

2 **The Resurrection of Group Selection as a Theory**
3 **of Human Cooperation**

4 **A Review of Foundations of Human Sociality: Economic Experi-**
5 **ments and Ethnographic Evidence from Fifteen Small-Scale**
6 **Societies, edited by J. Henrich, R. Boyd, S. Bowles, C. Camerer,**
7 **E. Fehr, & H. Gintis & Moral Sentiments and Material Interests:**
8 **The Foundations of Cooperation in Economic Life, edited by**
9 **H. Gintis, S. Bowles, R. Boyd & E. Fehr**

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14 **Abstract** Two books edited by members of the MacArthur Norms and Preferences
15 Network (an interdisciplinary group, mainly anthropologists and economists) are
16 reviewed here. These books in large part reflect a renewed interest in group selection
17 that has occurred among these researchers: they promote the theory that human
18 cooperative behavior evolved via selective processes which favored biological and/
19 or cultural group-level adaptations as opposed to individual-level adaptations. In
20 support of this theory, an impressive collection of cross-cultural data are presented
21 which suggest that participants in experimental economic games often do not behave
22 as self-interested income maximizers; this lack of self-interest is regarded as evi-
23 dence of group selection. In this review, problems with these data and with the
24 theory are discussed. On the data side, it is argued that even if a behavior seems
25 individually-maladaptive in a game context, there is no reason to believe that it
26 would have been that way in ancestral contexts, since the environments of experi-
27 mental games do not at all resemble those in which ancestral humans would have
28 interacted cooperatively. And on the theory side, it is argued that it is premature to
29 invoke group selection in order to explain human cooperation, because more par-
30 simonious individual-level theories have not yet been exhausted. In summary, these
31 books represent ambitious interdisciplinary contributions on an important topic, and
32 they include unique and useful data; however, they do not make a convincing case
33 that the evolution of human cooperation required group selection.

34 **Keywords** Evolution of cooperation · Altruism · Strong reciprocity ·
35 Experimental economics

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36 Both these books were edited by members of the Norms and Preferences
 37 Network, a MacArthur Foundation-funded group of behavioral scientists who
 38 share a strong interest in understanding the evolutionary origins of human
 39 cooperation. Over the past several years, the editors have produced a large
 40 number of publications promoting their perspective on how human cooperation
 41 evolved. The gist of this perspective is that people are more cooperative than the
 42 standard economic and evolutionary theory would predict. According to the
 43 editors, while standard theory predicts that all people will cooperate only when it
 44 is in their self-interest to do so, the truth is that many people will cooperate even
 45 when they have no chance of recovering the costs of cooperation via reciprocity
 46 or any other means. The editors somewhat confusingly term this unselfish
 47 cooperativeness “strong reciprocity,” in order to contrast it with regular
 48 reciprocity, which is what occurs when people cooperate in order to acquire
 49 return benefits from those whom they have assisted.

50 For years prior to the publication of these two volumes, the editors had been
 51 developing their empirical and theoretical case for strong reciprocity. Fehr had been
 52 especially active in making the empirical case; studies by himself and colleagues
 53 (e.g., Fehr & Gächter, 2000; Fehr & Fischbacher, 2004) suggested that a large
 54 fraction of undergraduate subjects in industrialized societies would spend their own
 55 money both to cooperatively benefit others, and to punish non-cooperators, even
 56 when there was no chance of recouping these expenditures via reciprocity.
 57 Meanwhile, on the theoretical side, Gintis, Bowles, Boyd, Henrich and other formal
 58 modelers were explaining how such strong reciprocity could evolve (e.g., Boyd,
 59 Gintis, Bowles & Richerson, 2003; Gintis, 2000). Since strong reciprocity is fitness-
 60 damaging to the individual strong reciprocator, they need to invoke some kind of
 61 selective process operating above the level of the individual. They argued, therefore,
 62 that human cooperative behavior must have evolved by biological and/or cultural
 63 group selection, and they backed up their arguments with mathematical models and
 64 computer simulations.

