agents perceive social decision problems (Zizzo 2002a), while dopamine might facilitate social learning processes (Zizzo 2002b). There is evidence suggesting a role for environmental input in how the serotonergic system works in individual brains, both with monkeys (Higley et al. 1993) and with humans (Oxenstierna et al. 1986). Monkeys growing up in a socially deprived environment have abnormally high levels of serotonin, related to inappropriate aggression (Higley et al. 1994; Kraemer et al. 1989; Lilly et al. 1992). In normally reared monkeys serotonin and dopamine are closely correlated, whereas in socially deprived monkeys they are not (Kraemer et al. 1989).

The authors' emphasis on the social learning of preferences is supported by heritability studies (e.g., Rutter 1997; Zizzo 2003a). For example, in Rushton et al. (1986), only around 50% of the variance of self-reported altruism, empathy, and aggressiveness is explained by the genes. Miles and Carey's (1997) meta-analysis found that genes might account for up to 50% of the variance in aggression in questionnaires and self-reports, but also that "observable ratings of laboratory behavior found no evidence for heritability and a very strong family environmental effect" (p. 207). Children growing up in different social environments may develop significantly different social preferences.

Self-interest, however, is not the only key assumption of "economic man," and the neurodevelopmental and heritability evidence can be interpreted both in terms of development of differential preferences as of differential social cognitive skills and perspectives. (Perfectly) rational choice – the idea that maximisation subject to informational and material constraints is all there is to choice – is the other key assumption, and the theoretical analysis provided by the authors is slightly unclear on this. Henrich et al. note the possibility of rationality limitations but claim that game playing does not require "very high levels of reasoning or omniscience" (sect. 9, para. 3). This may be so, but surely one possible source of cross-cultural variations lies in violations of the rationality rather than the self-interest axiom. Although this is not the focus of the authors' work, there are revealing signs that this is the case. The authors' largest dataset concerns ultimatum game offers, and they show that a possible explanation of ultimatum game offers behaviour lies in a combination of pessimistic beliefs and ambiguity aversion. Rubinstein (1998) defines the knowledge of the problem as one important dimension of economic rationality. Cross-cultural variations in how agents face up to uncertainty seem an obvious signal that there are not just differences in preferences, but also differences in cognition. It is suggestive that the Orma appeared to assimilate the public good game to what was for them a prototypical social setting, the *harambee*, because it indicates that something like similarity-based or case-based decision reasoning may be going on in the presence of an unfamiliar task (Gale et al. 1995; Gilboa & Schmeidler 2001; Zizzo 2003b). Indeed, as the authors recognize in their theoretical discussion, the correlation of the market integration index with behaviour can be explained in cognitive terms, in the development of "distinctive cognitive capacities and habits." Though the authors downplay the importance of framing in the discussion of the design, they themselves stress its possible role in the theoretical discussion. It is quite possible that some of the cognitive variations can be explained in terms of parsimonious and stable social utility functions; but whether this is generally true is very unclear, and decision-making approaches that explicitly recognise bounded rationality in determining the procedure of choice may be called for.

The attempts made by the authors to identify within-group variations in preferences and cognitive skills, and their impact on behaviour, were fairly unsystematic, so it is difficult to see what to make of them without additional research. This is not meant to be a criticism: in a first study of this scale, obviously not everything could be done. Still, that education does not predict game behaviour should not be taken as an indicator that cognitive abilities may not have played a role at the individual level. Transfer of knowledge from one task to another does take place in some cases but not in others (Reeves & Weisberg 1994; Zizzo 2005). Knowledge of the laws of physics may not be especially helpful to be an expert billiard player: there is a difference between explicit knowledge that people learn and store in memory and implicit knowledge of how to actually do things (Shanks & St John 1994). Therefore, that education should modify game play should not be taken as a foregone conclusion, as implicit cognitive skills may differ from, say, abstract numeracy skills. On the "heterogeneity of preferences" front, there is evidence pointing to large and systematic differences in preferences within fairly homogenous populations (e.g., Burlando & Guala 2005), but this requires more complex experimental designs than those used by the authors. They may also, no doubt, be harder to implement in the field, but this is a challenge worth taking, I think.

Authors' Response

Models of decision-making and the coevolution of social preferences

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Abstract: We would like to thank the commentators for their generous comments, valuable insights and helpful suggestions. We begin this response by discussing the selfishness axiom and the importance of the preferences, beliefs, and constraints framework as a way of modeling some of the proximate influences on human behavior. Next, we broaden the discussion to ultimate-level (that is evolutionary) explanations, where we review and clarify gene-culture coevolutionary theory, and then tackle the possibility that evolutionary approaches that exclude culture might be sufficient to explain the data. Finally, we consider various methodological and epistemological concerns expressed by our commentators.

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R1. The preferences, beliefs, and constraints approach

R1.1. The selfishness axiom

Our primary interest was to explore the between- and within- group variation in other-regarding social behavior by exploiting potential cross-cultural variation across a wide range of small-scale societies. Our experiments produced evidence inconsistent with the selfishness axiom. This aspect of our work has attracted critical attention. Most of the commentaries here focus on three challenges: (1) Proximate modeling of the observed behavior; (2) explaining the ultimate (evolutionary) origins of the behavior; and (3) methodological validity of the experimental evidence.

The *proximate* motivations and sentiments of the decision-maker provide a modeling framework that stands independent of the evolutionary origins of those motivations and sentiments. *Ultimate* explanations provide evolutionary foundations for proximate accounts. We discuss below the competing explanations at both levels raised by commentators. Many *methodological* questions arise as part of a debate concerning which theories are consistent with our results.

We interpret the experimental results as consistent with an ultimate-level gene-culture coevolutionary view described in our target article and later in this response. However, these experiments were not designed as a test of alternative evolutionary approaches (see commentaries by **Krupp**, **Barclay**, **Daly**, **Kiyonari**, **Dingle & Wilson** [**Krupp et al.**], **Sullivan & Lyle**, **E. A. Smith**, **Burnham & Kurzban**) and no single study – including ours – can definitively prove or disprove any ultimate-level theory of the evolution of human sociality. So, our efforts here are unlikely to convince all the researchers who prefer alternative interpretations. Therefore, our immediate goal is to clarify differences across theories, establish agreed-upon facts, and create an interest in further experimentation and theorizing.

The proximate explanation we adopt to interpret our data – the preferences, beliefs, and constraints framework – is rooted in game theory, and hence is not a theory of how people make decisions at the detailed level of cognitive processes and affective states (although research linking our approach to neuroscientific theory is proceeding rapidly). Rather, our framework provides a set of formal tools for capturing and precisely modeling the actions people take in given situations, allowing researchers to include self-regarding and other-regarding *preferences* (e.g., motivational concerns about equity or relative payoff), *beliefs* (mental states that describe or model that world), and *constraints* (rules, such as you cannot keep your share if you "reject") in a coherent account. An important interpretation of our findings is that *preferences* for other-regarding behavior are common, in some fashion, in every society studied, but that these preferences are heterogeneous within societies and vary across populations. Our results are also consistent with the view that preferences are context-dependent and subject to cueing and framing effects. Our experiments do not allow a conclusive determination of which social preferences are involved, or indeed, whether the behaviors observed might not be the result of beliefs about the game rather than of social preferences. For example, positive offers in the dictator game could be sensibly described as *altruistic behavior*, which could be explained by empathetic preferences (caring directly about the other's payoffs). However, from the preferences, beliefs, and constraints perspective, this could also result from other social preferences, such as an aversion to inequity, or from faulty beliefs – individuals with purely selfish preferences might have misunderstood the game, perceiving it as repeated even though it is a one-shot game.

