Altruism may arise from individual selection

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Abstract

The fact that humans cooperate with non-kin in large groups, or with people they will never meet again, is a long-standing evolutionary puzzle. Altruism, the capacity to perform costly acts that confer benefits on others, is at the core of cooperative behavior. Behavioral experiments show that humans have a predisposition to cooperate with others and to punish non-cooperators at personal cost (so-called strong reciprocity) which, according to standard evolutionary game theory arguments, cannot arise from selection acting on individuals. This has led to the suggestion of group and cultural selection as the only mechanisms that can explain the evolutionary origin of human altruism. We introduce an agent-based model inspired on the Ultimatum Game, that allows us to go beyond the limitations of standard evolutionary game theory and show that individual selection can indeed give rise to strong reciprocity. Our results are consistent with the existence of neural correlates of fairness and in good agreement with observations on humans and monkeys.
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1. Introduction

Ever since Darwin first faced this problem (Darwin, 1871; Gould, 2002), the arising of human cooperation has been a subject of intense debate within the framework of evolutionary theories. Cooperation has been linked to altruism, which can be defined as the capacity to perform costly acts that confer benefits on others (Fehr and Fischbacher, 2003). Previous theoretical approaches to altruism have shown that in many instances altruistic behavior is not truly so, in so far as they yield benefits for the altruist in the future. This is the case when the recipients of the altruistic act are relatives, well understood within kin selection theory (Hamilton, 1964). Altruism in the absence of kin relationships has also been explained in terms of repeated interaction leading to cooperation (Axelrod

and Hamilton, 1981; Trivers, 1971), indirect benefit through reputation gains (Leimar and Hammerstein, 2001; Milinski et al., 2002; Nowak and Sigmund, 1998) or costly signalling theories (Gintis et al., 2001). However, recent behavioral experiments show that humans can perform altruistic acts when interactions are anonymous and one-shot, i.e. in conditions which exclude all the explanations proposed so far (Fehr et al., 2002; Fehr and Gächter, 2002; Fehr and Rockenbach, 2003; Henrich et al., 2001). Indeed, it has been observed that individuals are ready to punish non-cooperators (altruistic punishment) as well as to reward cooperative behavior (altruistic rewarding) even when doing so will not produce any benefit for the punisher or rewarder. This set of behaviors has been termed strong reciprocity (Fehr et al., 2002; Gintis, 2000b) and, as such, it has been proposed as a schema for understanding altruism in humans (Fehr and Fischbacher, 2003; Gintis et al., 2003).

Substantial evidence in favor of the existence of strong reciprocity comes from experiments using the

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so-called Ultimatum Game (Güth et al., 1982), and from agent-based models (Bowles et al., 2003b; Bowles and Gintis, 2004; Boyd et al., 2003) [see (Fehr and Fischbacher, 2003; Gintis et al., 2003) for summaries]. In the Ultimatum Game, under conditions of anonymity, two players are shown a sum of money, say 100€. One of the players, the "proposer", is instructed to offer any amount, from 1€ to 100€, to the other, the "responder". The proposer can make only one offer, which the responder can accept or reject. If the offer is accepted, the money is shared accordingly; if rejected, both players receive nothing. Since the game is played only once (no repeated interactions) and anonymously (no reputation gain), a self-interested responder will accept any amount of money offered. Therefore, self-interested proposers will offer the minimum possible amount, 1€, which will be accepted. To be sure, this is a backward-induction way of reasoning, which leads to the conclusion that the subgame-perfect Nash equilibrium is the relevant one. However, the Ultimatum game has many Nash equilibria, which can play a role in the results we report below (see, e.g. Samuelson, 1997, or Gintis, 2000a, for complete game-theoretical discussions on this issue). We will come back to this question in Section 6. Notwithstanding, in actual Ultimatum Game experiments with human subjects, average offers do not even approximate the self-interested prediction. Generally speaking, proposers offer respondents very substantial amounts (50% being a typical modal offer) and respondents frequently reject offers below 30%. Most of the experiments have been carried out with university students in western countries, showing a large degree of individual variability but a striking uniformity between groups in average behavior. A recent experiment (Güth et al., 2003) used newspaper readers in order to have a population with broader characteristics and background, finding qualitatively similar results. Interestingly, a large study in 15 small-scale societies (Henrich et al., 2001) found that, in all cases, respondents or proposers behave in a reciprocal manner. Furthermore, the behavioral variability across groups was much larger than previously observed: while mean offers in the case of university students are in the range 43–48%, in the cross-cultural study they ranged from 26% to 58%.

