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Evolution

Chaos and the evolution of cooperation

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ABSTRACT The "iterated prisoner's dilemma" is the most widely used model for the evolution of cooperation in biological societies. Here we show that a heterogeneous population consisting of simple strategies, whose behavior is totally specified by the outcome of the previous round, can lead to persistent periodic or highly irregular (chaotic) oscillations in the frequencies of the strategies and the overall level of cooperation. The levels of cooperation jump up and down in an apparently unpredictable fashion. Small recurrent and simultaneous invasion attempts (caused by mutation) can change the evolutionary dynamics from converging to an evolutionarily stable strategy to periodic oscillations and chaos. Evolution can be twisted away from defection, toward cooperation. Adding "generous tit-for-tat" greatly increases the overall level of cooperation and can lead to long periods of steady cooperation. Since May's paper [May, R. M. (1976) *Nature (London)* 261, 459–467], "simple mathematical models with very complicated dynamics" have been found in many biological applications, but here we provide an example of a biologically relevant evolutionary game whose dynamics display deterministic chaos. The simulations bear some resemblance to the irregular cycles displayed by the frequencies of host genotypes and specialized parasites in evolutionary "arms races" [Hamilton, W. D., Axelrod, R. & Tanese, R. (1990) *Proc. Natl. Acad. Sci. USA* 87, 3566–3573; Seger, J. (1988) *Philos. Trans. R. Soc. London B* 319, 541–555].

The Prisoner's Dilemma (PD) is a two-player game: each player can opt for one of the two strategies C (to cooperate) and D (to defect). If both players cooperate, their payoff R is higher than the payoff P for joint defection. But a player defecting unilaterally obtains a payoff T, which is larger than R, while the opponent ends up with a payoff S, which is smaller than P. In addition to this rank ordering, one usually also assumes that $2R < S + T$. (For our numerical simulations we shall use the values $T = 5$, $R = 3$, $P = 1$, and $S = 0$.)

The rational decision in this game is to play D, since this yields the higher payoff no matter whether the opponent uses C or D. As a result, both players defect and earn P instead of the larger reward R for joint cooperation.

If the probability that the players repeat the interaction is sufficiently high, there is no longer a single best strategy for this iterated PD (IPD). But a series of computer tournaments by Axelrod (1) established the success of a remarkably simple strategy, TFT (tit-for-tat), which consists of playing C in the first round and from then on repeating whatever the adversary did in the previous round. This led Axelrod and Hamilton (2) to use the IPD for explaining the evolution of cooperation in biological interactions on the basis of reciprocity (see also ref. 3). This approach has proved to be extremely fruitful. It is not the only paradigm, but certainly it is the most current in the field (4–11).

While reciprocal interactions abound in nature, it is usually difficult to find clear-cut empirical evidence for the implementation of the TFT strategy (12–14). Furthermore, the uncertainties and mistakes surrounding most biological interactions penalize TFT populations, since any accidental defection entails a series of alternating retaliations. This vulnerability to errors is not evident under the clinical conditions of computer runs. In applications, however, it should not be overlooked: even human interactions are not immune from mistakes. Moreover, a TFT population can be subverted, through random drift, by unconditional cooperators who in turn can be invaded by defectors.

Generous TFT (GTFT) is a simple probabilistic strategy that can overcome mistakes; like TFT it cooperates after the opponent has cooperated in the previous round, but it also cooperates with probability $q = \min\{1 - (T - R)/(R - S), (R - P)/(T - P)\}$ after the opponent has defected (15–17). For our parameter values this is $q = 1/3$. This strategy has been very successful in evolutionary simulations of heterogeneous populations, and its emergence in populations is catalyzed by TFT (18).

Errors and contingent perturbations present difficulties for game-theory solutions—cf. the "trembling hand" behind Selten's notion of a perfect equilibrium (19). Biologically motivated concepts such as evolutionary stability or unbeatable strategies assume that the population is homogeneous and can repel mutant strategies invading one at a time (20, 21). However, an evolutionarily stable equilibrium need not be attainable (22). Furthermore, the population need not be able to repel several invaders at once. Like Binmore and Samuelson (23), we feel that "overlapping invasions seem more suited to a social context." No pure strategy in the IPD can be stable in this sense (24).

Here we investigate the evolutionary dynamics of strategy frequencies in heterogeneous populations subject to a background of continuous invasion attempts, and we consider the effects of chronic "noisiness" that blurs both the actions and the perceptions of individual players. We retain the simplifying assumption that the interactions between two players are repeated infinitely often. The qualitative results, however, do not depend on the assumption of an infinitely iterated PD.

