Conclusion. The fine anthropological work reported in Henrich et al. (2004; and target article) is at variance with the rhetoric with which it is introduced. Please do not throw away game theory and other approaches associated with "economic man." The ideas that motivate the folk theorem of repeated game theory remain our best hope of understanding how societies hold together and adapt to new challenges.

A cross-species perspective on the selfishness axiom

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Abstract: Henrich et al. describe an innovative research program investigating cross-cultural differences in the selfishness axiom (in economic games) in humans, yet humans are not the only species to show such variation. Chimpanzees and capuchin monkeys show signs of deviating from the standard self-interest paradigm in experimental settings by refusing to take foods that are less valuable than those earned by conspecifics, indicating that they, too, may pay attention to relative gains. However, it is less clear whether these species also show the other-regarding preferences seen in humans.

It is assumed, both explicitly and implicitly, that animals (including humans) attempt to maximize their own self interest. After all, this is fundamental to natural selection and many behaviors are demonstrably motivated by self-interest. In some areas of economics, this has been translated into an assumption that a truly self-regarding person would accept any offer that was positive, as, for instance, in the Ultimatum Game discussed in the target article. However, as Henrich et al. note, people from a variety of cultures appear more interested in relative than absolute benefits, indicating that interest in fairness is a universal human characteristic. Recent research has shown that two species of nonhuman primates, capuchin monkeys (*Cebus apella*) and chimpanzees (*Pan troglodytes*), may behave similarly. These primates will refuse previously acceptable rewards if their rewards differ from those of a companion (Brosnan & de Waal 2003; Brosnan et al. 2005), indicating that they are more interested in their *relative* benefit in comparison with a conspecific partner than in absolute benefits. This is similar to the logic explaining people's reactions to the Ultimatum Game and provides a beginning for the exploration of a "sense of fairness" in nonhuman species (Brosnan, in press).

Moreover, as with people from different cultures, chimpanzees show great variation in the level of response dependent upon the social group from which they originated. (Bear in mind that this variation may or may not be based on the same sorts of cultural or socioecological factors as it is in humans.) These differences are not based on the sex or the rank of the individual, nor relatedness, as all subjects tested were adults paired with nonkin. Chimpanzees from a social group in which virtually all of the individuals grew up together, showed virtually no reaction to inequity, while those in a more newly formed social group responded relatively strongly. Psychology research has shown that people respond very differently to inequity when in close or positive relationships than when in distant or negative ones (Clark & Grote 2003; Loewenstein et al. 1989), and perhaps nonhumans react similarly. Chimpanzees that grew up together may have intimate, kin-like relationships and hence respond to relative inequity quite differently than chimpanzees introduced to each other as adults.

Although nonhumans apparently react to inequity, and this reaction may be impacted by the social environment of the individual, the results do not perfectly mirror those of humans. This is in part because of experimental constraints (the primates did not have anonymous interactions, nor were they allowed to choose the reward distribution themselves), and in part because it is unclear how to compare these chimpanzee groups to human sociopolitical groups. Regarding the former, in a follow-up experiment with capuchin monkeys, individuals were paired with a group mate to solve a mutualistic cooperation task for two rewards. Rewards were sometimes the same and sometimes different (one better than the other). Pairs that were more equitable in the division of rewards in the unequal condition were far more successful in all situations than those in which one individual dominated the better rewards (Brosnan et al., submitted). While this is not a perfect match for games such as the Ultimatum Game, it indicates that monkeys do pay attention to their partner's actions in determining reward division. They may "reject" a partner who is not generous, perhaps by simply failing to cooperate, and "reward" a generous partner with continued cooperation (see also de Waal & Davis 2003). Regarding the latter constraint (comparing human and chimpanzee groups), male chimpanzees in particular may need to cooperate frequently for territory defense and hunting, indicating that, as with some human societies, these individuals should have an interest in fairness and, perhaps, display other-regarding preferences.