Some commentators (**Krupp et al.**[1] and **Burnham & Kurzban**) assert that our critique of the selfishness axiom is redundant in view of the fact that it has already been widely rejected on the basis of existing studies. Krupp et al., for example, state that "the Ultimatum Game had already debunked *Homo economicus* before anyone took it overseas." But the selfishness axiom, vis-à-vis the human species, *could not* possibly have been universally rejected on scientific grounds, since no one has executed a research plan that captured a sufficient diversity of human societies to substantiate such a claim. So, if many in the social sciences did in fact believe that the selfishness axiom had long been rejected, they did so with *insufficient evidence*. Burnham & Kurzban, for example, note the long history of research on the selfishness axiom, but they cite only work *with students* from industrialized societies. The value of "going overseas" is underscored by Krupp et al.'s observation of the number of times cross-cultural work has forced psychologists to retract universalist claims.[2]

Moreover, the selfishness axiom does survive across the human sciences and, seemingly among commentators **E. A. Smith**, **Binmore**, **Sullivan & Lyle**, and **Burnham & Kurzban**. Each argues that some combination of selfish preferences and faulty beliefs about the game can explain the results of the behavioral experiments (undertaken by us and others) that, in our view, provide evidence against the selfishness axiom. We will discuss the empirical challenges to this view further on.

The selfishness axiom certainly survives in economics, as any undergraduate economics student will confirm. Although the rational actor model that provides abstract theoretical foundations for economics does not require the selfishness axiom, it is consistently and routinely deployed in textbooks and journal articles without comment or justification. What could be greater evidence of an implicit ingrained axiom, than the fact that a major assumption about the nature of human motivations is so often omitted from a field which otherwise specifies each mathematical assumption with such great precision? Such an omission has not always been in fashion. In 1881, a founder of the neoclassical paradigm, F. Y. Edgeworth, wrote: "The first principle of economics is that every agent is actuated only by self-interest" (cited in Bowles 2004, p. 96). In the years since, this assumption has been routinely deployed in the general equilibrium model and influential applications, like financial markets and life-cycle savings. The Fundamental Theorem of Welfare Economics depends in a deep manner on self-regarding preferences. Without a set of preferences, economic theory cannot make predictions. So economists must assume something in addition to consistency. The routine assumption is that preferences are selfish.

Our critique of the selfishness axiom is not based on the view that those motivated by other regarding preferences are behaving *irrationally* (though some – **Yamagishi**, for example – describe deviations from the selfishness axiom in this way). As is standard in decision theory (and in the preferences, beliefs, and constraints approach), we use the term

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rationality to mean consistency of behavior *without any attribution of selfishness*. Therefore, our findings do not bear on "rationality" per se, but rather on the importance of, and between-group variation in, other-regarding or non-selfish preferences. People can be rational and still care about equity, or care about others. Indeed, preferences for fairness appear to have a high degree of consistency, responding to changes in prices and budget constraints as other types of preferences do, satisfying the Generalized Axiom of Revealed Preference (Andreoni & Miller 2002; Andreoni et al. 2003).

R1.2. What people bring into the experiment

Within the preferences, beliefs, and constraints model, individuals must bring beliefs and preferences to any decision-making situation; otherwise there could be no choice at all. Preferences specify how people rank outcomes, and beliefs specify how choices are mapped onto outcomes. Since peoples' psychology develops through the interaction of their genetic endowment and their environment, all preferences and beliefs are necessarily acquired in the "real world." Of course, people also form beliefs in response to the local conditions that surround any particular decision. Hence, we assume that people have preferences when they come into the game situation. They could be money maximizers, or they could prefer outcomes that place a positive value on the payoff of others, or they could have a taste for reciprocal behavior. But they must arrive with some preferences, which were at least partially constructed while growing up and living in a particular social and economic environment. Subjects also have to form beliefs about the experiment: Is the experimenter telling the truth? Will taking the money harm the experimenter? Will choices affect their reputations within their village? Subjects' inferences about these questions will certainly be affected by the beliefs that they bring to the experiment.

E. A. Smith is thus correct in asserting that experimental subjects bring what they have learned to the experimental setting. Indeed, among our findings, some of the most intriguing ones concern this process. But Smith's objection would have the most force if subjects failed to distinguish between the experimental situation and their natural social interactions. That is, can subjects adjust their beliefs to approximate the experimental reality? If not, they might, for example, act cooperatively in an experiment because they believed that non-cooperative acts would be punished in subsequent interactions (as they might be in a natural setting), and not as an expression of other-regarding preferences in a one-shot game. It is impossible to eliminate the latter possibility, but we believe that subjects' inferences are clearly affected by the reality of the experimental situation itself, for a number of reasons. In our studies, subjects' choices *were actually* anonymous, and could not affect their reputations with other locals. Every effort was made to provide cues that would lead subjects to recognize this reality. In most of the societies studied, subjects had developed a long-term relationship with the ethnographer and knew that he or she could be trusted. The structure of the experimental situation also made it as clear as possible that only the experimenter could find out what choices people made in the game. Since we expect that people will be good at making accurate inferences about these conditions (because of the nature of both our ancestral environments and daily life; see more on this below, contra **Heintz**), especially when significant resources are at stake, it is plausible that many, if not most, subjects made their choices knowing that their reputations would not be affected.

Thus, **E. A. Smith**'s claim that our explanatory proposals are "inconsistent" results from a failure to recognize the difference between preferences and beliefs in our model. We argued that preferences are influenced by learning and experience in growing up in a particular place, but that individuals retain an ability to adjust their beliefs to reality. This is consistent with the usual application of the preference, beliefs and constraints approach.

Moreover, **E. A. Smith**'s argument, interpreted within the preference, beliefs and constraints model, could be taken as arguing that preferences remain selfish, uninfluenced by learning or experience, while beliefs respond to life experience over years, but cannot readily adjust to the immediate decision situation. This approach suggests that certain aspects of belief formation are "cognitively impenetrable" psychological processes that lead people to behave as if they believed that their choices would affect reputations (**V. L. Smith**, **Heintz**, **Krupp et al.**, **Sullivan & Lyle**), and that this influence explains all the observed prosociality among non-relatives. But this interpretation of the source of their behavior is hard to reconcile *with the variation in offers cross-culturally* (analyses reviewed in section R2), with existing laboratory data from behavioral economics, and with our knowledge of human ancestral environments (Fehr & Henrich 2003). We address this at greater length in our discussion of non-cultural evolutionary approaches in section R2.1.

R1.3. Heuristic and behavioral game theory

Some commentators from psychology – **Gigerenzer & Gigerenzer**, **Fantino**, **Stolarz-Fantino**, **& Kennelly** [**Fantino et al.**], **Yamagishi**, and **Krupp et al.** – prefer an alternative conceptualization of decision-making to our preferences, beliefs, and constraints framework. Gigerenzer & Gigerenzer call theirs "adaptive tools" or "fast and frugal heuristics"; Yamagishi proposes a "social exchange" module; and Krupp et al. like "decision rules." We certainly appreciate the value of studying animal (including human) cognition in terms of heuristics and algorithms (*sensu* Herbert Simon). We are sympathetic to the views of these commentators and do not believe that our experiments provide (or could possibly have provided) telling evidence for the superiority of our decision-making framework over theirs. Moreover, we do not see these frameworks as true alternative conceptualizations, but rather as alternative descriptive languages. Often, a well-specified heuristic, module, or decision rule can be readily translated into the preferences, beliefs, and constraints framework. Contextually specific preferences, stochastic choice formulations, bounded degrees of induction, and biased belief formation can often express the essential behavior of heuristics (modules, etc.), while adding useful quantitative rigor in a flexible framework (e.g., **Ainslie**).

