moral behavior. Of course, it is also worth studying these behaviors in other species on their own merit.

Second, studying other species may also allow investigation of questions which are more difficult in humans. Of course, problems arise in studying both humans and non-humans in laboratories (Boesch, 2007), and field studies have their own set of issues (Burnham and Kurzban, 2005). Unique to humans, experimental factors such as anonymity and interaction with strangers are controversial (Fessler, 2009; Trivers, 2006), and social and environmental context can alter people's contributions in economic games (Hagan and Hammerstein, 2006). Studying captive animals avoids some of these issues, as interactions are occurring between individuals with very well known social histories (typically spanning the individuals' entire lifespans), allowing for more detailed investigations of the effects of relationships and social environment (Brosnan et al., 2009b).

This paper will address the evolution of one moral behavior, the sense of justice, from a biological perspective, using empirical data on how non-humans respond to inequitable and unequal outcomes. The goals of this paper are three-fold. First is to make the point that Adam Smith, despite the age in which he lived and his area of study, appeared to accept the continuity of species, including humans, an understanding which is sadly not as common as it ought to be today. Second is to propose that the non-human literature may be able to inform the human literature, specifically with regards to how context may affect perceptions of inequity. The final goal is to make the case that an evolutionary approach to economics is useful and worth engaging.

2. Smith, Darwin, and moral emotions

Not surprisingly, Charles Darwin was a strong proponent of the idea that humans and animals shared an evolutionary history. Although his most famous book, *The Origin of Species* (Darwin, 1964 [1859]), regarded primarily non-human species, two of his following books explicitly addressed humans and the role of evolutionary processes in shaping humans, including their behavior. In *The Descent of Man and Selection in Relation to Sex* (Darwin, 1981 [1871]), Darwin argues that the basis of morality is innate, rather than created *de novo* by humankind and provides a framework for the development of moral systems in any culture, group, or species:

The following proposition seems to me in a high degree probable – namely that any animal whatever, endowed with well-marked social instincts, the parental and filial affections being here included, would inevitably acquire a moral sense or conscience, as soon as its intellectual powers became as well developed, or nearly as well developed, as in man. For firstly, the social instincts lead an animal to take pleasure in the society of its fellows, to feel a certain amount of sympathy for them, and to perform various services for them. (pp. 71–2).

He goes on to argue that other animals feel at least some level of sympathy for one another. Although Darwin does believe that moral behavior requires fairly advanced intellectual ability, the primary feature he highlights as a necessity is “well-marked social instincts,” among which he included interactions with family. This encompasses a wide variety of animal species.

In *The Expression of the Emotions in Man and Animals* (Darwin, 1998 [1872]), Darwin made the case that moral emotions, like other traits, were the result of evolutionary continuity between humans and other animals. For this, Darwin relied on comparative data regarding facial expressions across both human cultures and different species, and addresses the reasons why these universal expressions take the form that they do.

Although he is better known for his ideas in economics than his evolutionary stance, Adam Smith appears to support this as well. While Smith does focus on human distinctiveness in his best known book, *The Wealth of Nations* (for instance asserting that only humans have developed barter and trade; Smith, 2000 [1776]), his approach is somewhat different in other writings spanning this publication. Smith's earlier work, *The Theory of Moral Sentiments* (Smith, 1817 [1759]) also focuses on human typical behaviors, however he appears open to – or even endorses – the idea of evolutionary continuity. In his discussion of ‘The Passions which take their origin from the Body’ (Part I, Section II, Chapter I), Smith explicitly argues against the ancient philosopher's conception that only our ‘brutish’ passions are shared with the animals, taking the position that both positive and negative passions are seen in common—in other words, that animals share many traits we consider human:

and has remained in both species. The second mechanism is convergence, in which behaviors emerged in two species independently because similar environmental pressures led to situations favorable for the maintenance of these behaviors when they emerged through chance evolutionary processes. To give an example, robins and eagles share wings through homology; their most recent shared ancestor had wings, and they both still have wings. On the other hand, robins, butterflies, and vampire bats share wings through convergence; all three species (or their ancestors) were in an environment in which wings provided a benefit, so when the appropriate genetic variation arose through chance (e.g. mutation, recombination), individuals with wings were favored by natural selection. These species have no common ancestor which had wings. Studying only one or a few species, it is difficult to determine which process led to similarities. However either way, the comparative approach can be useful in determining what environmental pressures led to the emergence of the behavior and which evolutionary trajectory it took upon the behaviors' emergence.

