Bulletin of Mathematical Biology (2002) **64**, 1101–1116
doi:10.1006/bulm.2002.0321
Available online at http://www.idealibrary.com on IDEAL®

Empathy Leads to Fairness

KAREN M. PAGE*
Bioinformatics Unit, Department of Computer Science,
University College London,
Gower Street,
London WC1E 6BT,
U.K.
E-mail: k.page@cs.ucl.ac.uk

MARTIN A. NOWAK
Institute for Advanced Study,
Einstein Drive,
Princeton,
NJ 08540,
U.S.A.

In the Ultimatum Game, two players are asked to split a prize. The first player, the proposer, makes an offer of how to split the prize. The second player, the responder, either accepts the offer, in which case the prize is split as agreed, or rejects it, in which case neither player receives anything. The rational strategy suggested by classical game theory is for the proposer to offer the smallest possible positive share and for the responder to accept. Humans do not play this way, however, and instead tend to offer 50% of the prize and to reject offers below 20%. Here we study the Ultimatum Game in an evolutionary context and show that empathy can lead to the evolution of fairness. Empathy means that individuals make offers which they themselves would be prepared to accept.

1. Introduction

An important aspect of understanding economic organizations and markets is studying the decisions made by individuals given well-defined choices. One model for human behavior in strategic interactions is given by the assumption of 'rationality', suggested by classical game theory. However, in many decision-making settings people do not behave as 'rational' agents who aim to maximize their own income. A simple example where such 'deviant' behavior arises, is given by the Ultimatum Game (Güth *et al.*, 1982).

*Author to whom correspondence should be addressed.

0092-8240/02/061101 + 16 $35.00/0

The rational solution in the Ultimatum Game emerges as follows: a rational responder, bent on maximizing his monetary payoff, should accept any nonzero offer. A rational proposer should therefore make the smallest nonzero offer, on the assumption that it will be accepted.

In experiments, human subjects do not play this way. They are far more apt to share the spoils and ready to punish individuals who do not want to share. The average offers are between 40 and 50% of the total sum, with 50% being the modal offer. One half of offers of 20% or less are rejected [see Thaler (1988), Güth and Tietze (1990), Roth *et al*. (1991), Bolton and Zwick (1995), Roth (1995), Sigmund *et al*. (2002)].

It has been suggested that people behave this way because they are maximizing a utility function which is not simply given by their monetary payoff, but rather includes some inequity aversion term (Kahnemann *et al*., 1986; Kirchsteiger, 1994; Bethwaite and Tompkinson, 1996; Fehr and Schmidt, 1999). Another explanation is that players do not understand that they play the game with each individual only once and so do not need to consider the effects of their behavior on future interaction (Rubinstein, 1982; Roth *et al*., 1991; Roth, 1995; Bolton and Ockenfels, 2000).

The Ultimatum Game has also been studied in the context of evolutionary game theory. In this framework players give rise to offspring in proportion to their total payoffs. Offspring inherit the strategies of their parents subject to a small mutational error. Evolutionary simulations of the standard Ultimatum Game lead to the evolution of strategies close to the rational strategy predicted by classical game theory, that is players offer negligible amounts and are prepared to accept those paltry offers. If, however, there is some probability of finding out about players' previous encounters and thus that reputation plays a role (Nowak *et al*., 2000) then fairness can evolve. Another mechanism for the evolution of fairness involves players playing with restricted groups of their spatial neighbors and competing with the same individuals for offspring (Page *et al*., 2000).

In this paper we show how empathy can lead to the evolution of fairness. In Section 2, we introduce a mechanism in which a fixed proportion, α, of players employ strategies with $p = q$, where p is the offer made by a player and q is the minimum offer that the player will accept. This leads to values of p and q close to $1/2$, the fair split. In this case, however, if α is allowed to evolve, it tends to zero and hence fairness does not evolve. We must therefore postulate that some other mechanism gives rise to a small proportion of 'empathic' players. We analyse the adaptive dynamics of this system in Section 2.2, first for the case of strong selection (Section 2.2.1) and then for the case of proportional selection (Section 2.2.2). In Section 3 we discuss an alternative approach to empathy in which players' strategies are given by their maximal offer p and minimum demand q. In this case players give offers uniformly distributed in $[0, p]$ with probability $1-\alpha$ and in $[q, p]$ with probability α. In this case α evolves towards 1 and fairness evolves. The adaptive dynamics of this system is analysed in the Appendix.

Table 1. Table of the time averages of the average offer and acceptance level within the population for different values of α. In each simulation, the population consists of 100 individuals and the time averages are performed over generations $10^5 - 10^6$. In the upper section, the mutation error $\mu = 0.01$ and in the lower section $\mu = 0.001$.

α	$\overline{p}$	$\overline{q}$
	$\mu = 0.01$	
0.0000	0.1115	0.0521
0.0010	0.1139	0.0542
0.0100	0.1443	0.0838
0.1000	0.3748	0.3236
0.2000	0.4448	0.3956
	$\mu = 0.001$	
0.0000	0.0557	0.0391
0.0010	0.0739	0.0568
0.0100	0.2944	0.2806
0.1000	0.4718	0.3236
0.2000	0.4919	0.3956

2. EMPATHY

We call the property of making offers the player himself would be prepared to accept, ‘empathy’. For a fuller discussion of the meaning and origin of empathy, see Preston and de Waal (2001). The following sections investigate the effects of empathy on the outcome of evolutionary simulations of the Ultimatum Game.

2.1. ***It only requires a small proportion of p = q-players to lead to the evolution of fair splits.*** Interestingly, we need only demand that a small proportion of players play strategies on the line $p = q$, to lead evolution towards strategies close to the fair split strategy. We assume that a proportion α of the total population plays $p = q$, either by offering their q-value or by demanding their p-value. We assume that this behavior is not passed on to their offspring who simply adopt the strategy (p, q) with probability $(1 - \alpha)$ and are randomly chosen to play a strategy on the line $p = q$ with probability α. The offspring are apportioned with probabilities proportional to the total scores of the parents.