65 These two volumes represent recent efforts by the editors to test, extend, and
 66 apply the theory of strong reciprocity. *Foundations* is more ambitious and unusual
 67 of the two books; in order to determine whether people behave as strong
 68 reciprocators not just in college environments in industrialized societies, but also in
 69 small-scale cultures around the world, the editors enlisted a small army of
 70 anthropologists to conduct experimental economic games in 15 societies on several
 71 different continents. In addition, though *Moral Sentiments* is a more typical edited
 72 volume, consisting of invited chapters on topics related to strong reciprocity and to
 73 the origins of cooperation more generally, it is unusual in its interdisciplinary scope:
 74 contributors include economists, anthropologists, primatologists and political
 75 scientists. The range of topics covered by these diverse contributors is wide, as
 76 one might expect, and includes outstanding and data-rich reviews of cooperation in
 77 primate groups (by Silk) and of food sharing in small-scale societies (by Kaplan &
 78 Gurven).

79 Strength of both volumes is the importance of their topic. Humans are capable
 80 of cooperating with unrelated individuals to an extent that is unprecedented
 81 among animals, and human society would be unrecognizable without this ability:

82 we would have no trade, no moral or legal systems, and no universities,
 83 religions, unions, armies, political parties, or organizations of any kind. However
 84 despite the centrality of cooperation to human social life, the issue of how
 85 human cooperativeness evolved is a contentious one that has been regarded as a
 86 major unsolved scientific puzzle for several decades. The basic puzzle is this: in
 87 a cooperative interaction that produces shared resources (e.g., a collective
 88 action), lower-contributing interactants ('free riders') will, all else equal, reap
 89 higher net benefits than higher-contributors (Olson, 1965). Unless the higher-
 90 contributors can solve this free-rider problem, they will be exploited to
 91 extinction, and cooperation will fail to evolve. The free-rider dilemma has been
 92 one of the more longstanding and intractable problems in behavioral science, and
 93 especially in behavioral biology, and the editors seem determined to solve it
 94 once and for all.

95 Another strength of these books is an emphasis on cross-cultural hypothesis
 96 testing. In order to thoroughly test any theory about the evolution of an aspect of
 97 human nature, it is necessary to study humans in as wide a range of cultures as
 98 possible, rather than studying only undergraduate samples. The contributors to
 99 *Moral Sentiments* review studies from a diverse sample of non-Western societies,
 100 and the 15-culture study chronicled in *Foundations* is one of the most expansive
 101 and ambitious cross-cultural research projects in history. Also admirable is the
 102 extent to which both books involve contributions by researchers from diverse
 103 fields. These contributors were able to see over the arbitrary boundaries that
 104 divide their disciplines, boundaries which continue to exist for historical,
 105 administrative, and professional reasons, but which have a little or nothing to do
 106 with scientific goals and the production of knowledge. When the topic is as basic
 107 to behavioral science as human cooperation, this kind of interdisciplinary
 108 approach is especially essential.

109 Despite these considerable strengths, however, these books suffer from a
 110 fundamental flaw: the theory of strong reciprocity, on which both books are based,
 111 is probably wrong. Understanding why this is so requires a thorough consideration
 112 not just of strong reciprocity itself, but also of the standard evolutionary theories of
 113 cooperation that strong reciprocity was designed to replace.

114 **Strong Reciprocity Defined**

115 In *Foundations*, the editors say “[s]trong reciprocity is a predisposition to cooperate
 116 with others, and to punish (at personal cost, if necessary) those who violate the
 117 norms of cooperation, even when it is implausible to expect that these costs will be
 118 recovered at a later date” (p. 8; italics in original). The above definition makes clear
 119 that strong reciprocity is actually decidedly non-reciprocal, in the respect that strong
 120 reciprocators do not expect to be compensated by the beneficiaries of their altruism.
 121 Hence, why was the term strong reciprocity chosen at all, instead of a seemingly
 122 more accurate term such as ‘non-reciprocal altruism’? Apparently because, as the
 123 above definition also makes clear, strong reciprocity is meant to refer to the negative
 124 reciprocity that strong reciprocators exhibit when they punish non-cooperators. The

125 punishment of non-cooperators is considered a kind of second-order cooperation,
 126 because the threat of such punishment often convinces would-be shirkers to
 127 contribute their fair share.