Such is our aversion for all the appetites which take their origin from the body: all strong expressions of them are loathsome and disagreeable. According to some ancient philosophers, these are the passions which we share in common with the brutes, and which having no connexion with the characteristic qualities of human nature, are upon that account beneath its dignity. But there are many other passions which we share in common with the brutes, such as resentment, natural affection, even gratitude, which do not, upon that account, appear to be so brutal. (Smith, 1817 [1759]), p. 30).

This idea that only negative passions are shared between humans and other species has not yet fully disappeared (de Waal, 1996).

Smith also uses comparisons between animals and humans to support his arguments about the nature of humanity. In *TMS*, he makes the point that all animals, including children, dogs, and ‘choleric man’ are likely to become angry at inanimate objects which hurt us (Part II, Section III, Chapter I). In his posthumously published *Essays on Philosophical Subjects* (Smith, 1982 [1795]), in the chapter on the external senses, Smith argues for the innateness of some human senses, particularly vision, from analogy with other animals. Smith’s discussion of the characteristics of the senses of other species additionally shows that he is informed about the Linnaean rank system for classifying organisms, and natural history in general.

Finally, for his time Smith had an advanced biological understanding of how human behavior functioned. Smith argued that human instincts were in place to promote survival and reproduction, an explicitly biological understanding of human behavior which preceded Darwin (Wight, 2009). He further believed that these instincts were initially experienced as emotion, rather than rational thought, and often served unconscious ends. Today we might refer to these motivations as ‘proximate causes²’ which explain how the behavior functions in the animal. Note that these motivations do not assume any understanding on the part of the animal (including humans). Although he does not explicitly refer to non-human species, this placement of human behavior firmly in the realm of the biological embeds humans in the natural world.

Hence, the idea of evolutionary continuity of behavior, even in realms often reserved for humans, such as the moral emotions, is not new. It was endorsed explicitly by both Smith and Darwin, then more or less disappeared in the last century, possibly due to the rise of foci on learning (behaviorism in psychology) and culture (in anthropology; Ekman, 1998). It seems likely that Smith and Darwin would have predominantly agreed with each other’s viewpoints, and in returning to their more inclusive approach, we may improve our understanding of human behavior.

3. Moral emotions and moral behaviors in non-humans

Moral emotions have been described as those emotions which focus on others, rather than the self, are elicited by stimuli which do not affect the self (e.g. inequality eliciting sympathy), and result in an outcome which helps others or society (Haidt, 2003). In other words, these emotions are among the proximate mechanisms which are necessary to uphold the rules of behavior underlying social norms and conventions. Moral emotions encompass different classes of emotions. For instance, they include both positive emotions, such as elevation, gratitude, or pride, and negative emotions, such as shame, guilt, and embarrassment (Tangney et al., 2007), as well as including both prosocial emotions, or those which improve the outcomes of other members of one’s group and antisocial emotions, which may decrease the fitness of other group members. Despite seeming contrary to morality, these latter emotions are moral if they change the recipient’s behavior to be more in line with the groups’ norms. While it is difficult to study emotions in non-verbal species, many scientists include other animals when discussing moral behaviors or moral emotions (Bonnie and de Waal, 2004; Flack and de Waal, 2000; Haidt, 2003). One such behavior for which there is a relatively extensive literature is responses to inequitable outcomes.

3.1. Justice, equity, and equality

Adam Smith refers to justice as “the main pillar that upholds the whole edifice [of human society]” (1817 [1759]; p. 115). Two related components of justice are equity and equality. Equality assumes identical outcomes, but fails to account for effort and deservedness. Equity does so. Since perception varies, an equal reward may be inequitable, or an equitable reward may be unequal. Because of this, this paper relies primarily on the concept of equity rather than equality. Although justice is difficult to study in non-verbal species, equity can be operationalized, allowing for an experimental approach.

In the fields of economics and psychology, equity is considered to consist of two components, one’s reactions to one’s own outcomes, and one’s reaction to others’ outcomes (Fehr and Schmidt, 1999; Walster et al., 1978). The former, disadvantageous inequity, is probably the most common, and is fairly easy to explain from an evolutionary perspective (Brosnan, 2006a,b). Individuals who notice that they receive less than another and change their behavior in ways that rectifies the inequity directly improve their outcomes, so this behavior is under strong positive selection.