Table 1 shows the average values of p and q obtained in simulations with various values of α. The number of individuals in the population was 100 and the mutational error was 0.01 and 0.001. The values were averaged over generations $10^5 - 10^6$. We can see that a small proportion of empathic ‘$p = q$’ players can lead to a significantly fairer outcome.

2.2. ***Adaptive dynamics.*** The standard adaptive dynamics framework derives a differential equation for the evolution of the average strategy within a population in terms of the continuous parameters describing the strategies. It is assumed that, at any one time, the population is homogeneous and a rare mutant with parameters close to those of the resident strategy is introduced. This strategy can invade if its payoff against the resident strategy is greater than the resident's own payoff against itself. The adaptive dynamical equation describes the evolution of the population strategy in the direction of the mutant which obtains the maximal payoff against the resident. For a parameter β, the equation is given by

$$\dot{\beta} = \left. \frac{\partial E(S'(\beta'), S(\beta))}{\partial \beta'} \right|_{S' \to S}. \tag{1}$$

This framework applies for a large population, provided that the payoffs are continuous in the parameters and there are no stable equilibria between strategies [see Nowak and Sigmund (1990), Metz *et al*. (1996), Geritz *et al*. (1997, 1998), Dieckmann (1997), Hofbauer and Sigmund (1998)].

The Ultimatum Game has payoffs which are discontinuous in p and q at the line $p = q$. In Page and Nowak (2001) we show how to extend the framework to apply to games which have discontinuities in their payoffs. We do so by replacing the payoff against a homogeneous resident by the average payoff against a slightly heterogeneous resident population.

Here we take the same approach for the game in which a player with strategy $S(p, q)$ plays (p, q) with probability $1 - \alpha$ and (q, q) with probability α. Thus the payoff obtained by a player with strategy $S'(p', q')$ against a population distributed in a small region around $S(p, q)$ is given by

$$\begin{aligned} E(S', \bar{S}) = (1-\alpha)^2 E_0(S'(p', q'), \bar{S}(p, q)) + \alpha(1-\alpha)[E_0(S'(q', q'), \bar{S}(p, q)) \\ + E_0(S'(p', q'), \bar{S}(q, q))] + \alpha^2 E_0(S'(q', q'), \bar{S}(q, q)), \end{aligned} \tag{2}$$

where E_0 represents the expected payoff in the standard Ultimatum Game.

We assume that the resident population has strategies uniformly distributed in an ϵ-neighborhood of (p, q), so that

$$E(S', \bar{S}) = \frac{1}{\epsilon^2} \int_{q-\epsilon/2}^{q+\epsilon/2} \int_{p-\epsilon/2}^{p+\epsilon/2} E(S', S_2) dp_2 dq_2. \tag{3}$$

The adaptive dynamical equations thus yield

$$\dot{p} = -(1-\alpha) \tag{4}$$

$$\dot{q} = \frac{\alpha}{\epsilon}(1-2q) - \frac{\alpha}{2}, \tag{5}$$

for $p > q + \epsilon/2$,

$$\dot{p} = 0 \tag{6}$$

$$\dot{q} = \frac{\alpha}{\epsilon}(1-2q) - \frac{\alpha}{2}, \tag{7}$$

for $p < q - \epsilon/2$ and

$$\dot{p} = \frac{1-\alpha}{\epsilon}\left(1 - 2p + q - \frac{\epsilon}{2}\right) \tag{8}$$

$$\dot{q} = \frac{\alpha}{\epsilon}(1-2q) - \frac{(1-\alpha)q}{\epsilon} - \frac{\alpha}{2}, \tag{9}$$

for $p \in [q - \epsilon/2, q + \epsilon/2]$.

Hence, for $p \in [q - \epsilon/2, q + \epsilon/2]$, p increases and q decreases, whereas for $p > q + \epsilon/2$, p decreases and q tends to a fixed value. Thus at equilibrium the system performs a two-cycle between two points close to and on opposite sides of the line $p = q + \epsilon/2$. We denote these two points by (p_1, q_1) and (p_2, q_2).

Close to the line $p = q + \epsilon/2$ we have to consider the exact type of selection. The dynamics depend on the way in which offspring are selected. We define 'proportional selection' to mean that each member of the subsequent generation is assigned a specific parent with probability proportional to that parent's total score. We define 'strong selection' to mean that the player with the highest total score in one generation gives rise to all the offspring in the next.

2.2.1. *Strong selection.* In the case of strong selection the point (p_1, q_1) will be the point with the highest score in the population uniformly distributed around (p_2, q_2) and vice versa.

We find that the score in a population centered around (p, q) is maximized by $p' = q + \epsilon/2$ and $q' = p - \epsilon/2$. Thus $p_1 \approx q_2 + \epsilon/2$ and $q_1 \approx p_2 - \epsilon/2$. In a finite population these equalities will not be exact and the score decreases from the maximum less rapidly on the sides $p' > q + \epsilon/2$ and $q' < p - \epsilon/2$, thus we expect $p_2 > q_1 - \epsilon/2$ and $q_2 < p_1 - \epsilon/2$. At equilibrium, we should have $p_2 + q_2 = p_1 + q_1$ and hence $\frac{\partial}{\partial t}(p+q) = 0$. Since $p_2 > q_1 - \epsilon/2$ and $q_2 < p_1 - \epsilon/2$, this implies [from equations (4) and (5)]

$$-(1-\alpha) + \frac{\alpha}{\epsilon}(1-2q) - \frac{\alpha}{2} = 0 \tag{10}$$

and hence

$$q = \frac{1}{2}\left(1 - \frac{(2-\alpha)\epsilon}{2\alpha}\right). \tag{11}$$

Thus the adaptive dynamics predict that for $\alpha \gg \epsilon$, the average strategy in the population will tend to a fair split.