Author Proof

128 **The Evidence for Strong Reciprocity Comes Mainly from Experimental**
 129 **Economics**

130 For evidence of strong reciprocity, the editors draw primarily on behavioral data
 131 from economics experiments such as dictator, ultimatum, and public good games.
 132 In all of these games, participants are endowed with a sum of money (or tokens
 133 that can be exchanged for money at the end of the game), and they are given an
 134 opportunity to either keep this money for themselves, or to give some or all of it
 135 to co-participants. For example, in the dictator game, a participant is endowed
 136 with (for example) £10 and then dictates how much of this amount will be gifted
 137 directly to one recipient co-player; what is not gifted is kept by the dictator. The
 138 ultimatum game is identical to the dictator game, except that the recipient of the
 139 gift has the opportunity either to accept or reject the offering; if the recipient
 140 accepts then the deal goes through, but if the recipient rejects then neither the
 141 recipient nor the offerer receives any money at all. In the public good game,
 142 participants play not with just one other co-player but with a small group of
 143 other co-players, and whatever portion of their endowment they choose to donate
 144 is multiplied by some factor >1.0 and then divided equally among all group
 145 members, including themselves. These games are typically conducted on
 146 computers in a university laboratory setting. All players usually play the game
 147 simultaneously in the same lab room, but the identity of each individual player is
 148 masked, so that a player cannot know the specific identity of his or her
 149 partner(s). Players can usually identify their co-players only by arbitrarily
 150 assigned anonymous titles such as Player 1, Player 2, etc. Therefore players
 151 never know which other participant in the lab is actually their partner in any one
 152 round.

153 All three of the above games are structured such that if a player is solely
 154 interested in achieving the maximum monetary payoff, then he or she should
 155 give the minimum possible amount to co-players. For example, in the dictator
 156 game, the dictator achieves maximal personal gain by offering the recipient as
 157 little as possible, and in the ultimatum game, the offerer gains maximally by
 158 offering the recipient as little as possible, and the recipient gains maximally by
 159 accepting whatever offer is made (because recipients who reject offers make
 160 nothing). In the public good game, all donations to the group are multiplied by
 161 some factor that is greater than 1.0 but less than the number of group members.
 162 As a result, while it is best for the group as a whole if each member donates as
 163 much as possible, each individual member has a personal incentive to donate as
 164 little as possible and to free ride on co-member donations. As the editors point
 165 out, any theory that regards people as being interested solely in maximizing their
 166 personal monetary gain would predict that participants in these games will
 167 behave as selfishly as the game allows. However, a large majority of players in

168 fact do not behave as income-maximizers. Players typically share from 40% to
 169 50% of their endowments with their co-players in the ultimatum game, for
 170 example, and from 40% to 60% in the initial rounds of the public good game.

171 **Is Generosity in Economics Games the Result of Hidden Reciprocal Motives**
 172 **and/or Western Cultural Bias?**

173 One plausible explanation for this generosity is that it is actually the product of
 174 reciprocal motives that are selfish in the long run: perhaps players realize that their co-
 175 players will behave generously only as long as they themselves do the same, so they
 176 contribute in order to maximize the amount that they can acquire from co-players; or,
 177 similarly, perhaps they contribute to signal their generosity to co-players, in order to
 178 build their own reputation for magnanimity so that their future partners will return this
 179 magnanimity. However, such claims are apparently only partially correct. These
 180 games can be structured so as to deny players the opportunity to acquire reciprocal
 181 returns, and when they have this structure, players do behave less generously. For
 182 example, when the game is one-shot (i.e., after a player has interacted with a particular
 183 co-player, there is no possibility that he or she will interact with that co-player again),
 184 and/or when players are given a new arbitrary identity after every round of the game
 185 (which makes it impossible to build a reputation for magnanimity), generosity is
 186 reduced. However, even under these reciprocity-precluding conditions, players
 187 continue to behave significantly more generously than would be predicted by any
 188 theory that casts humans as income-maximizers.

189 The tendency of economic game players from several different societies to engage
 190 in strong reciprocity (i.e., to continue to contribute above the required minimum, even
 191 when reciprocity and reputation are impossible) raised the question of whether strong
 192 reciprocity might be some kind of evolutionary adaptation. However, up until a few
 193 years ago, most economic games had involved only undergraduates from industrialized
 194 societies as subjects, which raised doubts about the extent to which strong
 195 reciprocity was culturally universal. In order to address this question, the editors
 196 recruited a research team of anthropologists and charged them with the task of
 197 conducting experimental games in a wide variety of 15 small-scale, non-western, non-
 198 industrialized societies. This effort became the research project that is detailed in
 199 *Foundations*. Members of the project team conducted ultimatum games in all 15 of the
 200 cultures, as well as public good games in six cultures and dictator games in three. The
 201 results of this research showed that players in all of these cultures, like undergraduates
 202 in industrialized societies, behave more generously than an income-maximization
 203 theory would predict: in no culture did players consistently contribute only the
 204 required minimum. However, there was some cross-cultural diversity in how the
 205 game was played, and some deviations from the Western undergraduate pattern of
 206 contributing roughly half of one's endowment initially. For example, mean offers in
 207 the ultimatum game ranged from 25% among the Quichua of Ecuador to 57% among
 208 the Lamalera of Indonesia. In order to explain the variation of mean offers in the
 209 ultimatum game, the cultures were ranked in terms of two factors: market integration
 210 (i.e., how much exposure the culture has to western-style market economies), and

211 payoffs to cooperation (i.e., the extent to which economic life in that culture depends
 212 on cooperation with non-kin). These two factors together explained 47% of the
 213 variance in mean ultimatum game offers.