However, this is entirely about one’s own outcomes. In order to qualify as a moral behavior, individuals must also notice and react when others are treated less well. These advantageous inequity responses are critical to a full-fledged moral system,

² Evolutionary biologists distinguish between proximate mechanisms and ultimate causes. Proximate mechanisms explain how the behavior functions within an individual while ultimate causes explain how the behavior evolved over the species’ history. For instance, the ultimate cause of eating is that it provides the energy and nutrients required for survival, but the proximate mechanism which leads individuals to consume food is the pleasure of doing so, not an understanding of its necessity.

yet it seems on the surface to be difficult to explain via natural selection. However, several good hypotheses exist to explain the evolution of the response. First, advantageous inequity responses also benefit the self, as a commitment device which demonstrates to others the actor's dedication to equity and general merit as a social partner (e.g. Frank, 1988, 2001). Humans' behavior supports this in some experimental settings, as people will make decisions which lower their absolute and relative outcomes, presumably to send a signal to their partner (Yamagishi et al., 2009). Related to this, responding to rectify inequity which is detrimental to another may also improve one's own reputation, providing benefits in the future (Milinski et al., 2002; Nowak and Sigmund, 1998; Wenekind and Milinski, 2000). Both of these functional explanations make clear why this prosocial behavior was selected, but more immediate proximate factors may be empathy and the 'warm glow' people get from helping others (Andreoni, 1989; Batson, 1991; Zak, 2010). It has been speculated that other primates, too, experience this (de Waal et al., 2008). Smith mentions this phenomenon in his own writing as well: "But whatever may be the cause of sympathy, or however it may be excited, nothing pleases us more than to observe in other men a fellow-feeling with all the emotions of our own breast" (Smith, 1817 [1759]), p. 13). Although advantageous inequity responses are ostensibly about benefiting others, because of the personal benefits (even in the case of the warm glow; Andreoni, 1989) they nonetheless benefit the self, explaining how they may evolve.

In the literature discussing justice or inequity in non-humans, it is fairly common to treat these two components separately, with the latter typically being pursued as 'other-regarding' or empathetic behavior. This discussion is beyond the scope of the paper, however the empirical evidence will be presented as it is relevant to question.

3.2. Equity and equality in non-humans

Several species respond negatively when they are treated less well than a social partner (Brosnan, 2006a,b, 2008a,b). Chimpanzees, capuchin monkeys, dogs, rabbits, and, possibly tamarins, all show responses which indicate frustration or distress, such as refusing food rewards or refusing to participate in interactions, when social partners receive better outcomes for completing a task (Brosnan and de Waal, 2003; Brosnan et al., 2005; Fletcher, 2008; Heidary et al., 2008; Neiworth et al., 2009; Range et al., 2008; van Wolkenten et al., 2007). This response is similar to that seen in humans when playing the impunity game (Yamagishi et al., 2009). This reaction is not surprising, as it is an extension of violation of expectation, which has been known in primates for almost 100 years (Tinklepaugh, 1928), and interacts with inequity (Brosnan et al., 2010). However the inequity response is based on an expectation set up by what someone else received, or a social expectation, rather than an individual expectation.

The reaction varies dependent upon the context. For instance, the response has thus far only been elicited in the context of a task to receive the reward, such as an exchange, which may indicate the importance of interaction or cooperation in determining whether outcomes are inequitable (Brosnan, 2008a; see Section 4.3 below for more details). Among chimpanzees, individuals' responses also differ depending on their social environment (Brosnan et al., 2005), perhaps based upon social relationships, as in humans (Clark and Grote, 2003). One study has found a sex difference in response, with males responding to social expectation and female to individual expectation (Brosnan et al., 2010). Finally, rank appears to make a difference in some situations, with dominant individuals responding more strongly than subordinates (Brosnan et al., 2010; Bräuer et al., 2009).

While primates respond strongly to inequitable outcomes, or distributional inequity, procedural inequity does not elicit a response. No study has found evidence of a negative response to effort differences, such as when only one individual must complete a task, or when one individual must complete a more difficult task, to get the reward (Fontenot et al., 2007; Roma et al., 2006; van Wolkenten et al., 2007; Brosnan et al., 2010). Moreover, other sorts of procedural differences do not affect responses; a time delay inserted between the task and the reward for only one individual does not affect subjects' reactions (Brosnan et al., 2010).