We simulate a population of players who each play one another and who offer their p-values in a proportion $(1-\alpha)$ of the interactions and their q-values in the remaining proportion α. We use a deterministic payoff in which the payoff between two players is given by $1-\alpha$ times the payoff when the offerer gives his p-value plus α times the payoff when he gives his q-value, rather than assuming that in

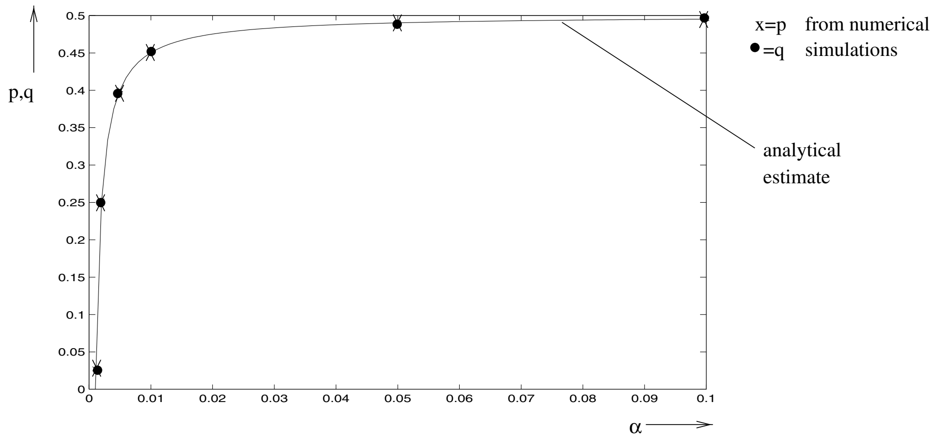

Figure 1. Plot of the time average of the population average of p (crosses) and q (dots) against α, in a simulation of the Ultimatum Game with strong selection, in which players offer their q-values a proportion α of the time. The line represents the analytical prediction from the adaptive dynamics. The values for p and q are almost identical. There were 100 individuals in the population, the mutation error/spread in the population was 0.001 and the averages were performed over generations 5000–50 000.

each interaction a player randomly chooses to offer his q-value with probability α. This corresponds to assuming that players interact many times. In each generation the player with the highest score is selected and gives rise to all the offspring in the following generation. These offspring have strategies uniformly distributed in an ϵ-neighborhood of the parental strategy. This process of strong selection means that we know that at any one time the population is uniformly distributed with spread ϵ.

Figure 1 shows the time average values of the average q-value in a population of 100 individuals with $\epsilon = 0.001$, for various values of α, compared with the analytical prediction for q of equation (15). There is good agreement.

2.2.2. *Proportional selection.* In the case of proportional selection, the strategies in the population will not be uniformly distributed, so that the calculations involved in the derivation of the adaptive dynamics will not be exact. However, we assume that they hold roughly and that ϵ is the effective spread in the population. In this case, the pressure to change p and q in the population centered around (p_1, q_1) must be equal and opposite to the pressure to change p and q in the population centered around (p_2, q_2). Thus, we should have $dp/dq(p_1, q_1) = dp/dq(p_2, q_2)$. Using equations (4), (5), (8) and (9) and assuming, without loss of generality, that $p_1 > q_1 + \epsilon/2$ and that $p_2 \in [q_2 - \epsilon/2, q_2 + \epsilon/2]$, we find that

$$\frac{-(1-\alpha)}{\frac{\alpha}{\epsilon}(1-2q_1) - \frac{\alpha}{2}} = \frac{\frac{1-\alpha}{\epsilon}(1 - 2p_2 + q_2 - \frac{\epsilon}{2})}{\frac{\alpha}{\epsilon}(1-2q_2) - \frac{(1-\alpha)q_2}{\epsilon} - \frac{\alpha}{2}}, \tag{12}$$

where $p_1 \approx p_2 \approx q_1 \approx q_2$.

To leading order in ϵ, this yields

$$a(1-2q_1)(1-q_1) = q_1 = p_1 = p_2 = q_2, \tag{13}$$

where $a = \alpha/(\epsilon(1-\alpha))$. This has solution

$$p_1 = q_1 = p_2 = q_2 = \frac{3a + 1 - \sqrt{1 + 6a + a^2}}{4a}. \tag{14}$$

For $a \gg 1$, $q \approx 1/2 - 1/(2a)$.

Thus, once again, the adaptive dynamics predict that for $\alpha \gg \epsilon$, the average strategy in the population will tend to a fair split.

We again perform numerical simulations in which players obtain payoffs equal to $1-\alpha$ times the payoff that they would get if they offered their p-values plus α times the payoff that they would get if they offered their q-values. Figure 2 shows the average p- and q-values in a population of 100 individuals, with mutational error 0.001, compared with the analytical estimate. In this case, we calculate the spread within the population from numerical simulations. We compute the standard deviation in p and in q within the population. We approximate the spread in the population by the value it would take if the population were uniformly distributed, that is $2\sqrt{3}\times$ the standard deviation. The agreement between the analytical estimate and the numerically computed average values of p and q, although less exact than in the strong selection case, is still good.

2.3. *Evolution of empathy.* Thus we have shown that fairness can evolve, if for some reason a fixed proportion of the population employs empathy. This proportion, α, can be very small and need only exceed the mutational spread, ϵ.