214 **Strong Reciprocity is Theorized to have Evolved by Group Selection**

215 The cross-cultural data presented in *Foundations* suggests to the editors that people
 216 all over the planet (and not just undergraduates in industrialized societies) act as
 217 “strong reciprocators” as opposed to income-maximizers, and that strong
 218 reciprocity could therefore be a universal aspect of human nature. The editors’
 219 theoretical work focuses primarily on how strong reciprocity could have evolved as
 220 a behavioral adaptation in human ancestral environments. Strong reciprocity would
 221 seem problematic for standard theories of behavioral biology, because most
 222 evolutionary biologists assume that genes promote their own replication, by
 223 encoding adaptations that promote the inclusive fitness (hereafter ‘fitness’) of the
 224 individuals who bear them. Since strong reciprocators are believed to cooperate
 225 even when they cannot recoup the costs of cooperating, they should be at a fitness
 226 disadvantage relative to the lesser-sacrificing beneficiaries of their altruism, and
 227 standard evolutionary theory would seem unable to explain their existence.
 228 Therefore, the editors see a need to develop an alternative to the theory that selfish
 229 genes promote individual fitness.

230 Their alternative theory, presented most completely in Chapter 7 of *Moral*
 231 *Sentiments*, suggests that although strong reciprocity harms the fitness of the
 232 individual strong reciprocator, its benefits to the strong reciprocator’s group are
 233 sufficient to permit its evolution. In other words, strong reciprocity may have
 234 evolved via a process of “group selection” whereby groups with more strong
 235 reciprocators are “less prone to extinction... because more cooperative groups are
 236 more effective in warfare, more successful in co-insuring, more adept at managing
 237 commons resources, or other similar reasons” (p. 217). The editors include a formal
 238 model suggesting that a strongly reciprocal strategy—which both cooperates and
 239 punishes non-cooperators—can more successfully evolve than a strategy that
 240 cooperates without punishing. They emphasize that “...the process modeled here is
 241 likely to be much less important for genetic evolution than for cultural evolution”
 242 (p. 239), because their model assumes a level of migration between groups that
 243 would seriously weaken the effects of biological group selection. However, in
 244 Chapter 1 of *Moral Sentiments*, the editors suggest “strong reciprocity, like kin
 245 altruism and reciprocal altruism, has a significant genetic component” (p. 22).
 246 While the theory is always presented as group selectionist, it not always clear
 247 whether the editors wish to argue for cultural or biological group selection.

248 **What Theories is Strong Reciprocity Designed to Replace?**

249 According to the editors, the fact that subjects in economic games tend to give more
 250 than the required minimum runs contrary to the “selfishness axiom” of traditional

251 economics and evolutionary biology, and suggests that these disciplines' "canonical
 252 model" (*Foundations*, p. 49) should be replaced by the theory of strong reciprocity.
 253 However, is it fair to say that standard economic and evolutionary theory is
 254 characterized by this selfishness axiom, or are the editors attempting to demolish a
 255 pair of straw men?

256 The editors' attack on standard economic theory would be more impressive if they
 257 cited examples of the selfish axiom being invoked by contemporary economists. I did
 258 not notice a single such reference in either book. In their *Behavioral and Brain*
 259 *Sciences* article (essentially a précis of *Foundations*), the editors do cite F. Y.
 260 Edgeworth as saying that the "first principle of economics is that every agent is
 261 actuated only by self-interest," (Henrich et al., 2005, p. 839) but Edgeworth does not
 262 qualify as a contemporary foil since this quote dates from 1881. The current standard
 263 perspective from economics is that people consistently "behave as though
 264 maximizing something... [called] utility... [but it is not] axiomatic that utility is
 265 the same as income" (Binmore, 2005, p. 817, italics in original). In other words, most
 266 contemporary economists would not expect for subjects in economic games to behave
 267 as income-maximizers. However, if there are any who would make this prediction,
 268 they will find that it has been falsified cross-culturally in *Foundations*.