The fact that indirect reciprocity is excluded by the anonymity condition and that interactions are one-shot allows one to interpret rejections in terms of strong reciprocity (Fehr et al., 2002; Gintis, 2000b). This amounts to considering that these behaviors are truly altruistic, i.e. that they are costly for the individual performing them in so far as they do not result in direct or indirect benefit. As a consequence, we immediately face an evolutionary puzzle: the negative effects of altruistic acts must decrease the altruist's fitness as compared to the that of the recipients of the benefit, ultimately leading to the extinction of altruists. Indeed,

standard evolutionary game theory arguments applied to the Ultimatum Game lead to the expectation that in a mixed population, punishers (individuals who reject low offers) have less chance to survive than rational players (individuals who accept any offer) and eventually disappear (Page and Nowak, 2000, 2002). Although much attention has been devoted to this issue by researchers in differents aspects of evolutionary theory, the problem is yet far from understood (Bowles et al., 2003a; Hammerstein, 2003; Vogel, 2004) To date, the only way out to this dilemma seems, following the original suggestion of Darwin (Darwin, 1871), to invoke group and cultural selection to compensate for the negative effects that reciprocity is assumed to have on individuals (Bowles et al., 2003b; Boyd et al., 2003; Hammerstein, 2003).

2. One-parameter model

In order to assess the possible evolutionary origins of these behaviors, we introduce and analyse here a drastically simplified model. Imagine a population of N players of the Ultimatum Game with a fixed sum of money M per game. Random pairs of players are chosen, of which one is the proposer and another one is the respondent. In its simplest version, we will assume that players are capable of other-regarding behavior (empathy); consequently, in order to optimize their gain, proposers offer the minimum amount of money that they would accept. Every agent has her own, fixed acceptance threshold, $1 \leqslant t_i \leqslant M$ (t_i are always integer numbers for simplicity). Agents have only one strategy: respondents reject any offer smaller than their own acceptance threshold, and accept offers otherwise. Although we believe that this is the way in which "empathic" agents will behave, in order not to hinder other strategies a priori, we have also considered the possibility that agents have two independent acceptance and offer thresholds. As we will see below, this does not change our main results and conclusions. Money shared as a consequence of accepted offers accumulates to the capital of each of the involved players. As our main aim is to study selection acting on modified descendants, hereafter we interpret this capital as "fitness" (here used in a loose, Darwinian sense, not in the more restrictive one of reproductive rate). After s games, the agent with the overall minimum fitness is removed (randomly picked if there are several) and a new agent is introduced by duplicating that with the maximum fitness, i.e. with the same threshold and the same fitness (again randomly picked if there are several). Mutation is introduced in the duplication process by allowing changes of ± 1 in the acceptance threshold of the newly generated player with probability $\frac{1}{3}$ each. Agents have no memory (i.e.

interactions are one-shot) and no information about other agents (i.e. no reputation gains are possible).

Two remarks about our model are in order before proceeding any further. First, we need to clarify the motivation for our choice of simple, memoryless agents. It is likely that in early human societies some degree of repeated interaction and reputation effects was present, factors that we have excluded from our model. In this respect, we stress that what we are actually trying to show is that the behavior observed in the experiments quoted above (Fehr and Fischbacher, 2003), can arise by individual selection in the absence of precisely those two ingredients, repeated interactions and reputation: In other words, the existence of repeated interactions and reputation is not a necessary condition for the selection of altruistic-like behaviors at the individual level. In that case, actual circumstances of human evolution would reinforce the tendency to the appearance of altruism. The fact that similar results are found in Ultimatum game experiments in a wide range of small-scale societies (Henrich et al., 2001) suggests that our conclusions will have to be kept in mind when dealing with early human behavior, as the relevance of these two influences is largely different in the studied societies. Second, we want to stress that our mutation rate, which we choose somewhat large to enhance the fluctuation effects (see related comments in Section 5 below), should not be understood from the genetic viewpoint, but rather from the phenotypical viewpoint. Indeed, the inheritance of an acceptance threshold like the one we are proposing may perfectly be also affected by cultural transmission, and it is therefore subject to a large individual variability. Observations reported in the literature (Fehr and Fischbacher, 2003; Gintis et al., 2003) support this great variability. On the other hand, it has to be borne in mind that even if the mutation rate may seem large, mutations are small, with relative changes of the order of $\frac{1}{100}$ in the acceptance threshold. We believe that such changes from parent to child are actually very likely, and hence our choice for the mutation rate.