The disadvantage of this approach as an explanation of the evolution of fairness is that, if α itself is allowed to evolve, then it tends to zero and the offers and demands also tend to zero. The adaptive dynamical equation in α, for the case in which players offer their q-values with probability α, is given by

$$\dot{\alpha} = \frac{1-q}{2} - \begin{cases} (1-p) & p > q + \epsilon/2 \\ \frac{(1-p)(p-q+\epsilon/2)}{\epsilon} & p \in [q - \epsilon/2, q + \epsilon/2] \\ 0 & p < q - \epsilon/2. \end{cases} \tag{15}$$

Thus $\dot{\alpha} < 0$ for $p > q$. So, according to the adaptive dynamics, α will evolve towards 0.

Hence, in the present framework, we require external reasons for the existence of empathy in order to explain the evolution of fairness.

We note that the use of $p = q$ to induce fairness can work the other way round. We can show that if a proportion α instead demand as responders their p-value, then the offer, p, evolves towards $1/2$, for $\alpha \gg \epsilon$, but the demand q does not change, provided it is less than p. In simulations of the evolutionary dynamics, q drifts randomly in the region $q < 1/2$.

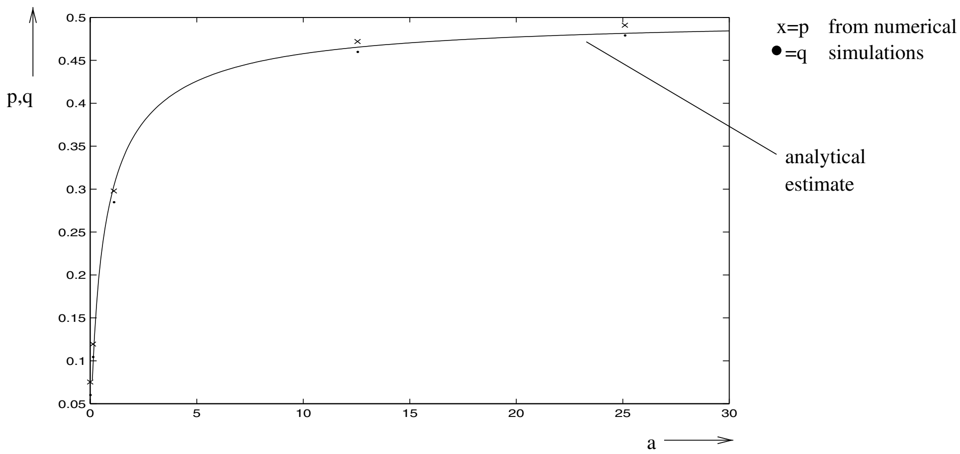

Figure 2. Plot of the time average of the population average of p (crosses) and q (dots) against $a = \alpha/(\text{spread}(1-\alpha))$, in a simulation of the Ultimatum Game with proportional selection, in which players offer their q-values a proportion α of the time. The line represents the analytical prediction from the adaptive dynamics. There were 100 individuals in the population, the mutation error was 0.001 and the averages were performed over generations 5000–50 000. The spread was estimated from the numerically computed standard deviations in p and q, which were roughly 0.0025 in all cases. The values of α range from 0.0 to 0.1.

3. An Alternative Approach to Empathy

Now we take a slightly different approach to the evolutionary Ultimatum Game. We once again assume that players have some minimal threshold proportion, q, of the sum which they are prepared to accept. This time we assume a more symmetrical form of strategy in which the players' p values determine the *maximum* offer that they are prepared to make. The actual offer in any one interaction is taken from a probability distribution on $[0, p]$. For simplicity we assume a uniform distribution on $[0, p]$. In each generation every player plays every other player once in the role of proposer and once in the role of responder. The payoffs from each interaction are added and the number of offspring that a player leaves is in proportion to his total payoff. Offspring inherit their parent's strategies plus or minus a small random error $\in [-\epsilon/2, \epsilon/2]$.

We numerically simulate this game with a population of 100 individuals and a mutational error of $\epsilon = 0.01$ over 100 000 generations. The results are shown in Fig. 3, where we plot the average offer ($= p/2$) and the average demand (q) in the population. As with the previous framework, the system evolves to one in which players offer and demand very small shares of the total sum.

Now, we introduce a probability α that a player always makes offers which he himself would be prepared to accept. The strategy of a player is now given by three parameters $S(p, q, \alpha)$. In any one interaction, with probability α, the player makes an offer from a uniform distribution in $[q, p]$ and, with probability $1-\alpha$, the player

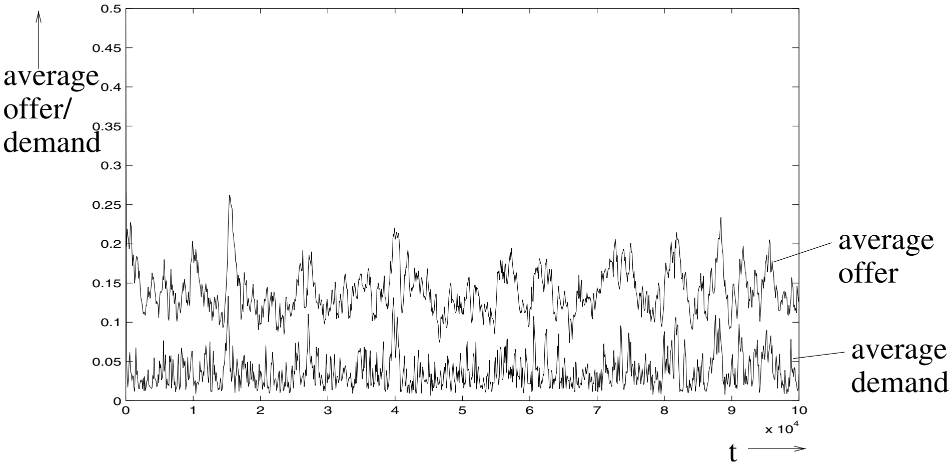

Figure 3. Numerical simulation of the evolutionary Ultimatum Game in which a player's strategy is determined by the parameters p, the maximum offer that he is prepared to make, and q, the minimum offer that he is prepared to accept. There are 100 individuals in the population, each of whom play one another once in the role of proposer and once in the role of responder. The number of offspring of a player is proportional to his total payoff. Offspring inherit their parent's strategies plus or minus a small random error in $[-0.005, 0.005]$. We plot the average offer $(p/2)$ in the population and the average demand (q) against time. We see that evolution leads near to the rational solution $p = q = 0$.