Finally, data from a more naturalistic study indicate that the long-term behavior of the partner is more important than the outcome of individual interactions. In an experimental cooperation task, subjects were much more likely to cooperate if they and their partner evenly shared the better rewards. For this task, capuchin monkeys had to work together to pull in a heavy tray which contained food for each of them. However, the foods were not always the same, and the monkeys had to decide whether they were willing to work for the food reward in front of them. Since they were not separated from each other, this was determined by the monkeys, rather than by the human experimenter. Subjects were willing to work for lower value rewards as long as they got about half of the higher value rewards across all of the trials with different foods. Pairs in which the partners shared the better rewards about half of the time were highly successful in this cooperative task, while pairs in which one partner excluded the other from receiving the higher value rewards rarely achieved cooperation. Hence, although the dominants in the second case (non-sharing dominants) received more higher value items than their partners, they received many fewer rewards overall than sharing dominants because of the lower success rate. (There was a condition in which both monkeys got high-value rewards, so this difference cannot be explained by an overall lack of motivation.) Thus, subordinates seemed to expect that working together on a task should lead to relative equity of reward outcome (Brosnan et al., 2006), and dominant partners who failed to do this received a form of punishment. The conclusion is that a critical factor in a naturalistic cooperative task is whether the partner's behavior is equitable, rather than whether the actual rewards on any given trial are so.

In the majority of these studies of inequity, there was little evidence that the advantaged partner was attempting to reconcile the discrepancy between the rewards (Brosnan, 2006a; although see Brosnan et al. (2010) and below for counter-

evidence in one group of chimpanzees). However, these experiments were not designed to measure advantageous inequity; food rewards were not easily divisible, requiring individuals to share all or nothing on an individual trial (a high cost). Moreover, only in the [Brosnan et al. \(2006\)](#) study was there any benefit to the individual for sharing. However, other studies have been done which were designed to minimize the cost to individuals for creating equality between themselves and a partner.

In most of these experiments, one primate is given a choice between an option which brings food both to itself and to a partner and an option which brings food only to itself ([Silk et al., 2005](#)). To make the task as simple as possible, the subjects' food rewards do not differ between the conditions, so self-interested motivation should not have differed. Subjects are typically tested in two different conditions, one in which they were paired with a social partner and one in which they were alone, as a response grounded in equity concerns must lead to an increase in sharing when a partner is present more than when the partner is absent. This differentiation helps control for the possibility that subjects' interest in the equal option is because it is a larger amount of food (even though they do not get it all).

Chimpanzees have been tested on this paradigm by two research teams at three different facilities. In each case, no subject behaved differently from chance, bringing food to their partners about half of the time whether the partner was present or absent ([Jensen et al., 2006](#); [Silk et al., 2005](#)). This remained true in a follow-up test in which the subjects could reward themselves and then their partners ([Vonk et al., 2008](#)). Even when the experiment was altered so that sharing was explicitly self-benefiting – by adding reciprocity within the session – chimpanzees were indifferent between the options ([Brosnan et al., 2009a](#)). However, chimpanzees do help others by completing simple tasks (fetching a pen, removing a blockade; [Warneken et al., 2006, 2007](#)). Finally, as mentioned above, in one study chimpanzees did refuse a grape as a reward more often when their partner got a cucumber (a less valuable reward) than when their partner also got a grape, although this may not have been due to prosocial motivations ([Brosnan et al., 2010](#)).

Several hypotheses have emerged to explain this apparent discrepancy within chimpanzee behavior, although none thus far satisfactorily explain all of the data. The first hypothesis is that food, as a limited resource, leads to the perception of a zero-sum game rather than an opportunity to share. Thus, the chimpanzee's goal in these experiments may be to avoid giving food to the competitor ([Warneken et al., 2007](#)). A second hypothesis is that explicit requests are required to generate prosocial behavior in chimpanzees ([Yamamoto and Tanaka, 2009](#)), although this does not seem to explain the behavior in other studies ([Cronin et al., 2009](#); [Silk et al., 2005](#)). More recently, marmosets, a new world monkey species, were found to show prosocial behavior ([Burkart et al., 2007](#)) in a situation very similar to that of [Silk et al. \(2005\)](#). The authors proposed that cooperative breeders have evolved to show more prosocial behaviors, due to selection for extensive prosocial interactions among non-kin. However, another recent study found that marmosets, which are very closely related to tamarins, do not show prosocial behavior in a similar paradigm ([Cronin et al., 2009](#); although see also [Cronin and Snowdon, 2008](#), for evidence of reciprocal behavior in tamarins). Moreover, capuchin monkeys, a non-cooperatively breeding new world monkey, albeit one with allomaternal care, do show prosocial behavior ([de Waal et al., 2008](#); [Lakshminarayanan and Santos, 2008](#); [Takimoto et al., 2010](#)), as do dominant long-tailed macaques ([Massen et al., 2010](#)). These results have led some to reject the cooperative breeding hypothesis as neither necessary nor sufficient ([Lakshminarayanan and Santos, 2008](#)).