For example, **Gigerenzer & Gigerenzer** mention the "tit-for-tat" strategy in a repeated game, which can be heuristically described as "cooperate first and then do whatever the other person does." Tit-for-tat is readily translated as a strategy which satisfies preferences for earning

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current and future rewards in the face of constraints imposed by repeated play, fully reflecting the perceived costs, benefits, and time horizon of future interaction.[3] All this "rationality" can be biased and bounded in theoretically precise ways that facilitate falsification. Indeed, Gigerenzer and his research group have demonstrated that many heuristics (including their successful Take-The-Best) can be written as general linear models (Gigerenzer et al. 1999; see also Martignon et al. 2003). Similarly, as alternatives to the "other-regarding preferences" view that we favor, **Yamagishi** makes two eminently plausible suggestions for interpreting our findings. The first suggestion, that heuristics are activated, parallels Gigerenzer & Gigerenzer's suggestion; the second, that cues activate a social exchange module, could be captured with context-specific preferences.[4] Given that it has already been shown that the *same* cues have different effects in different populations, if Yamagishi's "social exchange" module is conceptualized as context-specific preferences, it would necessarily result in between-group differences in behavior. Of course, in the end, it may well be that some empirically important heuristics or modules cannot be readily translated into the preferences, beliefs, and constraints framework. But, for the moment, we would like to pursue our current project of enriching the preferences, beliefs, and constraints framework to take account of the insights offered by the heuristic approach. A parallel, valuable project is to extend the heuristic approach to capture some of the key features of the preferences, beliefs, and constraints approach, such as intentionality.

We are inclined toward the preferences, beliefs, and constraints framework as represented by behavioral game theory, because a proper theory should:

1. Make quantitative predictions about how individuals and populations will respond to changes in a specific experimental setup (after calibration in a population). For example, what happens if the benefit-to-cost ratio is doubled, or subjects are told the game will be repeated (e.g., Fischbacher et al. 2002)? A good theory should make precise predictions about how behavior responds to such changes.
2. Make quantitative predictions across experiments, within a population. A researcher should be able to use one set of experiments to estimate the distribution of some aspect of preferences or beliefs in a population, develop a new experiment, and, using estimates as input, make quantitative predictions about what new subjects will do in aggregate, or the same subjects individually (e.g., Fehr & Schmidt 1999).
3. Provide a framework for quantitatively comparing individuals and populations in a manner that abstracts from the details of any particular experiment. (Phase II of our current project is endeavoring to accomplish this.)
4. Capture the dynamics of learning when the same game is played repeatedly (Camerer & Ho 1999).

We understand that the preferences, beliefs, and constraints approach does not provide a detailed description of real psychological processes,[5] but we prefer an approximation that is useful because it is easily formalized and, when suitably amended to take account of what we know empirically from experiments, seems to predict much real world behavior. If clearly specified general theories of adaptive heuristics and/or modules turn out to deliver on the abovementioned four requirements better than the preferences, beliefs, and constraints framework can, we will change our view. Or, more likely, a synthesis of the best parts of both approaches will emerge.

R1.4. Orthodox economics

Binmore says that the target article as well as our book, *Foundations of Human Sociality*, are "largely . . . devoted to claiming that 'economic man' is an experimental failure that needs to be replaced by an alternative paradigm." While some of the other commentators here do make such a broad claim, we do not. There is no doubt that self-interest is an important human motive, and that in "market-like" experiments (e.g., several agents competing for contracts, with limited or no ability to behave strategically, and limited or no direct interaction of subjects), the self-regarding actor model is well supported. However, in strategic interaction settings lacking this level of market anonymity and competition, the orthodox model predicts less well. We do not advocate – as Binmore fears – throwing out game theory or self-interest. Our moderate views on the appropriate behavioral foundations for social science are clearly laid out in: Gintis (2000) for game theory; Bowles (2004) for the preferences, beliefs, and constraints framework applied microeconomics; Camerer (2003) for behavioral game theory; Richerson and Boyd (2005) for gene-culture coevolution; and Henrich and Henrich (in press) for coevolutionary theory's application to the problem of cooperation.

Binmore worries that our results (and those of all other one-shot games) are due to "inexperienced subjects" and claims that "there is a huge literature which shows that adequately rewarded laboratory subjects learn to play income-maximizing Nash equilibria in a wide variety of games." It is certainly true that in many games, repeated play guides behavior in the direction of Nash equilibrium, often surprisingly rapidly. But repetition and experience do not generally lead to persistent income-maximizing play in games that involve other-regarding preferences, such as the ultimatum game (Abbink et al. 2001; Camerer 2003; Roth et al. 1991).[6]

Instead of using the ultimatum game, which is our primary focus, **Binmore** defends his learning claim by noting the well-known fact that in the public goods game subjects typically begin by contributing an average of half of their endowment, but finish, after 10 or so rounds, with about 90% of subjects entirely free-riding. This pattern is clearly a change in behavior over time, but it may not reflect learning (in the sense that subjects come to understand the game and its payoffs better). Players who conditionally cooperate – that is, cooperate because they expect others to do so – can only punish non-cooperation by giving less (Kiyonari et al. 2000; Kollock 1997; Watabe et al. 1996). So a decline in cooperation could simply reflect that conditionally cooperative subjects refuse to repeatedly subsidize free-riders, which leads to a decline in overall cooperation. Thus, because social preference models predict the same kind of decline as models of pure selfish interest (with learning), the public goods game is not the right place to look for decisive evidence against social preferences.

Furthermore, the learning interpretation is undermined by a key fact: Andreoni (1988) conducted a public goods game with several groups in which, after every series of rounds, group membership is reshuffled and the game is restarted. He found that after each restart, subjects' contributions jump back up to a mean of about half of the maxi-

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mum contribution, and then once again begin to decay as the rounds progress. Surely subjects did not "unlearn'" the money-maximizing behavior between restarts. This and much additional evidence (Andreoni 1995) supports the explanation that public-spirited contributors want to retaliate against free-riders, and the only way available to them in the game is by not contributing themselves, which leads to a gradual decline. Moreover, subjects often report a punishment motive for the unraveling of cooperation retrospectively. Other evidence for our interpretation comes from Page et al. (2003).

R1.5. Nonhuman primates and other-regarding preferences

Recent experiments have greatly illuminated the social behaviors of nonhuman primates, and may eventually document behaviors consistent with strong reciprocity, inequality aversion, and the other social preferences (Hauser et al. 2003; Brosnan & de Waal 2003). However, to date, we know of no published experimental positive evidence of other-regarding preferences in nonhuman primates (contra **Lucas & Wagner**), and recent experimental work among chimpanzees using economic experiments decisively demonstrates a lack of other-regarding preferences (Silk et al. 2005). This is consistent with our culture-gene coevolutionary approach to the phenomena in humans. Of course, we are optimistic about the use of theoretical and experimental tools from behavioral economics with nonhuman primates (some of us are even running such studies at this writing), but as yet the results are not very similar to those for humans.

First, although showing that tamarins, or any other animal (such as sticklebacks), will contingently cooperate in a repeated interaction (contingent on previous cooperation) is very important, it is not evidence of other-regarding preferences in one-shot games. Economists have long ago shown that purely self-interested preferences are sufficient to explain cooperation in dyadic interactions under conditions of repeated interaction.

Second, though **Brosnan & de Waal** do demonstrate that capuchins and chimpanzees can recognize social inequity, their findings show neither inequity aversion (as it has been defined in the economic literature) nor a consistency with actual human behavior in analogous circumstances. In their work, when a primate (either a capuchin monkey or a chimpanzee) sees another primate of the same species receive a larger reward, she sometimes trashes her (lesser) reward. This behavior is plausibly interpreted as a result of anger provoked by injustice. But, since discarding her own reward, without influencing the other player's reward, increases both her inequity vis-à-vis the other primate and her relative payoff difference (on the losing side), neither "inequity aversion" or "relative payoff maximization" can explain the behavior. Further, in linking the human and nonhuman literature, rejections in the ultimatum game have mistakenly been seen to be equivalent to the "discarding the reward" observed by Brosnan & de Waal. However, in the ultimatum game, unlike in Brosnan & de Waal's experiment, by rejecting the responder not only discards her own reward, but also discards an even larger reward for the proposer. The best human comparison for the primate experiment is the "impunity game" of Bolton and Zwick (1995). This game is a closer variant of the ultimatum game in which the proposer gets her payoff whether the responder rejects or not; so a rejection harms the responder but does not harm the proposer. In the impunity game, humans rarely reject, in contrast to Brosnan's experiments with primates. So, the closest analogous human result is the opposite of the nonhuman primate finding (Henrich 2004b).