269 Nor does the selfishness axiom appear to be a current characteristic of orthodox
 270 evolutionary theory. However, behavioral biology has been strongly associated with
 271 this axiom for several decades, particularly since Dawkins decided to give his
 272 bestselling 1976 popularization of Hamilton's theories the title *The Selfish Gene*. This
 273 title refers to the fact that genes which promote their own replication, by benefiting the
 274 fitness of the individuals in whom they are contained, will tend to proliferate in a
 275 population. Since genes often promote individual fitness by enabling individuals to
 276 cooperate with others, selfish genes often produce cooperative, rather than selfish,
 277 individuals: "Animals are sometimes nice and sometimes nasty, since either can suit
 278 the self-interest of genes at different times. That is precisely the reason for speaking of
 279 'the selfish gene' rather than, say, 'the selfish chimpanzee'" (Dawkins, 1998, p. 212).
 280 However, Dawkins himself has at times seemed confused on this point; for example
 281 when he stated that if you want people to "cooperate generously and selflessly
 282 towards a common good, you can expect little help from biological nature. Let us try
 283 and teach generosity and altruism because we are born selfish" (Dawkins, 1989
 284 [1976], p. 3). Dawkins' seemingly contradictory statements suggest how easy it can
 285 be to confuse selfish genes with selfish people. Nevertheless, while most behavioral
 286 biologists would certainly agree that genes replicate primarily by promoting
 287 individual fitness (and would therefore disagree with the editors' group selectionism),
 288 they would also agree that a crucial way in which genes promote fitness in humans is
 289 by building genuinely cooperative individuals.

290 **Problems with the Data: Minds are Executors of Adaptations, Rather than** 291 **Maximizers of Income, Fitness, or Anything Else**

292 As noted above, the editors' evidential case for strong reciprocity rests almost
 293 entirely on data from economic games. While these data are potentially useful, one

294 must be cautious in interpreting their meaning, especially with regard to what they
 295 imply about human psychological and behavioral adaptations for cooperative
 296 behavior. The editors seem to believe that if mainstream evolutionary theory
 297 subscribes to the selfish axiom, then in games designed to make reciprocity and
 298 reputation impossible, this theory should expect players to act as income-
 299 maximizers. In other words, they imply that evolutionary biologists would expect
 300 behavior in these games to be enabled by some kind of cognitive mechanism which
 301 simply calculates the range of monetary payoffs given the game's parameters, and
 302 then acts to maximize this payoff.

303 However, this view of the mind as an income-maximizing (or utility- or fitness-
 304 maximizing) device is certainly not the mainstream perspective among those who
 305 study the mind from an evolutionary perspective. Evolutionary psychologists regard
 306 the mind as an *executor of adaptations*, as opposed to a maximizer of fitness or of
 307 any other currency (Tooby & Cosmides, 1992). A cognitive adaptation can be
 308 thought of as a semi-autonomous 'if, then' mechanism: if a specific kind of
 309 informational input is present in the environment, then the mechanism generates a
 310 certain kind of psychological or behavioral output (for example, 'if you see a snake-
 311 like object, then become wary of this object'). Although the output would have
 312 been, on average, an adaptive response to the input in environments in which the
 313 input-output mechanism evolved, the mechanism itself can only execute its
 314 protocol and does not know how to generate adaptive behavior per se. A cognitive
 315 adaptation will produce its output in any environment that provides the kind of
 316 informational input that would have stimulated this execution in ancestral
 317 environments, even if some novel aspect of that environment causes the adaptation
 318 to fail to actually produce a fitness-enhancing outcome (Burnham & Johnson, 2005).
 319 This view of the mind has been standard among ethologists for decades (Burnham &
 320 Kurzban, 2005), and has always characterized modern mainstream evolutionary
 321 psychology. For example, in what many consider to be the first major contribution
 322 to evolutionary psychology to emerge following biology's 'new synthesis' in the
 323 1970s, Symons (1979) discusses the toad that continues to eat insect-sized metal
 324 pellets that an experimenter rolls past it, until it becomes "a living beanbag"
 325 (Symons, 1979, p. 21), and the herring gull that cares for eggs that are not its own
 326 (and that are not even the correct color), and that have been placed in its nest by an
 327 experimenter. These species did not evolve in environments characterized by pellet-
 328 rolling or egg-introducing scientists, and they both possess cognitive adaptations
 329 that fail to function adaptively in novel, experimental environments.