3. Results

Fig. 1 shows that strong reciprocity, in the form of altruistic punishment, can be selected for at the individual level in small populations ranging from $N = 10$ to $N = 10\,000$ agents when selection is strong ($s = 1$). The initial distribution of thresholds rapidly leads to a peaked function, with the range of acceptance thresholds for the agents covering about a 10% of the available ones. The position of the peak (understood as the mean acceptance threshold) fluctuates during the length of the simulation, never reaching a stationary value for the durations we have explored. The width of the peak fluctuates as well, but in a much smaller scale
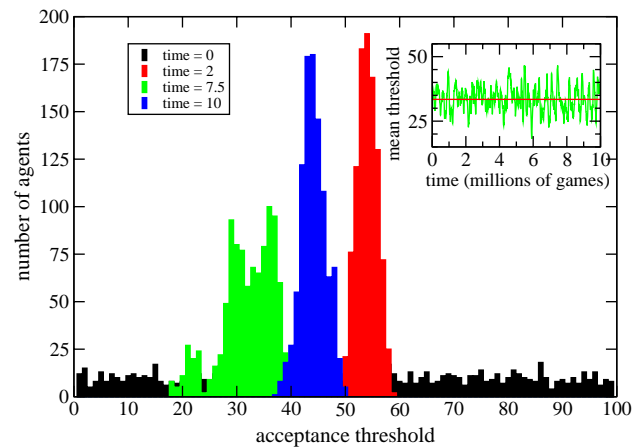

Fig. 1. Non-self-interested behavior establishes spontaneously on small populations. Population size is $N = 1000$, the capital to be shared per game is $M = 100$. Death and birth takes place after every game ($s = 1$). Initial acceptance thresholds are distributed uniformly ($t_i = t_0$ conditions lead to the same output). Plotted are the distributions of acceptance threshold at the beginning of the simulation and after 2, 7.5 and 10 million games. Inset: Mean acceptance threshold as a function of simulated time, is averaged over intervals of 10 000 games to reduce noise (in the raw data spikes appear that go above 50 or below 10). The red line in the inset is the average over all times of the mean, located at 33.45.

than the position. At certain instants the distribution exhibits two peaks (see distribution at 7.5 million games). This is the mechanism by which the position of the peak moves around the possible acceptance thresholds. Importantly, the typical evolution we are describing does not depend on the initial condition. In particular, a population consisting solely of self-interested agents, i.e. all initial thresholds are set to $t_i = 1$, evolves in the same fashion. The value M of the capital at stake in every game is not important either, and increasing M only leads to a higher resolution of the threshold distribution function.