R2. Ultimate (evolutionary) explanations of beliefs and preferences

The main focus of our target article was on the experimental results, but our "Discussion" section (sect. 9) also suggested an ultimate or evolutionary explanation of the observed patterns. As a theoretical framework for explaining both the origins of other-regarding preferences and the nature of their variation among populations, we introduced the gene-culture coevolution framework and indicated how it might inform our findings. Explaining the evolutionary origins of the behaviors observed in experiments, both our own and that of others, is an immensely challenging task. At this point, we can only offer scenarios that can be shown mathematically to be formally consistent and plausible in light of what we know about the conditions of life of our ancestors. Our experiments were not intended to distinguish among alternative models, although further research might do so.

The gene-culture coevolutionary approach begins from theoretical premises quite similar to those of evolutionary psychology and behavioral ecology. Our framework, however, emphasizes the additional possibility that adaptation to rapidly shifting evolutionary environments may have favored evolved psychological mechanisms that were specialized for various forms of learning, particularly complex forms of imitation (Richerson & Boyd 2000a; Tomasello 1999). We call the action of these mechanisms *cultural learning*. The idea is that, at a certain point in our cognitive evolution, the fidelity and frequency of cultural learning increased to the point that culturally transmitted ideas, technological know-how, ethical norms, and social strategies began to cumulate, adaptively, over generations. Once this cumulative threshold is passed, selection pressures for social learning or imitation, and the requisite cognitive abilities, take off. A species crossing this threshold becomes increasingly reliant on sophisticated social learning (Boyd & Richerson 1996). The fact that humans in all societies depend upon locally adaptive, complex behaviors and knowledge that no individual could learn individually (through direct experience) in a lifetime, motivates such a theory. The suggestion by **Kenrick & Sundie** that experiments pairing kin and nonkin could be a way of more precisely identifying the causal mechanisms of the gene-culture evolutionary process, is certainly a promising direction for new research.

Building on this foundation, in which individuals can acquire aspects of their psychology (e.g., motivations, skills, knowledge) *via* cultural learning, a substantial body of theoretical work shows how gene-culture interaction can explain human prosociality more plausibly than purely genetic inheritance models. In one class of these gene-culture models, combinations of culturally transmitted cooperation and punishment can spread through a population *via* cultural group selection. This spread alters the selective social environment faced by genes, so that within-group forces fa-

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vor alleles that create components of prosociality (Boyd & Richerson 2002; Boyd et al. 2003; Henrich 2004a; Henrich & Boyd 2001). A complementary approach shows that the capacity to internalize norms can favor significant levels of altruism (Gintis 2003a). These gene-culture coevolutionary processes are hypothesized to have occurred in ancestral human populations, but it is also plausible that purely cultural evolution has been contributing to the prosociality of human behavior (and perhaps in human dispositions) more rapidly over the last 10,000 years, since the environmentally stable Holocene began (Richerson & Boyd 2000a).

An important implication of these theories is that learning mechanisms operating on payoffs derived from social interaction typically produce multiple locally stable equilibria that vary in their overall group payoffs – some equilibria are more conducive to group survival and expansion than are others (Boyd & Richerson 1992; Henrich & Boyd 2001; Young 1998). As groups at different equilibria compete militarily for command over resources and in other ways, the social groups that landed on stable equilibria with greater group benefits from prosociality will proliferate at the expense of groups stuck at less group-beneficial local equilibria. This approach therefore allows different human groups to exhibit distinct culturally evolved equilibria with differing degrees of prosociality, along with a long-term trend towards more overall cooperation and greater social complexity over the last several thousand years (Diamond 1997). Cultural group selection therefore provides a foundation for **Markman et al**.'s comment that "social structures are designed for the long-term, and punishing other members of a culture who are acting selfishly may provide the best long-term reward for members of that culture."

Since culture-gene evolution will often lead to multiple equilibria, and this can be interpreted as differing moral systems which, to participants, appear morally sound, we agree with **Machery**, **Kelly & Stich** (**Machery et al**.), who view the empirical variability we observed as evidence for "a moderate form of moral anti-realism," denying the existence of a convincing universal morality.

Lucas & Wagner were concerned that we thought other-regarding preferences resulted entirely from cultural evolution. To the contrary, our gene-culture coevolutionary approach provides a mechanism by which natural selection acting on genes could have favored the kind of social behavior that Lucas & Wagner discuss and observe in kids.

Gene-culture coevolution can explain: (1) why humans are seemingly more prosocial than would be predicted by models that ignore cultural learning; (2) how learning processes and cultural evolution can modify our motivations – within the confines of universal constraints – to generate patterns of between-group variation, and why variables like market integration and the presence of local cooperative institutions might predict between-group variation (but not within-group variation); (3) why children and adults so readily imitate altruism in anonymous interactions (as described in the target article); and (4) why people seem to have both generalized-dispositional preferences and contextually specific preferences, the details of which vary across human societies. Before discussing the alternative (non-cultural) evolutionary approaches highlighted by several commentators, we will first address claims (2) through (4) above, since doing so allows us to confront several of the commentators' concerns.

The application of a theory with learning dynamics solves what some commentators (**E. A. Smith**, **Yamagishi**) took to be a puzzling feature of our data: Why do we observe such a strong effect of market integration at the group-level, but few examples of such relationships at the individual-level, within groups? The reason could be that most people acquire most of their dispositions by imitating the dispositions of others in their group, but occasional individual experience and interaction between groups cause the distribution of attitudes within a group to adjust over time to the average level of market contact. For example, it might be that individuals who actively trade in markets tend to be considered more successful (because of wealth or language skills), causing their attitudes and dispositions to spread more rapidly (if imitation is payoff-dependent). Because the combination of learning and social interaction creates equilibria, which are characteristics of groups that cannot be reduced to accumulated individual effects, the forces creating variation *within* groups may not be the same as the forces creating variation *among* groups. Therefore, group-level variables which correlate with behavior may not bear any relation to individual-level variables.

Applying this framework to our experimental results, market integration may correlate with ultimatum game behavior because (1) contact and interaction in markets by some members of the population – via the imitation of successful or prestigious individuals – may have tipped the group into a different social equilibrium (which will affect everyone's preferences), or (2) because groups that are already at certain social equilibria may be more likely to diffuse market practices (i.e., markets may not lead to success, and thus spread, unless the group already has certain preferences and beliefs). Both of these are forms of cultural group selection that have been carefully modeled (Bowles 1998; Boyd & Richerson 2002). We agree with **Jankowiak** that we are far from having a good explanation for the fact that market integration is associated statistically with higher ultimatum game offers. He may be right in thinking (like many 18th century philosophers, including Adam Smith of "invisible hand" fame; see Ashraf et al., in press) that markets contribute to moral empathy and altruism toward strangers, but we are unaware of any very convincing evidence of this as yet.

Although our target article highlighted the predictive power of market integration and cooperative institutions, theoretical findings from gene-culture coevolution are highly consistent with **Gächter**, **Herrmann**, **& Thöni**'s (**Gächter et al**.'s) findings from Russia. Cultural evolutionary models of cooperation and punishment have shown that while punishment can stabilize cooperative behavior, it can also stabilize other norms (Boyd & Richerson 1992; Henrich & Boyd 2001). Gächter et al. confirm that people don't necessarily punish non-cooperators; instead they punish those who deviate from a group norm, even if that norm is far from cooperative or prosocial. In response to their comments, our focus on only two important dimensions of between-population variation (market integration and local cooperation) is certainly not meant to suggest there are no other important dimensions of cross-group variation, as their data helpfully illustrate.