330 When subjects play economic games, their psychological adaptations for social
 331 behavior are being deployed in environments that are radically different from those
 332 in which they evolved. As a result, these adaptations may produce behaviors which
 333 seem maladaptive for individual fitness (if income-maximization is seen, as it is by
 334 the editors, as a proxy for fitness-maximization). However, this result does not
 335 necessarily falsify the theory that these adaptations evolved because they promoted
 336 individual fitness in ancestral environments; instead, it may merely suggest that
 337 these adaptations will continue to execute their protocols, even in environments
 338 where experimenters have introduced novel conditions that make it impossible for
 339 these protocols to lead to adaptive outcomes.

340 In what important ways are the environments of economic games different from
 341 those of ancestral human social interaction? To answer this question, consider that,
 342 as discussed above, these games are often designed so as to minimize the extent to
 343 which subjects can gain via reciprocity and reputation. For example, the ultimatum
 344 game that was played in 15 different cultures was anonymous and one-shot, so
 345 players could not know the identities of their partners, and would expect to interact
 346 with each partner only once. The editors intended this design to eliminate the
 347 possibility that players would cooperate only in order to elicit more generous
 348 contributions from co-players, as the result of either direct reciprocity or indirect
 349 (i.e., reputation-dependent) reciprocity. After thus ruling out all cooperation
 350 motivated by long-term selfishness, the editors believed that any remaining
 351 cooperativeness would constitute evidence for truly unselfish strong reciprocity. In
 352 addition after observing significant levels of this remaining cooperativeness, the
 353 editors concluded that just as modern humans engage in strong reciprocity in
 354 experimental anonymous one-shot interactions, ancestral humans also engaged in
 355 strong reciprocity in real-life anonymous one-shot interactions; and although this
 356 behavior was individually fitness-damaging for ancestral strong reciprocators, it
 357 evolved nonetheless because it was favored by group selection. For the editors'
 358 reasoning to be accurate, it must be true that the anonymous one-shot interactions
 359 they created were similar to the anonymous one-shot interactions that occurred
 360 naturally in ancestral environments; otherwise, there is no reason to believe that
 361 their subjects' behavior in these interactions reveals anything about how ancestral
 362 humans behaved in these interactions.

363 It is unlikely, however, that ancestral humans would have routinely encountered
 364 anonymous one-shot interactions of the kind modeled in experimental games. In the
 365 first place, in the small, face-to-face social environments of ancestral humans,
 366 encounters with complete strangers would have been rare. Rarer still would have
 367 been encounters with strangers that would have been truly anonymous or one-shot.
 368 For example, say an ancestral individual encounters an unfamiliar person one day
 369 while they were both out hunting for gazelle in a remote location, and he interacts in
 370 some way with the person. For the interaction to be and to remain anonymous, he
 371 would have to be certain that the stranger did not already know who he was; and
 372 even if he could be certain of this, he would have to also be certain that the stranger
 373 would never see him again, discover his identity, or be able to describe him (and his
 374 actions) to anyone who might know his identity. A truly one-shot interaction would
 375 also be unlikely, because no experimenter would be present to ensure the
 376 termination of the interaction. If the interaction left one hunter feeling grateful (or
 377 angry), for example, he may decide to repay (or attack) the other, either on the spot
 378 or at some later date. As Trivers notes, “[s]ocial interactions are intrinsically repeat
 379 interactions - at least over short periods of time and usually over much longer
 380 periods as well. So the natural assumption is that in life we will respond to social
 381 situations as if there were later repercussions to our actions” (Trivers, 2004, p. 965).
 382 In light of the social reality that exists outside of experimental labs, it seems
 383 unlikely that ancestral individuals would have had much opportunity to engage in
 384 social interactions that they could safely expect to be truly anonymous and one-shot.
 385 In natural social environments, the only way to thoroughly ensure that one's

386 interactant partner does not tell others about one's actions is to completely destroy
 387 that partner's ability to communicate with others (e.g., via homicide). However, the
 388 editors do not theorize that anonymity must be maintained through anything like
 389 homicide; they just assume that ancestral individuals could often have correctly
 390 expected interactions to be anonymous and one-shot, and that strong reciprocity
 391 evolved (by group selection) under such conditions.