makes an offer from a uniform distribution in $[0, p]$. Figure 4 shows the results of a numerical simulation for a fixed value of α which is the same for all players. We see that, unlike in the model described above in which α refers to the probability of offering exactly one's q value, small α values do not have a dramatic impact on the long-term evolution and once again near rational strategies are obtained.

We now ask, however, what happens if α is allowed to evolve. Figure 5 shows the results of numerical simulations. We find that α tends to almost one and hence, ultimately, players are almost certain to make offers which they themselves would be prepared to accept. This empathy for their coplayers leads to the evolution of fair offers and demands.

We once again apply the modified adaptive dynamics (Page and Nowak, 2001) to the model described in this paper (see Appendix for details). We find

$$\dot{\alpha} = \left[\frac{1}{p-q} - \frac{1}{p}\right](1 - p/2 - q/2)(p-q) \tag{16}$$

and hence $\alpha \to 1$, provided $p > q$. For $\alpha = 1$,

$$\dot{p} = \frac{1}{(p-q)}\left[\begin{cases} \frac{q-p}{2} + \frac{\epsilon}{8}\frac{(1-q)}{(p-q)} + O\left(\frac{\epsilon^2}{p-q}\right) & p > q + \epsilon/2 \\ \frac{(1-p)(p-q)}{\epsilon} - 1/2 + \frac{q}{2} + \frac{\epsilon}{8}\frac{(1-q)}{(p-q)} + O\left(\frac{\epsilon^2}{p-q}\right) & q < p < q + \epsilon/2 \end{cases}\right] \tag{17}$$

$$\dot{q} = \frac{1 - p - q}{2(p-q)} + o(1). \tag{18}$$

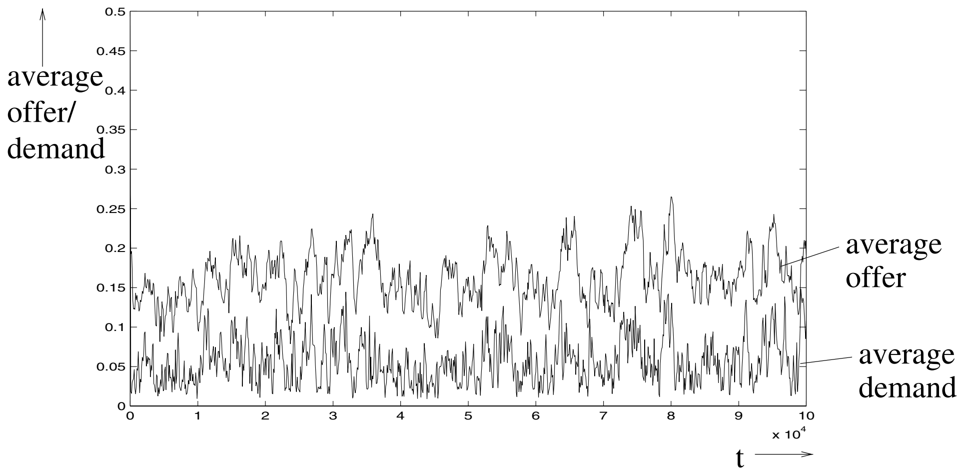

Figure 4. Numerical simulation of the evolutionary Ultimatum Game in which a player's strategy is determined by the parameters p, the maximum offer that he is prepared to make, and q, the minimum offer that he is prepared to accept. There are 100 individuals in the population, each of whom play one another once in the role of proposer and once in the role of responder. The number of offspring of a player is proportional to his total payoff. Offspring inherit their parent's strategies plus or minus a small random error in $[-0.005, 0.005]$. We plot the average offer $(p/2+\alpha q/2)$ in the population and the average demand (q) against time. In these simulations a player has a probability 0.1 of always making offers in the range $[q, p]$ rather than $[0, p]$. The average offers and demands are not very different from the case $\alpha = 0.0$ shown in Fig. 1.

Thus, to leading order, at equilibrium

$$p = q = \tfrac{1}{2}. \tag{19}$$

Thus, the modified adaptive dynamics support the results of these simulations and predict the emergence of fairness in this case.

4. Conclusions

For the Ultimatum Game, both classical game theory and standard evolutionary game theory predict that players will offer and accept negligibly small proportions of the total sum to be shared. In experiments, human subjects do not play that way. They usually reject offers as high as 30% of the total and offer between 40 and 50%. Here, we show that, if a small proportion of players project their acceptance thresholds on to others and offer what they themselves would be prepared to accept, then this leads to the evolution of players who demand and offer a fair share of the total sum. We show that this evolution is predicted by (a modified version of) the adaptive dynamics. The analysis shows that offering one's q-value introduces a pressure for q to increase in order to avoid rejection. This pressure on q to increase