The success of reciprocators does not depend on the selection rate (although the detailed dynamics does). Fig. 2 shows the result of a simulation with 1000 agents in which the removal-duplication process takes place once every $s = 10\,000$ games. To show further that the initial conditions are irrelevant, for this plot we have chosen an initial population of self-interested agents. As we may see, the evolution is now much less noisy, and the distribution is narrower, becoming highly peaked and immobile after a transient. The value of s at which this regime appears increases with the population size. The final mean acceptance threshold at which simulations stabilize depends on the specific run, but it is very generally a value between 40 and 50. We thus see that the selection rate may be responsible for the particulars of the simulation outcome, but it is not a key factor for the emergence of strong reciprocity in our model. We note, however, that taking very large values for s or,
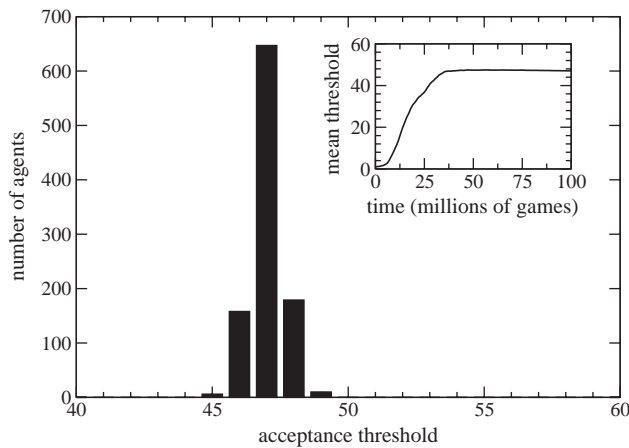
Fig. 2. Slow selection rates lead to stationary acceptance threshold distributions very narrowly peaked. Population size is $N = 1000$, the capital to be shared per game is $M = 100$ and selection is weak ($s = 10\,000$). Initial agents are all self-interested ($t_i = 1$). Plotted is the distribution of acceptance threshold at the end of the simulation. There are no agents with thresholds outside the plotted range. Inset: Mean acceptance threshold as a function of simulated time. The asymptotically stable mean is very slowly approaching 47.

strictly speaking, considering the limit $s/N \to \infty$, does lead to different results. See next section for a detailed discussion.

4. Discussion

Among the results summarized above, the evolution of a population entirely formed by self-interested players into a diversified population with a large majority of altruists is the most relevant and surprising one. We will now argue that the underlying reason for this is the presence of fluctuations (or noise) in our model. For the sake of definiteness, let us consider the case $s = 1$ (agent replacement takes place after every game) although the discussion applies to larger (but finite) values of s as well. After one or more games, a mutation event will take place and a "weak altruistic punisher" (an agent with $t_i = 2$) will appear in the population, with a fitness inherited from its ancestor. For this new agent to be removed at the next iteration so that the population reverts to its uniform state, our model rules imply that this agent has to have the lowest fitness, that is the only one with that value of fitness, *and also* that it does not play as a proposer in the next game (if playing as a responder the agent will earn nothing because of her threshold). In any other event this altruistic punisher will survive at least one cycle, in which an additional one can appear by mutation. Note also that in case a "weak altruistic punisher" is chosen to act as a proposer, she earns a large amount of fitness, which would allow her to survive for many death–birth cycles, and during those

she could even accumulate more fitness in case she is selected to play again as proposer. It is important to realize that this does not imply any constraint on the number of times the emergent weak punisher is picked up as respondent: in that case, and until a second punisher arises from mutation, acting as a respondent the punisher will simply earn nothing, while the selfish agent playing the role of proposer in that game would not earn the 99 fitness units she would earn if she met another selfish agent. Therefore, the survival of the first punisher does not depend on (and it may actually be favored by) the number of times she acts as respondent, as one would expect in a realistic situation.

The above discussion is in fact an example, something like a worst-case scenario for the $s = 1$ case, and one can easily imagine other ways a newly created punisher may survive. Our intention is to illustrate the crucial fact that fluctuations (i.e. the fact that the recently appeared altruist is chosen to play or not, or that it is chosen to be removed if there are more than one with the lowest fitness, or other, selfish agents are not selected to play in one or several intervals) allow for survival and growth of the population of altruists. It is interesting to note that in the dynamics in which all players play against every other once, i.e. in the replicator dynamics (see next paragraph for more on this), the average fitness earned by each type of agent can be computed analytically as a function of the frequency of the types in the population. From that result, it is easy to find out the threshold value required for one type to have a fitness advantage on the other. In particular, it can be shown that if a 3% of an initial $t_i = 1$ population turns to $t_i = 2$, the latter ones will outperform the originally self-interested agents. Note also that, in our model, it can also be shown that the number of times a particular agent is chosen to play is a random variable given by a Poisson distribution of mean s/N (and of standard deviation $\sqrt{s/N}$, which for $s/N \gg 1$ becomes negligible with respect to the mean). Therefore, irrespective of their threshold, some agents will have played more than others and may have accumulated more capital, subsequently being less exposed to removal. All this scenario is what we refer to as "dynamics governed by fluctuations."