392 For the sake of argument, however, imagine that relatively anonymous one-shot
 393 interactions did sometimes occur in ancestral environments, and that modern humans
 394 do have psychological adaptations for negotiating such social landscapes. If so, then
 395 experimenters would be able to observe the deployment of these adaptations, if they
 396 designed an experiment that convincingly simulated the conditions under which
 397 these ancestral interactions occurred. Would such an ecologically valid experiment
 398 be at all similar to the one designed by the editors? Probably not. Ancestral
 399 interactions would have been relatively anonymous and one-shot only if they
 400 occurred in socially remote locations in the absence of witnesses, and especially of
 401 witnesses who were particularly interested in interactant behavior. Economic game
 402 environments do not resemble such social scenarios at all: games are conducted in
 403 lab or lab-like spaces that are crowded with subjects and experimenters, and subjects
 404 know that experimenters are intensely interested in their decisions and behaviors
 405 (after all, the whole point of the experiment is to evaluate behavior). Even if players
 406 are told that the games are anonymous, and even if they consciously believe that their
 407 identities will be shielded from co-players (and also from experimenters, if the
 408 design is double-blind), the semi-autonomous psychological mechanisms which
 409 regulate players' cooperative behavior might not recognize the situation as one that
 410 would ensure anonymity. Unless these mechanisms are given information from the
 411 game environment that they are operating in the kind of social situation that would
 412 have afforded relative anonymity in the ancestral past, there is no reason to predict
 413 that players should act as if their actions will be relatively invisible to others. There
 414 is thus little reason to expect that players in the editors' games should behave as if
 415 they are participating in an ecologically valid, anonymous one-shot encounter.

416 The editors are aware of the general criticism that economic games do not
 417 resemble real-life ancestral social interactions, and that human minds should
 418 therefore not be expected to be adapted for such games. They respond by saying that
 419 players must be able to understand the cues to social context that are provided by the
 420 game environment, because when these cues are more indicative of an anonymous
 421 one-shot interaction, players behave more selfishly. For example, in a game where
 422 players have repeated interactions with the same player, they are more generous
 423 than in a one-shot game (presumably because the repeated game allows them to
 424 selfishly sustain a reciprocal relationship); or in a game where players are
 425 identifiable to co-players only via ID numbers which are reassigned arbitrarily after
 426 every round, thus making it impossible to build reputations over the course of the
 427 game, players are more selfish than in games where reputation-building is possible.
 428 While such evidence supports the view that people are indeed motivated by
 429 'ultimately selfish' concerns about reputation and reciprocity, the editors attempt to
 430 turn this evidence on its head by emphasizing that players still contribute
 431 significantly more than nothing, even in games where reciprocity and reputation are

432 impossible, behaviors which they interpret as group-selected strong reciprocity. In
 433 other words, since players can apparently tell the difference between anonymous
 434 and non-anonymous games and between iterated and one-shot games, they should
 435 be able to detect anonymous one-shot conditions; and if their cooperative behavior
 436 were the product only of individual-level psychological adaptations, they would be
 437 completely unmotivated to contribute under such conditions.

438 The editors are incorrect, however, in asserting that individual-level cooperative
 439 adaptations should necessarily contribute nothing in games that are designed to
 440 prohibit reciprocity and reputation. Again, just because the experimenters are
 441 convinced that they have designed a truly anonymous one-shot game, their subjects'
 442 cognitive mechanisms for cooperation may not be similarly 'convinced.' There is no
 443 reason to expect that the baseline rate of cooperativeness in such games should be
 444 zero, even if the mechanisms producing cooperative behavior are individual-level
 445 adaptations.

446 **Problems with the Theory: Group Selection has Never Worked as an** 447 **Evolutionary Explanation for Human Cooperation**

448 As noted above, the editors are impressed by the fact that subjects in economics
 449 experiments continue to behave somewhat generously, even after experimentalists
 450 have attempted to rule out the possibility that subjects could be motivated by
 451 concerns related to reciprocity and reputation. In both *Foundations* and *Moral*
 452 *Sentiments*, the editors advocate a group selectionist theory of strong reciprocity in
 453 order to account for this residual cooperativeness. Their theory is by no means the
 454 first attempt to explain apparently altruistic behavior in terms of group selection;
 455 even Darwin (1871) resorted to group selectionism in order to explain human self-
 456 sacrifice, and 'naïve' group selectionist accounts of behavior were relatively
 457 common in behavioral biology prior to Williams' (1966) deeply influential critique
 458 of these approaches. The general problem with group selectionist approaches, as
 459 Williams and many since have pointed out, is that they leapfrog lower levels of
 460 selection in order to explain adaptation at higher levels, even though selection's
 461 power to sculpt adaptations is much stronger at lower levels. Parsimony demands
 462 that we attempt to exhaust all plausible lower-level adaptationist explanations for
 463 behavior, before we resort to higher-level, group selectionist explanations: "When
 464 recognized, adaptation should be attributed to no higher a level of organization than
 465 is demanded by the evidence" (Williams, 1966, p. v).