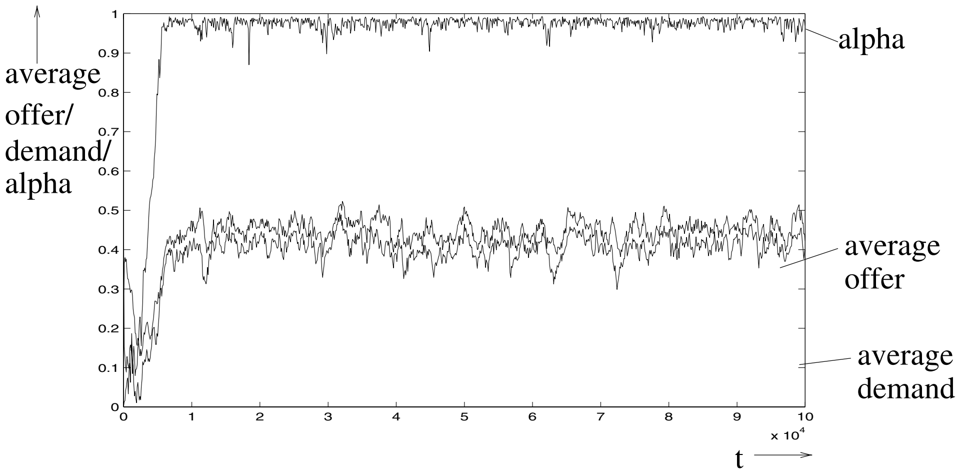

Figure 5. Numerical simulation of the evolutionary Ultimatum Game in which a player's strategy is determined by the parameters p, the maximum offer that he is prepared to make, and q, the minimum offer that he is prepared to accept. There are 100 individuals in the population, each of whom play one another once in the role of proposer and once in the role of responder. The number of offspring of a player is proportional to his total payoff. Offspring inherit their parent's strategies plus or minus a small random error in $[-0.005, 0.005]$. We plot the average offer $(p/2+\alpha q/2)$ in the population and the average demand (q) against time. In these simulations a player has a probability α of always making offers in the range $[q, p]$ rather than $[0, p]$. Initially all players have $\alpha = 0.0$, but α is allowed to evolve and is subject to a mutational error in each generation which is randomly distributed in $[-0.005, 0.005]$. We plot the average value of α within the population against time. We see that α evolves towards 1.0 and that the fact that players always make offers that they themselves would accept leads to the evolution of equal sharing of the total prize.

in turn creates a pressure for p to increase. However, in this context, evolution favors $\alpha \rightarrow 0$, where α is the probability that a player offers his acceptance threshold, and hence neither empathy nor fairness will evolve. Thus we must rely on α being set by other processes if we are to see the evolution of fairness. We should note that by fairness, in this context, we refer to an even split of the total sum to be shared. It is of interest that fairness has been described by others as 'some type of do-as-you-would-be-done-by principle' (Binmore, 2001), which in our discussion is somewhat similar to the notion of empathy and offering what you yourself would accept.

We have also studied an alternative set-up in which a player offers anything up to his p-value with probability $1 - \alpha$. With probability α he offers at least his q-value. We have found that in this context in the Ultimatum Game, empathy is evolutionarily favored and results also in the evolution of equal sharing of the prize. This is independent of an assortative structuring of the population or of knowledge of other players' strategies, such as is necessary in reputation effects and strategies designed for repeated interactions, or of the possession of a utility function more complicated than the monetary payoff. We have shown how evolutionary game theory can explain human behavior in the Ultimatum Game, which is not explicable by classical game theory. In this context players' strategies have an intermediate level of complexity. They are more sophisticated than the simple prescribed strategies in which a player offers p and demands q, according to his genetic programming, but they do not require the level of reasoning of the classical 'rational' player who must reason about his opponent's rationality. Here he simply asks, 'how would I behave in his place?'

APPENDIX

Strategies are given by the maximal offer, p, that a player is prepared to make, the minimal offer, q, that he will accept and the probability, α, that he always makes an offer that he himself would accept. The actual offer, x, made by a player in a given interaction is uniformly distributed in $[0, p]$, with probability $1-\alpha$ and in $[q, p]$ with probability α.

Thus the expected score obtained by a player with strategy $S'(p', q', \alpha')$ against a player with strategy $S(p, q, \alpha)$ is given by

$$\begin{aligned} E(S', S) = &\frac{\alpha'}{p'-q'}\int_{q'}^{p'}(1-x')H(x'-q)dx' \\ &+ \frac{(1-\alpha')}{p'}\int_0^{p'}(1-x')H(x'-q)dx' \\ &+ \frac{\alpha}{p-q}\int_q^p xH(x-q')dx + \frac{(1-\alpha)}{p}\int_0^p xH(x-q')dx, \end{aligned} \tag{A.1}$$

where H is the Heaviside function.

Thus against a population with strategies (p, q) uniformly distributed in $[p - \epsilon/2, p+\epsilon/2] \times [q-\epsilon/2, q+\epsilon/2]$, the player with strategy S' scores on average

$$E(S', \bar{S}) = \frac{1}{\epsilon^2}\int_{p-\epsilon/2}^{p+\epsilon/2}\int_{q-\epsilon/2}^{q+\epsilon/2} E(S', S)dqdp. \tag{A.2}$$

The modified adaptive dynamics [see Page and Nowak (2001)] thus yields

$$\begin{aligned} \dot{\alpha} = &\left.\frac{\partial E(S', \bar{S})}{\partial \alpha'}\right|_{S'\to S} \\ = &\frac{1}{p-q}\int_q^p (1-x')H(x'-q)dx' - \frac{1}{p}\int_0^p (1-x')H(x'-q)dx' \\ = &\left[\frac{1}{p-q} - \frac{1}{p}\right]\int_q^p (1-x')dx' \\ > &\, 0 \text{ (provided } p > q). \end{aligned} \tag{A.3}$$