Our focus on the possible use of various cultural learning mechanisms to adaptively acquire, modify, or hone motivations and preferences (among others things) provides an entry point for thinking about the continuum from gener-

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alized (dispositional) to contextually specific preferences. In social life, learners will always need to infer the underlying preferences or motivations from the behavior of those they want to learn from (e.g., successful people) *in specific situations*. As a hedge against the costs of overgeneralization from specific situations (leading possibly to norm violations, punishment, and exploitation), learners might make inferences that confine preferences, at least initially, to a rather narrow set of circumstances consistent with direct observation. Studies of the development of prosocial behavior show that children first learn to be prosocial, often by imitation, in specific circumstances and don't generalize this prosociality to other situations. Over time, and through repeated exposure to stimuli favoring prosociality, children expand the range of circumstances in which they apply these patterns (Eisenberg & Mussen 1989). People reared in different societies are likely to have developed generalized dispositions related to fairness and punishment (of unfairness) to differing degrees – so sometimes we are measuring more dispositional traits that have been generalized to include the ambiguous game situations, and other times we may be measuring a context-specific trait/preference that the game is mapped onto. Furthermore, as **Zizzo**'s summary of the influence of environment on neurotransmitters suggests, culture and the culturally constructed environment may have numerous neurobiological pathways into brains, especially human brains.

In market societies, for example, the use of money in the game may be sufficient to cue very general dispositions towards "fairness" in market transactions (cues of anonymity, money, and strangers may activate default norms and the associated preferences for such situations). As noted in the target article, among American children in an ultimatum game involving money, fairness emerges first, then a "taste for punishing unfairness," but neither achieves "adult levels" until age 22. So, age matters a lot for ultimatum game play in the first two decades of life (Harbaugh et al. 2002), but then matters little after that point (Henrich, in press). In small-scale societies, where the nature of daily transactions is not highly variable, people may not have any generalized prosocial dispositions that apply to "ambiguous situations involving money and strangers." When we see fair offers in these places, it may be because people were able to map the game onto a local context associated with prosocial norms (as the Orma did, linking the public goods game to *harambee*). Thus, the correlation we found between ultimatum game offers and payoffs to cooperation may arise from context-specific cueing between local institutions and the game, whereas the correlation of ultimatum game offers with aggregate market integration could arise from cuing a more generalized set of preferences, which apply to situations involving money and anonymity. Of course, our data are silent on the plausibility of these interpretations.

This brings us to **Lucas & Wagner**'s additional data on prosocial behavior in children. They note that other research, which did not use money, found different results than those we described. We defend our use of Harbaugh et al.'s data as the appropriate set of comparative developmental data because they used money as we did.[7] But we also agree entirely with commentators who thought the results might have been different if payoffs were in a currency other than money, such as tobacco (in the case of Lamalera), honey, or meat. Given the manner in which preferences emerge, different exchange mediums could certainly evoke different preferences, with different developmental trajectories. Children may first attach prosocial preferences to food because this is an early and frequent context in which kids observe prosocial behaviors by others.

The same line of thinking about developmental process and preference formation may help explain the pattern of rejections across societies. If people from a society mapped the game structure onto a local norm (and associated preferences) that called for the punishment of norm violations, responders would be likely to reject inappropriate offers. But if the game could not be readily linked to some context, people's decisions could be biased towards accepting whatever they were offered (without a norm to direct motivation, why give up free money?). This would explain the prevalence of groups that were unwilling to reject low offers (no norm mappings), and sheds light on the Au and Gnau's surprising tendency to reject offers that were *both* too high and too low. (In fact, the tendency to reject offers that are "too high" turns up in many other places in our more recent, as yet unpublished, work.)

This line of thinking may also illuminate the relationship that we observed between within-group variation in the ultimatum game (the standard deviation in ultimatum game offer for each group) and market integration, which are correlated -0.75 ($p = 0.0003$). Groups with less market integration were less able to consistently map the game onto a specific context, leading to a larger variance in offers in those groups.

Our findings do not provide strong support for either dispositional or contextually specific preferences. Post-game debriefings provided mixed insights as to whether "dispositions" or "contexts" were driving players' motivations. Despite efforts by many of the ethnographers, most participants did not spontaneously and clearly see the games as linked to a real life context. Whatever subjects were bringing into the game situation, a consciously accessible mapping between the game and a real life context was not common (of course, this mapping might occur unconsciously, in a manner that was not accessible even upon reflection). But it did exist in some cases, as the Orma analogizing our public goods game to their *harambee* showed.

R2.1. Non-cultural evolutionary approaches

If the game payoffs contribute to fitness, a fitness maximizer should never reject a positive offer in the one-shot anonymous ultimatum game. If our fitness maximizer is the proposer and she knew that the respondent is also a fitness maximizer, she should offer the smallest positive amount possible, knowing that the fitness-maximizing respondent will accept any positive offer. This *simple* fitness maximizing prediction is not supported in any society. Thus, our work provides an empirical challenge to evolutionary theory.

Many feel there is an immediate answer to this challenge: These apparent anomalies can be explained as the byproduct of selection in ancestral environments. This line of argument comes in two versions. One version emphasizes *preferences* and the second emphasizes *beliefs*. Both versions share a common opening: Natural selection faces constraints in constructing brains – even human ones – and we cannot expect individuals to make fitness-maximizing decisions in every case, especially in such artificial laboratory circumstances. In dealing with these constraints, the argument goes, natural selection should use the reliable features

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of ancestral human societies to build in assumptions to calibrate our motivations and perceptions of the world (Johnson et at. 2003; Nowak et al. 2000).[8]

The belief version goes on to suggest that there may be certain assumptions built-in to our cognitive processing of social dilemmas that leads members of our species to systematically misunderstand (or disbelieve) some aspect of the experimental game. For example, if life in ancestral societies lacked fitness-relevant low-frequency interactions (like one-shot games), selection might have built human brains to default to the assumption that all interactions are repeated or reputational (Samuelson 2001). But people clearly are more prosocial in experiments with repeated interaction or reputation, vis-à-vis one-shot games (e.g., Camerer & Weigelt 1988). So the problem cannot lie in the inability to tell a one-shot game from a repeated interaction; the problem must be an inability to properly calibrate one's belief about the likelihood of reputational consequences all the way to zero (Fehr & Fischbacher 2003; Fehr & Henrich 2003; Fehr et al. 2002). This is the aforementioned "cognitive impenetrability" argument.

The preference version of this argument is very similar, except it asserts that natural selection built other-regarding preferences into our motivational system, perhaps to avoid making costly errors or as a short-cut heuristic device to save on information processing (**Heintz**), rather than operating through belief calibration.

There are two problems with this response to our work. First, these hypotheses proceed from factual assumptions about the nature of human ancestral environments, which, to our knowledge, have never been empirically scrutinized. Fehr and Henrich (2003) provide some (however limited) evidence from nonhuman primates, paleoanthropology, and foraging populations suggesting that "low-frequency fitness-relevant" interactions were important. If ancestral environments did have such interactions, natural selection should have calibrated our psychology to handle them – and the prediction might be that people accurately calibrate their beliefs and preferences to the game context. Furthermore, a general capacity to distinguish decisions with short-run and long-run consequences (e.g., fishing versus building shelter) surely developed in nonstrategic domains, and that capacity would only need a few add-ons to be part of a general neural circuit to successfully distinguish one-shot and reputational strategic interactions with other humans.