466 That is not to say that all forms of group selection have necessarily been
 467 irrelevant in shaping aspects of human psychology and culture. On the contrary,
 468 some form of cultural group selection seems central to explaining why certain
 469 cultural characteristics come to proliferate in the world. For example, cultural traits
 470 associated with a relatively powerful society may spread throughout the world, as
 471 that society imposes its culture on other societies via conquest, and as it is imitated
 472 by other societies who wish to emulate its power. But while cultural group selection
 473 is probably important for explaining the origins of some human behaviors, it cannot
 474 provide an adequate theory for the ultimate origins of human cooperation (Burnham

475 & Johnson, 2005). The ability to engage in cooperative interactions, including
 476 complex ones such as collective actions, is a fundamental attribute of human
 477 sociality that probably has biological roots. By being well adapted for cooperation
 478 in groups, ancestral individuals would have been able to engage in a variety of
 479 fitness-promoting activities, for example, cooperative hunting and foraging, and
 480 group defense against predators (Price, Cosmides & Tooby, 2002), while at the
 481 same avoiding being exploited to extinction by free riders. To discover the deepest
 482 origins of the human ability to cooperate, the editors should be focusing not on
 483 cultural evolution but on human biological nature.

484 Fortunately, since biology's new synthesis in the second half of the twentieth
 485 century, behavioral scientists have been gifted a new set of tools with which to solve
 486 the puzzle of human cooperation. The most crucial of these tools are the theories of
 487 genic self-favoritism (Hamilton, 1964) and reciprocal altruism (Trivers, 1971).
 488 Since we already have these tools at hand, there is no need to reinvent the wheel in
 489 order to solve the puzzle, let alone a square wheel like group selectionism, which has
 490 always been a non-starter as an explanation for human cooperation. There is a need,
 491 however, for more research that extends and synthesizes the theories of Hamilton
 492 and Trivers, in order to explain the more complex forms of human *n*-person
 493 cooperation, such as collective action. While Hamilton and Trivers' theories have
 494 successfully explained several general types of animal cooperation (e.g., altruism
 495 among close genetic kin, reciprocal exchange between dyadic partners), their
 496 potential to explain complex human cooperation is only now beginning to be fully
 497 exploited (Brown & Moore, 2002; Brown, Palameta & Moore, 2003; Frank, 2005;
 498 Tooby, Cosmides & Price, 2006). The basic prediction of Hamilton and Trivers is
 499 that collective action participants ought to *cooperate with other cooperators*, that is,
 500 preferentially form groups with individuals whom they expect will cooperate, and
 501 behave cooperatively only to the extent that their co-members reciprocate their
 502 cooperativeness. In this way, cooperators can avoid being exploited to extinction by
 503 lower-contributing free riders, and cooperation can evolve via individual-level
 504 adaptation. A growing body of experimental and field data suggests that cooperation
 505 with other cooperators is indeed the most common behavioral pattern of collective
 506 action participants cross-culturally (review in Price, 2006), and formal models
 507 suggest that such behavior could evolve via individual-level adaptation (Johnson,
 508 Price, & Takezawa, [in press](#); Takezawa & Price, [in preparation](#)).

509 Conclusion

510 Much of the content of these volumes rests on a wobbly theoretical foundation that is
 511 unlikely to succeed as an explanation for the ultimate origins of human cooperation.
 512 Nevertheless, these books' contributions should not be underestimated. *Foundations*
 513 is one of the most ambitious cross-cultural research projects ever in behavioral
 514 science, and *Moral Sentiments* includes several outstanding chapters from an
 515 interdisciplinary group of experts on cooperation. Finally, both books draw attention
 516 to one of the most longstanding and fundamental puzzles in social science and
 517 behavioral biology: the evolution of complex cooperation in humans. All of

518 behavioral science will benefit when this puzzle is finally solved, and it benefits today
 519 from the discussion and controversy generated by such serious attempts to solve it.

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