Thus, the adaptive dynamics predicts that $\alpha \to 1$, as $t \to \infty$.
So we consider the dynamics for p and q, with $\alpha = 1$. We have

$$\dot{p} = \frac{\partial}{\partial p'}\left[\frac{1}{p'-q'}\frac{1}{\epsilon^2}\int_{p-\epsilon/2}^{p+\epsilon/2}\int_{q-\epsilon/2}^{q+\epsilon/2}\int_{q'}^{p'}(1-x')H(x'-q)dx'\right]dqdp\Bigg|_{S'\to S} \tag{A.4}$$

$$= \frac{1}{p-q}\frac{1}{\epsilon}\int_{q-\epsilon/2}^{q+\epsilon/2}(1-p)H(p-q)dq$$

$$-\frac{1}{(p-q)^2}\frac{1}{\epsilon}\int_{q-\epsilon/2}^{q+\epsilon/2}\int_{q}^{p}(1-x')H(x'-q)dx'dq$$

$$= \frac{1}{(p-q)^2}\frac{1}{\epsilon}\left[(1-p)(p-q)\begin{cases}\epsilon & p>q+\epsilon/2\\ p-q+\epsilon/2 & q<p<q+\epsilon/2\end{cases}\right.$$

$$\left.-\int_{q-\epsilon/2}^{q+\epsilon/2} p - Max(q,q') - p^2/2 + Max(q,q')^2/2dq\right]$$

$$= \frac{1}{(p-q)^2}\left[(1-p)(p-q)\begin{cases}\epsilon & p>q+\epsilon/2\\ \frac{p-q}{\epsilon}+1/2 & q<p<q+\epsilon/2\end{cases}\right.$$

$$\left.-p+p^2/2+\frac{1}{\epsilon}\int_{q}^{q+\epsilon/2}(q-q^2/2)dq+\frac{1}{2}(q-q^2/2)\right]$$

$$= \frac{1}{(p-q)^2}\left[(1-p)(p-q)\begin{cases}\epsilon & p>q+\epsilon/2\\ \frac{p-q}{\epsilon}+1/2 & q<p<q+\epsilon/2\end{cases}\right.$$

$$\left.-p+p^2/2+\frac{[(q+\epsilon/2)^2-q^2]}{2\epsilon}-\frac{[(q+\epsilon/2)^3-q^3]}{6\epsilon}+\frac{1}{2}(q-q^2/2)\right]$$

$$= \frac{1}{(p-q)}\left[(1-p)\begin{cases}1 & p>q+\epsilon/2\\ \frac{p-q}{\epsilon}+1/2 & q<p<q+\epsilon/2\end{cases} -1+\frac{p+q}{2}+\frac{1}{(p-q)}\left(\frac{\epsilon}{8}-\frac{\epsilon}{8}q-\frac{\epsilon^2}{48}\right)\right]$$

$$= \frac{1}{(p-q)}\left[\begin{cases}\frac{q-p}{2}+\frac{\epsilon}{8}\frac{(1-q)}{(p-q)}+O\left(\frac{\epsilon^2}{p-q}\right) & p>q+\epsilon/2\\ \frac{(1-p)(p-q)}{\epsilon}-1/2+\frac{q}{2}+\frac{\epsilon}{8}\frac{(1-q)}{(p-q)}+O\left(\frac{\epsilon^2}{p-q}\right) & q<p<q+\epsilon/2\end{cases}\right]. \tag{A.5}$$

Thus we find that $\dot{p} > 0$ when $0 < p - q < 1/2\sqrt{\epsilon(1-q)}$. Now

$$\dot{q} = -\frac{1}{p-q}(1-q)\frac{1}{\epsilon}\int_{q-\epsilon/2}^{q+\epsilon/2}H(q'-q)dq$$

$$+\frac{1}{(p-q)^2}\frac{1}{\epsilon}\int_{q-\epsilon/2}^{q+\epsilon/2}\int_{q'}^{p}(1-x')H(x'-q)dx'dq$$

$$-\frac{1}{\epsilon^2}\int_{p-\epsilon/2}^{p+\epsilon/2}\int_{q-\epsilon/2}^{q+\epsilon/2}\int_{q}^{p}x\delta(x-q')dxdqdp \tag{A.6}$$

$$= -\frac{1-q}{2(p-q)}+\frac{1}{(p-q)^2}\frac{1}{\epsilon}\int_{q-\epsilon/2}^{q+\epsilon/2}p-p^2/2-Max(q,q')+Max(q,q')^2/2dq$$

$$-\frac{1}{\epsilon^2}\int_{p-\epsilon/2}^{p+\epsilon/2}\int_{q-\epsilon/2}^{q+\epsilon/2}\frac{q'H(q'-q)H(p-q')}{p-q}dpdq$$
$$=-\frac{1-q}{2(p-q)}+\frac{1}{(p-q)^2}\Bigg[p-p^2/2-\frac{1}{2}(q-q^2/2)-\frac{1}{2\epsilon}\Bigg[(q+\epsilon/2)^2-q^2$$
$$-\frac{1}{3}(q+\epsilon/2)^3+\frac{1}{3}q^3\Bigg]\Bigg]-\frac{q}{\epsilon^2}\int_{p-\epsilon/2}^{p+\epsilon/2}\int_{q-\epsilon/2}^{q}\frac{H(p-q')}{p-q}dqdp$$
$$=\frac{1}{(p-q)^2}\Bigg[-\frac{(1-q)(p-q)}{2}+p-p^2/2-\frac{1}{2}(q-q^2/2)-q/2$$
$$-\epsilon/8+q^2/4+\epsilon q/8+\epsilon^2/48\Bigg]+\frac{q}{\epsilon^2}\int_{p-\epsilon/2}^{p+\epsilon/2}ln\left(\frac{p-q}{p-q+\epsilon/2}\right)H(p-q)dp.$$