In the context of the above discussion, it is very illustrative to compare our results with previous studies of the Ultimatum Game by Page and Nowak (Page and Nowak, 2000, 2002). The model introduced in those works has a dynamics completely different from ours: following standard evolutionary game theory, every player plays every other one in both roles (proponent and respondent), and afterwards players reproduce with probability proportional to their payoff (which is fitness in the reproductive sense). Simulations and adaptive dynamics equations show then that the population ends up composed by players with fair (50%) thresholds. This

is different from our observations, in which we hardly ever reach an equilibrium (only for large s) and even then equilibria set up at values different from the fair share. The reason for this difference is that the Page–Nowak model dynamics describes the $s/N \to \infty$ limit of our model, in which between death-reproduction events the time average gain all players obtain is the mean payoff with high accuracy. We thus see that our model is more general because it has one free parameter, s, that allows selecting different regimes whereas the Page–Nowak dynamics is only one limiting case. Those different regimes are what we have described as fluctuation dominated (when s/N is finite and not too large) and the regime analysed by Page and Nowak (when $s/N \to \infty$). This amounts to saying that by varying s we can study regimes far from the standard evolutionary game theory limit. As a result, we find a variability of outcomes for the acceptance threshold consistent with the observations in real human societies (Fehr and Fischbacher, 2003; Gintis et al., 2003; Henrich et al., 2001).

5. Two-parameter model

To further confirm the differences between our approach and Page and Nowak's one, we have considered the same alternative as they did, namely to assign agents a new strategical variable, o_i, defined as the amount offered by player i when acting as proponent, and subject to the same mutation rules as the acceptance threshold, t_i. While Page and Nowak observed that in their setup, this modification of the model led to fully rational players (i.e. in our model, $t_i = o_i = 1$), except for fluctuations due to mutations. Fig. 3 shows clearly that in our model the dynamics remains very complicated and equilibria are never reached within the duration of our simulations. Once again, this is due to the fact that the dynamics we propose does not remove the fluctuations of the payoff obtained by the players as the limit $s/N \to \infty$ does. It is clear that many other choices for the dynamics are possible, aside from choosing different values for s. For instance, a certain percentage of the population could be replaced in reproduction events instead of just the least fit individual. Another possibility would be the selection of individuals to be replaced with probability given by their fitness. Notwithstanding, our main point here is that our dynamics is far away from the replicator or adaptive ones, and the form we choose for the replacement is intended to make easier and faster to visualize the fluctuation effects. Our choice for the large mutation rate points in the same direction as well, i.e. helps amplify the effect of fluctuations. In this respect, the question arises as to the influence of such a large mutation rate in our results. To exclude any dependence
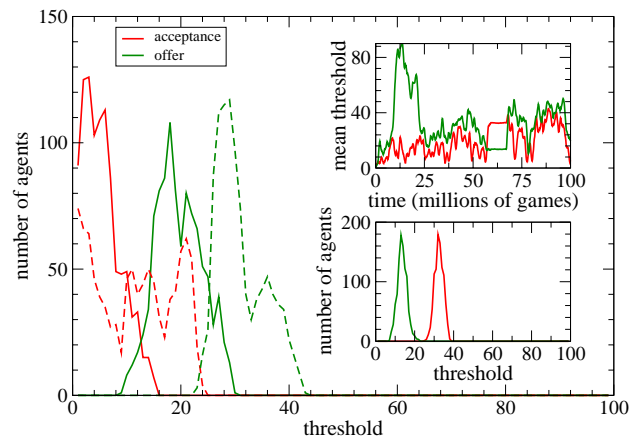

Fig. 3. Introduction of an independent level for the amount of money offered by the agents does not change our conclusions. Population size is $N = 1000$, the capital to be shared per game is $M = 100$ and selection is intermediate ($s = 1000$). Initial agents are all fully rational ($t_i = o_i = 1$). Plotted are the distribution of acceptance threshold (red) and offered amount (green) after 50 million games (dashed) and 100 million games (solid). Upper inset: Mean acceptance threshold and offered amount as a function of simulated time. The offered amount is most of the time larger than the acceptance threshold, and occasional crosses lead to a very slow dynamics until the situation is restored (see the plateaus around 62.5 million games, and corresponding distributions in the lower inset).