We know that some nonhuman primates react to being relatively underbenefitted compared to a conspecific, which is irrational according to a strict self-interest paradigm. However, due to factors such as the primates being unable to determine the distribution of resources (excepting in the Brosnan et al. [submitted] study mentioned above), this research cannot compare partner response directly to any of the games discussed in Henrich et al's target article, nor can we effectively comment on the potential for other-regarding preferences in chimpanzees or capuchin monkeys. However, one bit of evidence indicates that these primates may be less other-regarding than humans are. In the experimental setup for the exchange tests, the primates were able to share food with each other if they so chose. However, there was virtually no sharing between the privileged individual and their less well-endowed partner (no instances in capuchin monkeys and less that 1% of interaction in the chimpanzees). Both of these species are known to be good food sharers and, indeed, we saw some sharing in the other direction (the privileged individual consuming the less valuable food). Previous research has indicated far greater levels of food sharing. It is interesting, therefore, that the relatively benefited individuals did not exert more effort to equalize rewards.

Studying such behaviors in nonhuman species may be an excellent way to further our knowledge of the selfishness axiom and other-regarding behavior. Not only do nonhuman primates provide a possible glimpse of the evolutionary trajectory of these behaviors, but investigation of their behavior may give us a greater insight into our own behavior. Other socially complex food-sharing species, such as the social carnivores, may display similar tendencies and provide further insight (e.g., Bekoff 2004).

On the limitations of quasi-experiments

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Abstract: Although provocative, the data reported in Henrich et al.'s target article suffer from limitations, including the fact that the "selfishness axiom" is not an interesting null hypothesis, and the intrinsic limitations of quasi-experimental designs, in which random assignment is impossible. True experiments, in the laboratory or in the field, will continue to be crucial for settling core issues associated with human economic behavior.

The wealth of data reported in the target article is a welcome addition to the study of economic behavior, which has, with impor-

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tant exceptions (e.g., Buchan & Croson 2004), only rarely concerned itself with populations outside of the industrialized West. Moving beyond the convenience samples so frequently used by researchers in this area is an important step in broadening our understanding of issues related to prosocial behavior, altruism, and cooperation.

We focus here on three points. First, we question the continued use of the "selfishness axiom" as a null hypothesis. Second, we point to the advantages of experiments on the cognitive mechanisms that produce prosocial behavior. Third, we question what inferences are licensed by the present studies.

The first of the authors' five main conclusions from their data is a rejection of the "selfishness axiom" (target article, sect. 1, para. 4). As the authors themselves acknowledge, however, a massive amount of data has already accumulated that undermines this axiom. In 1965, for example, participants showed high levels of cooperation in finitely repeated prisoners' dilemmas (Rapoport & Chammah 1965). Because defection is a dominant strategy in the last round, researchers expressed surprise that even in the last round many people cooperated, earning less money than they could have. Similarly, in 1982, some ultimatum game responders chose less money than was feasible when they rejected offers that were a small percentage of the total (Guth et al. 1982).

The hypothesis that people maximize monetary payoffs in all environments (an unsophisticated interpretation of self-interest) has failed so vividly and so frequently that it is not clear that continued falsification adds to our understanding. Indeed, recent work has shifted towards much more sophisticated models of human economic behavior, which has yielded a bounty of theoretical and empirical fruit (Camerer 2003; Gintis 2000).

This leads to our second point, the success of recent experiments in shedding light on the mechanisms that underlie the behavior discussed in the target article. Tinbergen provided a framework that explained both maximizing behavior and persistent failures to maximize in particular settings (Tinbergen 1968), and this framework has become the standard for the study of the behavior of all animals except humans.

As an example of Tinbergen's approach, consider work showing that herring gulls fail to maximize in environments constructed to include artificial eggs. Careful experimental studies were able to pick apart the mechanisms that gulls use for egg selection (Baerends & Drent 1982a; 1982b). These mechanisms (1) arose by natural selection, (2) advanced the inclusive fitness of the individuals in natural environments, and, crucially, (3) failed spectacularly in particular, artificial settings.