Now at equilibrium, we will have $p-q$ is $O(\sqrt{\epsilon})$ and so $p-\epsilon/2>q$ and $H(p-q)$ is 1 for all values of p in the above integral. Thus

$$\dot{q}=\frac{1}{p-q}\Bigg[-(1-q)/2+1-(p+q)/2-\frac{\epsilon(1-q)}{8(p-q)}+\frac{O(\epsilon^2)}{p-q}\Bigg]$$
$$+\frac{q}{\epsilon^2}\int_{p-\epsilon/2}^{p+\epsilon/2}ln\Bigg[1-\frac{\epsilon/2}{p-q+\epsilon/2}\Bigg]dp$$
$$=\frac{1}{p-q}\Bigg[\frac{1-p}{2}-\frac{\epsilon(1-q)}{8(p-q)}+\frac{O(\epsilon^2)}{p-q}\Bigg]$$
$$+\frac{q}{\epsilon^2}\int_{p-\epsilon/2}^{p+\epsilon/2}ln\Bigg[1-\frac{\epsilon/2}{p-q+\epsilon/2}\Bigg]dp$$
$$=\frac{1}{p-q}\frac{1-p}{2}-\frac{q}{2\epsilon}\int_{p-\epsilon/2}^{p+\epsilon/2}\frac{1}{p-q+\epsilon/2}dp+o(1)$$
$$=\frac{1}{p-q}\frac{1-p}{2}-\frac{q}{2\epsilon}ln\frac{p-q+\epsilon}{p-q}+o(1)$$
$$=\frac{1}{p-q}\frac{1-p}{2}-\frac{q}{2(p-q)}+o(1)$$
$$=\frac{1-p-q}{2(p-q)}+o(1). \tag{A.7}$$

Thus to leading order, at equilibrium,

$$p=q=\tfrac{1}{2}. \tag{A.8}$$

So the adaptive dynamics agrees with numerical simulations in predicting that $\alpha\to 1$ and $p,q\to\frac{1}{2}$ as $t\to\infty$.

References

Bethwaite, J. and P. Tompkinson (1996). The ultimatum game and non-selfish utility functions. *J. Econ. Psychol.* **17**, 259–271.

Binmore, K. (2001). How and why did fairness norms evolve? *Proc. British Acad.* **110**, 149–170.

Bolton, G. E. and A. Ockenfels (2000). A theory of equity, reciprocation and competition. *Am. Econ. Rev.* **90**, 166–193.

Bolton, G. E. and R. Zwick (1995). Anonymity versus punishment in ultimatum bargaining. *Game Econ. Behav.* **10**, 95–121.

Dieckmann, U. (1997). Can adaptive dynamics invade? *Trends Ecol. Evol.* **12**, 128–131.

Fehr, E. and K. M. Schmidt (1999). A theory of fairness, competition and cooperation. *Q. J. Econ.* **114**, 817–868.

Geritz, S. A. H., J. A. J. Metz, E. Kisdi and G. Meszena (1997). Dynamics of adaptation and evolutionary branching. *Phys. Rev. Lett.* **78**, 2024–2027.

Geritz, S. A. H., E. Kisdi, G. Meszena and J. A. J. Metz (1998). Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.* **12**, 35–37.

Güth, W., R. Schmittberger and B. Schwarze (1982). An experimental analysis of ultimatum bargaining. *J. Econ. Behavior Organization* **3**, 367–388.

Güth, W. and R. Tietze (1990). Ultimatum bargaining behavior, a survey and comparison of experimental results. *J. Econ. Psychol.* **11**, 417–449.

Hofbauer, J. and K. Sigmund (1998). *Evolutionary Games and Population Dynamics*, Cambridge: Cambridge University Press.

Kahnemann, D., J. L. Knetsch and R. Thaler (1986). Fairness and the assumptions of economics. *J. Bus.* **59**, S258–S300.

Kirchsteiger, G. (1994). The role of envy in ultimatum games. *J. Econ. Behavior Organisation* **25**, 373–389.

Metz, J. A. J., S. A. H. Geritz, F. J. Meszena, F. J. A. Jacobs and J. S. van Heerwaardenm (1996). Adaptive dynamics: a geometrical study of the consequences of nearly faithful reproduction, in *Stochastic and Spatial Structures in Dynamical Systems*, S. J. Van Strien and S. M. Verduyn Lunel (Eds), Amsterdam: North Holland, pp. 183–231.

Nowak, M. A., K. M. Page and K. Sigmund (2000). Fairness versus reason in the Ultimatum Game. *Science* **289**, 1773–1775.

Nowak, M. A. and K. Sigmund (1990). The evolution of reactive strategies in iterated games. *Acta Applicandae Math.* **20**, 247–265.

Page, K. M. and M. A. Nowak (2001). A generalized adaptive dynamics framework can describe the evolutionary Ultimatum Game. *J. Theor. Biol.* **209**, 173–179.

Page, K. M., M. A. Nowak and K. Sigmund (2000). The spatial ultimatum game. *Proc. Roy. Soc. Lond. B* **267**, 2177–2182.

Preston, S. D. and F. B. M. de Waal (2001). Empathy: Its ultimate and proximate bases. *Behav. Brain Sci.* (in press).

Roth, A. E., V. Prasknikar, M. Okuno-Fujiwara and S. Zamir (1991). Bargaining and market power in Jerusalem, Ljubljana, Pittsburgh and Tokyo. *Am. Econ. Review* **81**, 1068–1095.

Roth, A. E. (1995). Bargaining experiments, in *Handbook of Experimental Economics*, J. Kagel and A. E. Roth (Eds), Princeton University Press.

Rubinstein, A. (1982). Perfect equilibrium in a bargaining model. *Econometrica* **50**, 97–110.

Sigmund, K., E. Fehr and M. A. Nowak (2002). The economics of fair play. *Sci. Am.* **286**, 82–87.

Thaler, R. H. (1988). The Ultimatum Game. *J. Econ. Perspectives* **2**, 195–206.

Received 15 May 2002 and accepted 28 August 2002