of our main conclusion, namely the appearance of altruistic punishers even in an initially selfish population, on the value of this quantity, we simulated the same model for smaller mutation rates. Fig. 4 shows clearly that even for mutation rates as small as $\frac{1}{3000}$ the population is taken over by the altruistic punishers, although at a correspondingly larger time. Of course, the larger the mutation rate, the wider the histogram of the population, and therefore, for the smallest values the acceptance threshold distribution is very sharply peaked around the mean value (see inset in Fig. 3). For even smaller rates (of the order of 10^{-4} or similar genetic mutation rates) the amount of time needed for altruistic individuals to establish becomes exceedingly large, and out of the scope of our computing capabilities. We believe that different rules for the dynamics would lead to qualitatively similar results in so far as they do not approach Page and Nowak's (which we could call deterministic) limit.

6. Conclusions

In this paper, we have shown that altruistic-like behavior, specifically, altruistic punishment, may arise by means of exclusive individual selection even in the absence of repeated interactions and reputation gains. Our conclusion is important in so far as it is generally believed that some kind of group selection is needed to
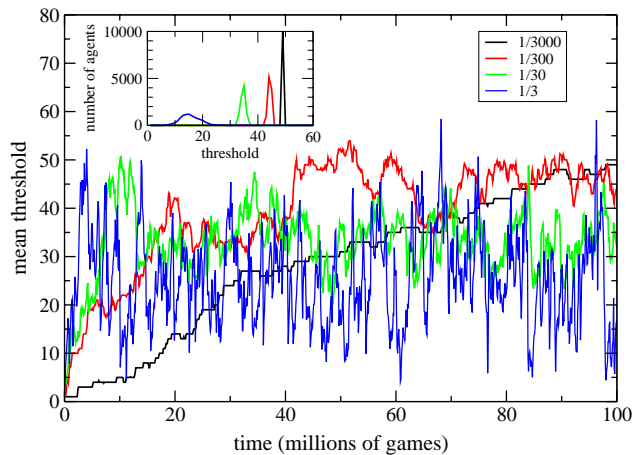
Fig. 4. Simulation results do not depend on the mutation rate. Population size is $N = 10\,000$, the capital to be shared per game is $M = 100$. Death and birth takes place after every game ($s = 1$). Initial agents are all self-interested ($t_i = 1$). Plotted is the mean value of the acceptance threshold vs. time in number of games (which for $s = 1$ equals the number of generations). Mutation rates are as indicated in the plot. Inset: Distribution of the acceptance threshold at the end of each of the simulations. The fact that the peak of every distribution is displaced to the left for larger mutation rates is an irrelevant coincidence: The peak positions fluctuate in time (as indicated by the mean value in the main plot).

understand the observed human behavior. The reason for that is that game theoretical arguments apparently show that altruists are at disadvantage with respect to selfish individual. In this respect, another relevant conclusion of the present work is that perspectives and approaches alternative to standard evolutionary game theory may be needed in order to understand paradoxical features such as the appearance of altruistic punishment. We begin by discussing this second conclusion and proceed to the first one afterwards.

As we have seen, in our model the effects of finite time between generations (more precisely, the effect of keeping s finite) and of stochasticity play a non trivial role and sustain strong reciprocity (existence of players with $t_i > 1$) even if acceptance and offer obey independent rules. Regarding this, it is important to notice that the way fluctuations enter our model is directly through the evolutionary dynamics we propose. Other important effects of noise have been reported in the literature (Gale et al., 1995; Binmore and Samuelson, 1999) in which fluctuations are included into a replicator dynamics for the Ultimatum game to account for imperfections in the learning process. In our case, there is no learning at all (agents have no memory) and therefore the source of noise is the dynamics itself, i.e. the random differences between the number of games every player plays between selection events. Interestingly, randomness arising from finiteness of the population has also been shown to change the evolutionary stability of cooperation (Nowak et al., 2004). In a related context, it has