Second, even if this canonical view of ancestral environments is accurate, recent modeling work exploring the emergence of cooperation via reciprocity has, for the first time, explicitly addressed the issue of whether the logic of reciprocal altruism will lead individuals to cooperate broadly, with any member of their group (as the above hypothesis requires), or only with their preferred partners (Hruschka & Henrich, in press). The findings are decisive: direct reciprocity does *not* predict some generalized prosociality towards other members of one's group. Instead, it predicts defection on most individuals in one's group, and only cooperation with a select set of partners. This runs directly counter to **Heintz**'s claim about strategies of "niceness."[9]

Our empirical findings present another challenge for these hypotheses. If humans, as a species, are generally geared to "assume" repeated interaction, and therefore offer 50/50 and reject low offers, why are there so many groups with few rejections of low offers? In a repeated ultimatum game, especially one with a long time horizon, individuals should reject low offers (Page 2000). If *Homo sapiens* cannot "understand" a one-shot game (because of their programming in ancestral environments), and preferences or beliefs automatically anticipate repeated interactions or reputational effects, responders should always reject low offers – *but subjects from many societies rarely do*. Moreover, some of the societies which generally don't reject low offers are considered to be much more similar to the conditions associated with ancestral human environments than other societies with high rejection rates. These societies should be more likely to impute a reputational or repeated interpretation to the game. We found the opposite.

Recent findings among chimpanzees using experimental games add a third puzzle for these hypotheses. Chimpanzees live in, and likely evolved in, small groups that interact frequently, and observational studies show evidence consistent with reciprocal altruism. However, in one-shot experiments, chimpanzees behave in a manner consistent with pure self-interest (Silk et al. 2005). So, despite their ancestral past and reliance on reciprocity, chimpanzees appear to have retained the ability to readily calibrate their beliefs to a one-shot game, while humans – under this hypothesis – apparently have not.

Since word of the variation in ultimatum game behavior observed in our project spread, new versions of this argument have emerged, based on the canonical evolutionary model. These arguments suggest that human minds should be selected to be sensitive to certain kinds of "contextual cues," and in particular, those that would have been essential to adaptively negotiating social life and managing reputation (Nowak et al. 2000) in our ancestral environments (**Krupp et al**., **Burnham & Kurzban**). Some examples might involve (1) the apparent degree of anonymity and possibilities for repeated interaction, (2) status differences, (3) property rights, and (4) signaling opportunities. Such suggestions are consistent with some experimental findings from students (Haley & Fessler 2005; Hoffman et al. 1994; Hoffman et al. 1998).

With this kind of context sensitivity potentially built into our evolved cognition, some have hypothesized that minor methodological variations across the experimental sites might have inadvertently cued universal human sensitivities to context, resulting in the group-level variation.

There are both theoretical shortcomings and empirical obstacles to consider in judging whether this argument can fully explain our results. Theoretically, this interpretation is underspecified in its current form. A good theory should delineate what contextual variations (and corresponding methodological modifications) will produce what changes in behavior. With such a specification, we could actually test to see if our methodological variations predict the differences in behavior – and thereby provide evidence concerning this hypothesis.

Empirically, four lines of evidence are inconsistent with this idea. First, as we explained in the target article and will return to in this response, the methodological variations that occurred across our work have not been shown to have important effects in the cases where they have been carefully tested, and do not appear to explain the variation across our sites. Several subsets of our data, in which neither the experimenters nor the protocols were varied, still showed substantial variation between groups.

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Second, it is difficult to see how the correlation with market integration and payoffs to cooperation might be explained from the view that all cross-group variation is due to methodological variation.

Third, suppose our evolved cognition is sensitive to the local intensity of repeated interaction and reputational consequences (and, say, the paucity of one-shots). Now, in most of the small-scale societies, individuals interact all the time in small groups and have intense reputational effects, compared to most Western groups and student populations. The evolved cognition hypothesis therefore predicts *more* rejections in small-scale societies, and *fewer* rejections in developed sites. But rejection rates are quite low in many of the small-scale societies. Furthermore, even across the small-scale societies, there is substantial variation in the measures that might covary inversely with the intensity of reputation and repeated interaction (complexity, market integration, privacy, anonymous roles, settlement size). These variables are either *positively* correlated with mean ultimatum game offers, or bear no relationship. None of these variables produces the negative correlation between offers and repeated interaction frequency that the evolved cognition hypothesis predicts.[10]

Fourth, an ongoing Phase II of this project has largely eliminated methodological variation across sites and arrived at very similar findings for the ultimatum game, both within and across sites. This replication is powerful in two ways. First, we still obtain the same degree and patterns of variation between groups. Second, researchers redoing the ultimatum game among the populations, now using modified protocols which are more uniform across sites, still get the same answers. Thus, the results are replicated despite the difference between our first and second protocols.

R2.2. What do the canonical evolutionary models actually predict?

Several commentators (**E. A. Smith**, **Krupp et. al.**, **Sullivan & Lyle**, **Lucas & Wagner**) have quite a different notion of what the extensive body of formal models from evolutionary biology actually tells us about cooperation based on reciprocity and reputations than we do. In reciprocity models with repeated direct interactions, cooperation is unlikely to emerge if the size of cooperative groups is even moderately large (Boyd & Richerson 1988; Joshi 1987). Reputation-based cooperation in large groups – in which a defector's reputation is broadcasted widely to others with whom the defector did not interact directly – depend critically on high fidelity information about past behavior (Brandt & Sigmund 2004; Leimar & Hammerstein 2001; Mohtashemi & Mui 2003; Panchanathan & Boyd 2003). Panchanathan and Boyd show that if reputational information is even moderately noisy, or moderately unavailable (i.e., there is moderate anonymity), individuals should defect. Together, these acultural models suggest that natural selection acting in ancestral environments should have shaped our psychology in a manner that *immunized us* from cooperating in many of the real world and laboratory circumstances that we do cooperate in.

One of the larger problems we see in the interpretation of the work coming from evolutionary biology is the insufficient attention given to the issue of multiple stable equilibria. **E. A. Smith**'s commentary (see also **Burnham & Kurzban**), for example, claims that behaviors "that sacrifice short-turn self-interest can be shown to be favored in various evolutionary regimes."[11] However, the formal models themselves show that the emergence of cooperation is but *one possible equilibrium* (Gintis et al. 2001; Panchanathan & Boyd 2004). E. A. Smith's joint work with Gintis and Bowles nicely illustrates this: it shows that any behavior that provides an honest signal of certain underlying qualities can be maintained – it need not have anything to do with cooperation or altruism (in fact, the signal can be wasteful, extravagant, and reduce a group's overall payoff; beating up one's neighbor is as good a demonstration of prowess in combat as warding off the enemy). Similarly, the Panchanathan and Boyd model shows that linking reputation to both a dyadic "helping game" and to an *n-person* interaction can create a stable cooperative outcome, in which people cooperate in both games. However, the model also shows that *n*-person interaction need not be a cooperative interaction: reputation can potentially stabilize *any behavior* in the *n*-person game, even behavior that reduces the group's overall payoff. Without specifying an *equilibrium selection mechanism*, these models are incomplete.

There is clearly variability in "costly signals" (turtle hunting in some places, alligator wrestling and mountain climbing in others) and in "what goes into a good reputation" across human societies. Models of culture-gene evolutionary processes produce such variation naturally. Cultural evolution can "experiment" with many stable equilibria, involving different costly signals and different ingredients for reputations. Cultural group selection can then favor those equilibria that provide the most group beneficial properties (it can build the observed link between costly signals and "providing group benefits"). Overall, this approach yields (1) an equilibrium selection mechanism that delivers more cooperative equilibria, (2) an explanation as to why the human species seems to have so many different kinds of costly signals and kinds of reputation, and (3) a mechanism for explaining the nature of the variation in costly signals and reputations – why do costly signals, for example, vary mostly between social groups (and much less within).

R3. Methodological concerns

R3.1. Protocols, anonymity, and the three-body problems

This brings us to **V. L. Smith**'s methodological concern, which we and many of the commentators share: While the payoff and rules of the game were held as constant as we could hold them across sites, the game as understood and experienced by our subjects must have varied from site to site. For obvious reasons we cannot offer decisive evidence that these differences had little effect on our results; but on balance we do not think that they explain the main findings as summarized in our target article.