Tinbergen's theory and its applications suggest a similar explanation for human economic behavior that fails to maximize, and this approach is already providing novel insights. For example, it has long been known that humans fail to maximize in many experimental settings involving time discounting (Ainslie 1974; Rachlin 1970). A recent study manipulated the mechanism of discounting and caused an increase or decrease in the deviation from maximization (Wilson & Daly 2004). By illuminating one aspect of the cognitive architecture behind discounting, this work suggests that the apparently puzzling economic behavior is simply caused by adaptive mechanisms interacting with particular and peculiar environments.

Similarly, a growing body of research investigates the mechanisms that modulate prosocial behavior as a function of anonymity. Models based on signaling (Smith & Bliege Bird 2000) or reputation (Panchanathan & Boyd 2003; Trivers 1971) predict the adaptive value of psychological mechanisms sensitive to cues of anonymity. Indeed, people modulate their behavior as a function of anonymity (Burnham 2003; Hoffman et al. 1996b; Rege & Telle 2004) and prosociality is more likely when actions are observed.

In fact, the data in the target article would not be surprising at all if they took place in a repeated, non-anonymous setting with an ability to generate reputations. Is this failure to maximize – like that of gulls with artificial eggs and people discounting in the laboratory – caused by mechanisms interacting with specific environmental cues? If so, it might be possible to create prosociality using cues to social presence. In particular, a powerful cue is likely to be the presence or absence of eyes, which is used to modulate behavior across many species (Call et al. 2003; Hampton 1994; Hare et al. 2001).

This hypothesis that eyes will produce prosocial economic behavior has been tested and confirmed in two studies. Contributions to a public good game increased by 29% in the presence of human eyes (Burnham & Hare, in press; see also Kurzban 2001). Similarly, contributions in a dictator game were increased 32% by the presentation of eyespots (Haley & Fessler 2005). We are optimistic that the continued application of Tinbergen's framework to human economic decisions may provide both proximate and ultimate explanations for prosocial behavior.

This brings us to our third and final point, which concerns the inferences that one can draw from studies of this nature. As the authors point out, the use of "culture" as an independent variable places severe restrictions on what can be learned. Because "culture" cannot be experimentally manipulated, causal claims are necessarily problematic (and indeed, section 4 should properly be labeled "Quasi-experimental results"). This is important because the issues that are at stake in this arena surround the underlying psychological mechanisms that cause the observed behavior.

The difficulty with the cross-cultural work described here is that it speaks only obliquely to centrally debated questions. The authors, for example, favor a proximate explanation that makes reference to socially acquired preferences and norms, a model that differs importantly from other approaches in that the postulated psychology is, broadly, a domain-general learning psychology. Such a model (Note 17 of the target article notwithstanding) does indeed imply something about cognitive architecture because the acquisition of any information necessarily entails a mechanism by which the information is acquired. To the extent that this constitutes a key element of debate, research will need to be directed squarely at this issue. Findings such as the one concerning market integration, while interesting, lend themselves to extremely wide interpretation.

In summary, the data showing that people fail to maximize monetary outcomes in some settings and that there is cross-cultural variability, are useful, but do not directly address the key debates in the area. Accordingly, we suggest that research should be carefully directed towards resolving the relevant central theoretical issues, with a focus on the nature of the psychological mechanisms that underpin economic behavior.

Psychology and groups at the junction of genes and culture

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Abstract: Replacements for the self-interest axiom may posit weak to strong theories of sociality. Strong sociality may be useful for positing social cognitive mechanisms and their evolution, but weak sociality may work better for identifying interesting group-level outcomes by focusing on deviations from self-interested psychological assumptions. Such theoretical differences are likely to be based on disciplinary expertise, and the challenge for Darwinian integration is to keep the conversation flowing.

Henrich and his colleagues have made an outstanding contribution with an illuminating study combining descriptive and experimental methods. They not only expand the challenge to the canonical model of self interest, they also present remarkable cross-cultural evidence that local, group-level effects explain substantially more of the variance in choice behavior than do individual-level variables. (And, of course, the opening line with its allusion to Caporael et al. [1989] was just perfect from my perspective.) My com-

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