been recently reported that spatial structure, previously regarded as beneficial for the evolution of cooperation on the basis of results on the evolutionary Prisoner's Dilemma, may in fact inhibit it (Hauert and Doebeli, 2004). Finally, let us also mention the recent results about the evolution of strong altruism in randomly formed groups when they exist for more than one generation (Fletcher and Zwick, 2004). All these unexpected and non-trivial results, along with our present report suggest that general approaches, involving different, non-standard dynamics, beyond standard evolutionary game theory, and particularly computer simulations of agent models, may provide insights into the issue of how cooperation arises. Interestingly, it has been argued that empathy (or fairness), i.e. the fact that agents offer what they themselves are prepared to accept, does not arise evolutionary on its own (Page and Nowak, 2002). While those results are not questioned, they have been obtained in the framework of adaptive dynamics. We believe, along the same line of reasoning we are presenting here, that the effect of fluctuations as described in the previous section may be enough to originate and sustain fairness in finite populations, which would in turn justify our model from the game theoretical viewpoint. In this regard, an interesting question arises when one considers the possibility of observing similar behavior in dilemma-type games (such as the prisoner's dilemma, see Axelrod and Hamilton, 1981). In that kind of games, the Nash equilibrium structure is much simpler than in the Ultimatum game: Usually, they have only one equilibrium. It may then be that in those situations, departure from that equilibrium by individual selection alone without additional ingredients is much more difficult. In other words, the existence of numerous Nash equilibria in the Ultimatum game may facilitate the creative role of the fluctuations in leading the population away from the self-interested type. It would be interesting to analyse the case of dilemma-type games in the light of our findings here. Work along these lines is in progress.

Evolutionary explanations of strong reciprocity have been advanced in terms of gene-culture coevolution (Bowles et al., 2003b; Bowles and Gintis, 2004; Boyd et al., 2003; Gintis, 2003; Hammerstein, 2003; Henrich and Boyd, 2001). The underlying rationale is that altruistic behavior leads to fitness disadvantages at the individual level. But why must strong reciprocators have lower fitness than other members of their group? While alternative compensating factors (e.g. sexual selection) have been suggested (Bowles et al., 2003a), our results show clearly that, in the context of the Ultimatum Game, altruistic punishment (Fehr and Gächter, 2002) may be established by individual selection alone. Our simulations are consistent with the large degree of variability among individuals (Fehr and Fischbacher,

2003; Gintis et al., 2003) and among societies (Henrich et al., 2001), and reproduce the fact that typical offers are much larger than self-interested ones, but lower than a fair share. While in our model agents have other-regarding behavior (empathy), i.e. agents offer the minimum they would accept if offered to them, this is not a requisite for the emergence of strong reciprocators as the two-threshold simulations show. The population evolves by descent with modification and individual selection, as the model does not implement cultural (other than parent-to-child transmission) or group selection of any kind. To be sure, we do not mean that these mechanisms are irrelevant for the appearance and shaping of altruism: what we are showing is that strong reciprocity (and hence altruism) may arise in their absence. Observations of strongly reciprocal behavior in capucin monkeys (Brosnan and de Waal, 2003), where cultural transmission, if any, is weak, strengthens this conclusion. Further support for our thesis comes from reports of individual, pre-existent acceptance thresholds shown by neural activity measurements in (Sanfey et al., 2003). In this respect, neural mechanisms gratifying cooperation as those demonstrated in (Rilling et al., 2002) may have evolved to reinforce behaviors selected for at the individual level as we are suggesting. Of course, those results do not preclude cultural influences in the brain control of altruistic behavior, which may play an important part in determining the experimentally observed thresholds. What is more relevant here is that individual thresholds do exist, with a large amount of individual variability, much like in our model, instead of a single culturally prescribed threshold. Evidence seems to favor one common threshold for acceptance and rejection but it is not strong enough to exclude the other version of the model. The detrimental effects of unfair sanctions on altruism (Fehr and Rockenbach, 2003) is yet another piece of evidence in favor of the existence of such individual acceptance ("fairness") thresholds.

In closing, let us emphasize that our conclusion that altruism does not necessarily have negative consequences for individuals draws such theories nearer to a biological perspective. Indeed, our results suggest that, despite its not being self-evident, altruistic strategies may do better in terms of fitness than selfish ones, even without repeated interactions or reputation gain. This conclusion, which would imply that strictly speaking there is no truly altruistic behavior, may have far-reaching implications in decision-making models and the design of public policies (Bowles et al., 2003a; Vogel, 2004).

Acknowledgments

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