Sosis suggests that our methods vary in a manner that explains the variation. But his Table I leaves out our UCLA student control group, which had a high mean offer at 48%, but no corralling and only individual instruction. Adding UCLA to Sosis's table substantially shifts the balance. This table also disguises the fact that the Machiguenga experiment was done with half the sample using "corralling with talking" (but not about the game) and half using "instructions to individuals" only. These conditions produced no difference in behavior. The UCLA and Machiguenga stud-

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ies provide controls at both ends of the offer spectrum and suggest that these differences do not dramatically influence the results. Finally, most of us did post-game interviews as Sosis did. However, unlike Sosis, we did not find players across sites with low offers or few rejections explaining that they did this because they wanted compensation for their time investment.

Gigerenzer & Gigerenzer suggest that subjects could have perceived the experimenter as a third player in the game, and that the presence of the experimenter may have had more influence than in university experiments. Ethnographers are even more acutely aware, than are experimental social scientists who interact with undergraduate subjects, of how the relationship between subject and experimenter could influence subjects' behavior. We worried mightily about this issue from the earliest stages of the project and offer three lines of evidence indicating the "three-body problem" is probably less severe in anthropological settings than in university laboratories.

First, as explained in the target article, an "experimenter experience" variable (the number of months the experimenter had spent at that field site prior to administering the game, ranging from 1 to 75 months) was *not* a significant predictor of between-group variation in mean offers, standard deviations, or responder rejections. Whatever influence the experimenter has does not correlate with the group's exposure to the experimenter.

Second, given the close relationship between subjects in small-scale societies and experimenters (compared to the relationships in university experiments), one might expect that offers (and perhaps rejections) would have increased, as subjects strive to impress the more influential experimenter with the subject's sense of equity or willingness to drive a hard bargain. Contrary to this conjecture, subjects in small-scale societies offered less, and rejected less frequently, than most student groups.

Third, among the Mapuche in Chile, Henrich explored experimenter effects by using four different experimenters (using a Prisoner's Dilemma Game), three locals from two ethnic groups, and one anthropologist (JH). Using a male experimenter from the Mapuche ethnic group as the point of reference for experimenter effects (in a multivariate regression), the sole anthropologist did *not influence* the chances of a Mapuche cooperating. However, when the experimenter was of a different, *locally salient*, ethnic group (a non-Mapuche Chilean) *and* male, the Mapuche cooperated less. It seems that local subjects are more concerned with how they might appear in front of some locals, within their social system of status and obligations, than they are about the anthropologist, who stands well outside their system. Further confirming this minimal outside-experimenter effect, Henrich and Smith (2004) also compared a single and a double-blind public good game protocol among the Mapuche, and found no additional influence of the double-blind treatment. In several societies, our post-game interviews and ad-hoc discussions with players and local assistants after the game also revealed nothing that suggested an experimenter effect, except in the case of Gil-White's Mongolian work (Gil-White [2004] responded in the best possible way – empirically – by simply redoing his experiment to clarify his position vis-à-vis the money).

The best evidence that methodological variation across sites does not explain our central findings comes from a second phase of the cross-cultural games project, using many of the same societies, along with some new field sites. In this second project, we eliminated many sources of methodological variation by using (1) identical procedures across sites (e.g., uniformly corralling subjects and paying show-up fees), (2) a standardized game script (which was back-translated for each site for linguistic comparability), and (3) more tightly controlled stakes, involving only money. The results for ultimatum game offers across sites from this second phase are strikingly similar to the original results reported in our target article, with mean offers ranging from 25% to 51%. In sites such as the Hadza and Tsimane, where the most different procedures were used in Phase I, the more uniform Phase II experimental data look very much like the Phase I data; so the Phase I differences in procedures did not substantially affect the results. The widespread replication in Phase II gives the best possible assurance that the methodological variations described in the target article (and noted by **Sosis** and others) are not driving the between-group variation found in Phase I.

The Phase II results also address the three-body concern of **Gigerenzer & Gigerenzer**. In Phase II, we included four sets of double-blind dictator games, including one among U.S adults (non-students) from a small town in rural Missouri. Of these four data sets, the double-blind treatment matters only in the single U.S. group, and the effect size was much smaller than observed for the same treatment among university students (Cardenas 2005; Ensminger 2005; Lesorogol 2005a). These findings suggest that the differences between small-scale societies and students are not to be primarily explained by the three-body problem, though of course, three-body effects could exist in many other populations or protocols.[12]

Sullivan & Lyle questioned the effect of player-player anonymity, emphasizing that the imperfectness of the anonymity might have influenced play. First, weakening anonymity is typically thought to promote prosocial behavior, but the lower offers in most of the small-scale societies, compared to students (particularly the UCLA control) suggest the opposite effect. Second, among the Machiguenga (Henrich and Smith) and Ache (Hill and Gurven) player-player anonymity was manipulated using a public and private version of the public goods game and little or no effect was found (Henrich & Smith 2004; Hill & Gurven 2004). These results suggest that anonymity may matter to different degrees in the different places. So far, it appears that anonymity may matter less (not more) in populations from non-industrialized countries. Sullivan & Lyle also propose, despite the anonymity in the game, that relative status in the community may influence offers. We too suspect that in some societies people of different statuses might play differently when anonymity is relaxed (or if subjects don't believe that the game is anonymous). However, in most small-scale societies, higher status is highly correlated with age and male gender. The fact that age, sex, and age-times-sex interactions have little effect on offers and rejections indicate that these status effects are unlikely to have been an important force in our findings. Phase II made an even more explicitly study of status; thus far, no striking within-group status effects have emerged.

R3.2. Contextual effects in experiments

As we noted in the target article, one of the problems with discussing the importance of "context" in experimental

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games is that context effects are large in some games and small in others. We were keenly aware of potential contextual effects early in the design process. We decided to focus on the ultimatum game *precisely because* it had been shown to be more resistant to easy contextual manipulation than, for example, the dictator game – which is well known to be the most susceptible to framing effects.

Despite our deliberate choice of ultimatum rather than dictator game, several commentators nonetheless pointed to experiments involving dictator games, and in particular to Haley and Fessler's recent paper (**E. A. Smith**, **Sullivan & Lyle**, **Burnham & Kurzban**). Haley and Fessler (2005) manipulated two possible cues of anonymity in the dictator game (*not* in the ultimatum game). One treatment involved the presence of "eyes" on the gaming screen (cue of less anonymity). The other treatment required subjects to wear noise-reducing ear muffs (cue of more anonymity). Haley and Fessler found that one of their cues affected offers. We find the results plausible and not at all inconsistent with our views. The eyes may have indicated that moral behavior is appropriate in this situation, rather than that this is an opportunity to establish a reputation for morality. Moreover, this result, even if interpreted as a reputation effect, in no way contradicts our view: we of course accept the idea that forming reputations may affect behavior, sometimes in prosocial ways (Fehr & Fischbacher 2003); what we contest is the claim that *all* of the seemingly prosocial behavior in the experiments can be attributed to reputation building.

An important issue is also the *size* of any context effect (not just its statistical significance). A statistical regression of Haley and Fessler's data showed that "the presence of eyes" increased offers by 83 cents (out of a $10 stake). Wearing ear muffs decreased offers by 63 cents.[13] These effects are, in fact, the same size or smaller than other framing effects (e.g., Eckel & Grossman 1996; Camerer 2003, Ch. 2), and do not seem as "dramatic" as **Sullivan & Lyle** suggest.

Haley and Fessler's hypothesis is that the presence of eyes, even highly stylized inanimate one, always cues an evolved reputational psychology. We do not find this hypothesis convincing. Presumably, as in many of the small-scale societies we lived among, there are irrelevant pairs of eyes everywhere. Rats, chickens, pigs, tapirs, monkeys, and human infants all have "eyes" which should not influence one's reputation. A mutant who reacts to just any "eyes" would presumably be selected against. Moreover, the contention that eyes always cue a reputational psychology is not consistent with the fact that ultimatum game offers among students do not differ substantially between games administered by a computer and games administered by a person. This means that the "eyes" (real eyes in this case) *in the ultimatum game* do not produce important effects. Using real eyes is presumably a more direct and powerful test than stylized eyes. These concerns also apply to **Burnham & Kurzban**'s claims about "eyes," and the weak effects of robot eyes on game play they cite.