3.3. The context of inequity

Humans respond differently to inequity depending upon the source. In experimental games, for instance, humans change their pattern of responses if there appears to be a reason for inequity. Subjects offer less and partners accept this inequity more readily if the subject is perceived to have earned the right to it (e.g. by performing well on a test; [Hoffman et al., 1994](#); [List and Cherry, 2008](#)). Humans also respond more strongly to inequity which is caused by another human directly than to inequity resulting from chance (e.g. a computer-generated response; [Blount, 1995](#); [Knoch et al., 2006](#)). Despite these few studies, little research has been done on how the framing of the inequitable outcome affects perception. This may be particularly important since most payoffs in experimental economics occur in the context of 'free' money which the subjects receive when they walk through the door ([Wight, 2009](#)).

Non-human primates respond very differently to inequity which results following a task than to that which is due to 'free' handouts. This evidence emerges from the consistent finding that most primates respond to inequity only when the payoffs are framed as a 'payment' for completing a task, but not when rewards are framed as a 'gift' which is handed to participants for free. In these studies, subjects typically either earn rewards by exchanging a token with a human experimenter (for which they receive a food item in payment) or are simply handed food rewards by the experimenter, with no task.

No apes show a response to inequity without a task ([Bräuer et al., 2006](#); [Brosnan et al., 2010](#)). When a task is included, results are variable; bonobos seem to respond, orangutans do not, and chimpanzees' responses vary both between and within studies ([Bräuer et al., 2009](#); [Brosnan et al., 2005, 2010](#); [Brosnan et al., in preparation](#)). Thus, it is probable that there are other ecological, experimental, or social factors which are affecting the response ([Brosnan et al., 2010](#)). Among monkeys, tamarins do not show an inequity response when there is no task present, but increase their refusal rates over time when a task is present ([Neiworth et al., 2009](#)). Among capuchins, the same pattern holds as in the chimpanzees ([Brosnan and de Waal, 2003](#); [Fletcher, 2008](#); [van Wolkenten et al., 2007](#); [Dindo and de Waal, 2006](#); [Dubreuil et al., 2006](#); [Fontenot et al., 2007](#); [Roma et al., 2006](#)), with subjects in the exceptional study showing no response to a contrast effect, either, indicating that there may have been another reason that the subjects did not respond ([Silberberg et al., 2009](#)). Notably three of these studies used the same group of capuchin subjects, and the one which did not use a task ([Dindo and de Waal, 2006](#)) found no response to

inequity while those which did use a task (Brosnan and de Waal, 2003; van Wolkenten et al., 2007) found that monkeys did respond when receiving less good food rewards than their partners. Although all of the abovementioned examples are only correlational evidence, a recent study including both conditions counterbalanced within the same experiment has supported this in chimpanzees (Brosnan et al., 2010). Thus, something about the task seems to be critical in triggering expectation.

There are several hypotheses for this behavior (Brosnan et al., 2010). First, this could be due to the typical captive environment, in which food is routinely handed to subjects by humans. They may have become accustomed to inequity in this context. However, another possibility is that subjects react to inequity only in situations which require some sort of effort. There seems to be a fundamental difference in the way inequity is perceived between situations in which the rewards are unearned (received for 'free') and those in which rewards result from an effortful task. It may be that joint efforts lead to the expectation of joint payoffs (van Wolkenten et al., 2007), thus animals may not expect equity in situation in which there is no perception of working with another. This is reminiscent of humans accepting more unequal rewards when they believe a computer chose a division, as opposed to when they believe that a human partner did so (Blount, 1995; Knoch et al., 2006). Given that both situations involving free rewards and those involving effort are prevalent in the real world, it seems essential to an understanding humans' responses to inequity to better distinguish the differences in response they generate. Aside from providing an interesting new line of research in human populations, this distinction is one that is mostly absent from the models of inequity common in the literature. Including this distinction, and the differences in response resulting from it, may even affect existing theories on reactions to inequity in humans (Khalil, 2009).