A much higher-level effect of context comes from an analysis **Grace & Kemp** report in their commentary. They correlate measures of public spending on health and pensions (as a fraction of gross domestic product) with ultimatum offers and rejections across studies in different countries, using Oosterbeek et al.'s (2004) meta-analysis data. Higher public spending correlates with more rejections and with lower offers. Grace & Kemp suggest that responders in high-spending countries expect some equity (and hence reject low offers), but proposers expect the state to provide (and hence offer less). These intriguing findings suggest the value of using experimental data to study behavior at many levels, from the societies we studied to the national level (where a wide variety of statistics are often readily available).

Heintz proposes that our experiments lack ethnography. However, many of us applaud or have fully engaged the program Heintz suggests (combining "multivariate analysis" with qualitative ethnography), as presented in Henrich et al. (2004), and in other venues where we link to economic anthropology (Ensminger 2002; Henrich 2002; Tracer 2003).

R4. Conclusion

As some commentators suggested (e.g., **Ostrom**, **Caporael**), the project of understanding the nature of human sociality depends on the integration of theories and methods from across the human sciences. Data must come from the entire range of human societies and social roles within them, as well as from nonhuman primates and other relevant species (e.g., cetaceans). Methods must integrate meticulous field observations with experiments as well as physiological measures. Both evolutionary theory and proximate psychological or behavioral theories need to continue to press towards increasingly rigorous formalizations, which facilitate testing, model comparison, and the assessment of both individual and population level heterogeneity (**Davies**), while sticking closely to the incoming empirical findings.

Despite lingering disciplinary prejudices in many academic institutions, this project is already well advanced, in part by the important research of many of our commentators. We are grateful for this opportunity to join with them and with our readers in facing these challenges.

NOTES

1. It is notable that the phrase "straw man" was used by **Krupp et al**. to argue that *Homo economicus* is long dead, and it is also used by **Binmore** to argue that *Homo economicus* is actually healthy and robust. The fact that such prestigious commentators can't agree on the state of health of *Homo economicus* is inconsistent with the assertion that we manufactured a straw man.

2. Some readers may have gotten the impression that economists had not done any cross-cultural work prior to our project from **Krupp et al**.'s statement that, "Any experimental economist implicitly operating on the premise that American undergraduates are representative of humankind must feel chastened. To some extent, this is *déjà vu* for psychologists, who have repeatedly seen cross-cultural studies complicate simple views of human nature." To clarify: The first ultimatum game (Güth et al. 1982) was done in Germany, and the literature jointly emerged from the U.S. and Europe. Within a decade, Roth et al. (1991) had done a good comparative study among students from Pittsburgh, Jerusalem, Ljubljana, and Tokyo showing little variation in offers. Then, and still before our project, a 1996 working paper appeared by Lisa Cameron using students and faculty in Indonesia (Yogyakarata), which also showed little variation in offers from previous studies (Cameron 1999).

3. In a roughly similar way, **Ainslie** sees ultimatum game offers and responses as heuristic byproducts of evolved emotions (like proposer guilt), or reflecting "self-signaling" (e.g., responders reject to convince themselves they are not meek).

4. Note that the broadest interpretation allows preferences to

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depend on "states" – just as the taste for food depends on hunger. Many kinds of context dependence can be interpreted as state-dependence. Others depend on cognitive or perceptual interpretations of rewards or their value ("framing").

5. Neurobiologists could rightly argue that heuristics do not provide accurate descriptions of psychological processes, but progress in neuroeconomics is closing the gap between abstract reduced-form descriptions and neural detail (e.g., Camerer et al. 2005).

6. We note that if players in the ultimatum game are income-maximizers, and if each knows the other is an income-maximizer, then the unique subgame perfect equilibrium requires the responder to accept any positive amount and the proposer to offer the minimum possible amount. Although this is uncontroversial, **Binmore** notes that there are other Nash equilibria of the game which are not subgame perfect but are compatible with self-interest – e.g., the proposer could offer half because she fears (mistakenly) that the responder would reject anything less. However, this sort of "incredible threat" – a threat or fear that will not be carried out if tested – is precisely what subgame perfection was designed to rule out, mathematically. The weaker set of Nash equilibria Binmore refers to also includes all possible offers – so the Nash equilibrium offer prediction can never be falsified by offer data. However, in any Nash equilibrium, there should be no rejections; so rejections cast doubt on the weaker Nash equilibrium account. Furthermore, even in the Nash equilibrium analysis, if players occasionally make errors, then the minimal-offer prediction is the only equilibrium.

7. We are less enthusiastic about the result on empathy discussed by **Lucas & Wagner**. Empathy should not be conflated with other-regarding preferences, since empathy is possibly an excellent tool for a fully self-interested individual to figure out how to manipulate conspecifics.

8. Price et al. (2002) have suggested that individuals *should* reject in the ultimatum game because they are really trying to maximize their fitness *relative* to the proposer. This suggestion is flawed because an individual who rejects a positive offer in order to eliminate their fitness deficit vis-à-vis *their* proposer will lose relative to other proposers and responders in the group who earn money. So the fitness advantage of rejection only holds if ancestral human groups were extremely small (Gintis et al. 2003; Hück & Oechssler 1999) – much smaller than any empirical data has yet suggested.

9. Heintz cites Axelrod's (1984) seminal work of two decades ago (see also Axelrod & Hamilton 1981). Substantial research since then – hundreds of papers – have modified and overturned some of Axelrod's findings (e.g., Bendor 1987; 1993; Bendor et al. 1996; Bendor et al. 1991; for a brief introduction to work since Axelrod, see Henrich & Henrich, in press: Ch. 3). In one instance of this literature, by allowing individuals to develop social networks of cooperative relationships, Hruschka and Henrich relaxed the assumption that individuals' payoffs are independent of the decisions of individuals they did not play directly and show that "niceness" (cooperate on first interaction) toward other group members is *not* a general characteristic of successful strategies in pairwise interactions (Hruschka & Henrich, in press).

10. An alternative way to think about this prediction is that those less familiar with one-shot interactions with strangers in real life may be less able to comprehend the one-shot anonymous character of the games, and hence perhaps be more likely to behave "as if" it is a repeated or reputational situation. That is, small-scale societies will offer more and reject more because they are less able to grasp the game. However, in fact, the people least familiar with one-shot, anonymous interactions are the ones who offered the least and failed to reject (ironically, coming closest to the prediction of game theory assuming selfishness).

11. Burnham & Kurzban cite models "based on signaling [. . .] or reputation" that they perceive as showing how people will modulate their behavior in response to anonymity. Their first citation for this, Smith and Bliege Bird (2000), is not a formal model. The second, Panchanthan and Boyd (2003), predicts that unless the fidelity of reputation is quite high (corresponding to essentially no anonymity), people should defect, which does not fit the experimental data at all. The third, Trivers (1971), deals with neither costly signaling nor reputation (it is about repeated interaction).

12. One reason why the experimenter might matter less in small-scale societies is that locals do not know what the anthropologist would consider a "good" offer (i.e., an offer that would cause an anthropologist to admire them). Outsiders to the field might be surprised to know that the people anthropologists study do not necessarily seek the approval of anthropologists; more often, they regard the anthropologists as mysterious or indecipherable. And you can't "please or impress the experimenter" unless you know what would please or impress him or her.

13. We used Haley and Fessler's (2005) data (which they generously supplied) in an ordinary least-squares regression predicting dictator game offers based on dummy variables for "wearing ear muffs" and "presence of eyes," in order to estimate the coefficients reported in the text.

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Letters "a" and "r" appearing before authors' initials refer to target article and response respectively.

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