3.4. The evolution of the sense of justice

The previous section demonstrates that primate experiments reveal a behavioral response to inequity, supporting the hypothesis that behavior relevant to at least one moral behavior, the sense of justice, does exist in species other than humans. Several species of non-human primates (and several non-primates) respond negatively to earning less preferred rewards than a social partner. Some species even respond behaviorally to rectify inequity which affects a partner, although the context in which this occurs is still not entirely clear. These behaviors may have emerged through either convergence or homology (see Sections 1 and 2). Evidence from capuchins, chimpanzees, and humans, even with the addition of dogs, is not sufficient to distinguish between these possibilities since all three species share in common traits (cooperation, gregariousness) which have been linked to negative responses to inequity. In particular, cooperation has previously been linked to the inequity response (Fehr and Schmidt, 1999; Brosnan et al., 2006), meaning that it may be the critical environmental factor that led to selection for the behavior. Regardless of whether these behaviors emerged once in a common ancestor and represent an evolutionary homology or arose in parallel several different times, we can use the comparative approach to track the evolutionary trajectory of this response. In this way we can understand more about the features which are important for the inequity response.

The inequity response likely evolved in four steps (Brosnan, 2006a). Note that although these steps represent a process of cumulative behavioral complexity, at each step there is some benefit to the individual. Moreover, not all species will exhibit all of the steps. Thus, when looking for sensitivity to inequity it is important to look for *any* of the stages of the behavior, and not focus on solely the more complex behaviors. A first necessary step is to notice inequity. This may have been a byproduct of any other behavior that selected individuals to pay attention to conspecifics, such as social learning (which is present in many species). In and of itself, noticing inequity may not be beneficial, however, if these individuals took the next step and began to respond negatively to inequity, even in a non-targeted way, they would benefit. If individuals began to react negatively to individuals who treated them inequitably, this could lead them to cease interactions with those partners and seek out others. By chance alone it is likely that some new partners will behave more equitably. In this case, they have benefited, even if they did not recognize why they responded negatively or that their change in behavior provided a benefit. This would enhance the individual's fitness, resulting in positive selection for the behavior. Most of the evidence for inequity responses is at this stage: individuals respond negatively to inequity and, based on the one test in which subjects could choose whether or not to participate (Brosnan et al., 2006), seem to cease interacting with partners who are not equitable. In the third step, individuals understand that they have received less and actively take steps to rectify inequity. This is likely the stage at which humans operate, for example, by punishing individuals who do not play fairly (Fehr and Gächter, 2002). Thus far, only scant evidence exists that non-humans show this reaction. For example, if it turns out that capuchins are punishing social partners who do not share by ceasing to cooperate (Brosnan et al., 2006), this would be an example of this stage of the response.

The final stage of the response was likely responding when advantaged, or rectifying inequity in others. Although advantageous inequity responses are also explicable via individual natural selection, disadvantageous inequity responses are more straightforward as there is a more immediate benefit to the partner. In the case of advantageous inequity, however, individuals must actually act against their own short-term self interest, giving up rewards to benefit partners. However, despite the short term cost, this behavior may increase long-term benefit (see Section 4.1). Responses which assist another individual are seen in non-human primates, as discussed above (Section 4.2). However, these behaviors do not appear to be as easy to elicit in non-human primates as in humans. One possibility, of course, is that we have not designed tests that do a good job of exploring these other species' capacities. Another possibility is that human prosocial responses are more fully developed than those of other species. This may be indication that prosocial behaviors (e.g., strong reciprocity; Gintis, 2000) were particularly important in humans' evolution.

4. Conclusion

Moral emotions are not the only area of economics in which studies from non-human species are being used to inform our understanding of human behavior. For instance, other species show behavior which is in line with Prospect Theory (Kahneman and Tversky, 1979) in the same ways as do humans (Brosnan et al., 2007; Chen et al., 2006; Lakshminarayanan et al., 2008). This indicates that humans' 'irrational' behaviors (Ariely, 2008) are not unique, and that these behaviors were likely beneficial at some point in our evolutionary history (Jones and Brosnan, 2008). For example, constraints such as the lack of language would have inhibited the growth of institutions that could protect against losses (Brosnan et al., 2008).

With respect to moral behaviors and emotions, by understanding precursors, such as the inequity response, we have a better understanding of the evolution of moral behaviors. These behaviors will not likely be identical to those of humans, but in examining them we see the connection between our behaviors and those of other species. Far from being simply an academic exercise, the study of these behaviors helps to clarify how our own behaviors evolved and the constraints which may be encountered. This line of thinking is not new; Charles Darwin clearly saw continuity between the species, and, though he was not a biologist, Adam Smith did as well. Perhaps in the future this evolutionary approach to human behavior will once again span disciplinary boundaries.

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