Let us consider strategies which are entirely specified by the outcome of the previous round. Such strategies can be described by a quadruple of parameters, (p_1, p_2, p_3, p_4), which denote the probabilities to cooperate after receiving payoffs R, S, T, and P, respectively, in the previous round. A strategy is deterministic if all four p values are exactly either 0 or 1. For example, (0, 0, 0, 0) is the deterministic rule that always defects (AllD), whereas (1, 0, 1, 0) cooperates after receiving R or T but defects after S or P. This means that it imitates the adversary's previous move. A strategy with this rule and initial move C plays TFT; with initial move D, it plays "suspicious" TFT. The strategy (1, 1, 0, 0) remains in its initial state forever. With initial state C, the rule (1, 0, 0, 0) plays GRIM: after a single D of the adversary, it never

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Abbreviations: PD, Prisoner's Dilemma; IPD, iterated PD; TFT, tit-for-tat; GTFT, generous TFT; AllD, always defect; AllC, always cooperate.

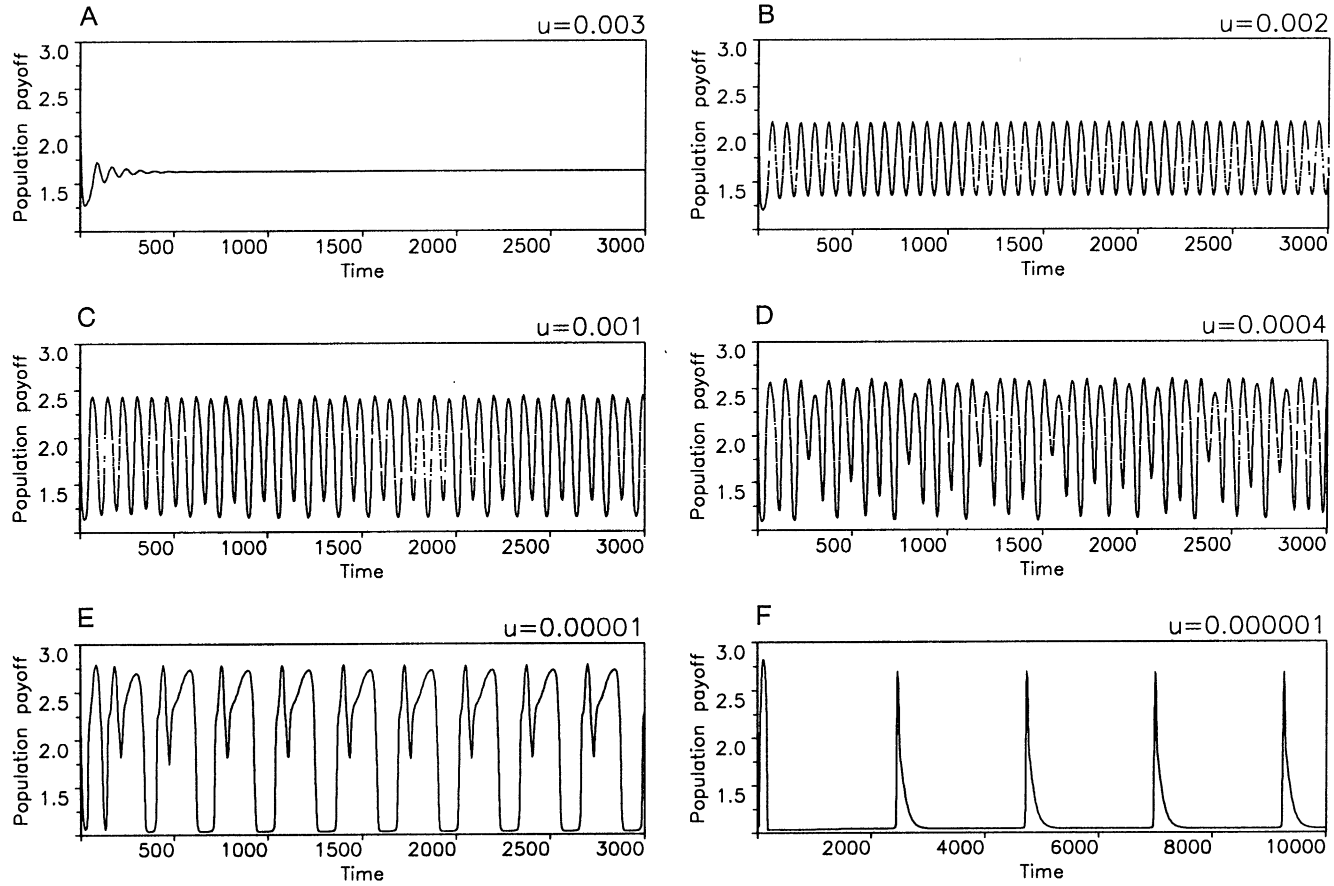

FIG. 1. Oscillations and chaos for a system containing the 16 (deterministic, but including a small amount of noise) strategies which are totally specified by the outcome of the previous round. If the mutation rate, u, is sufficiently high, we obtain a stable equilibrium among all the 16 strategies. For $u = 0.003$ this equilibrium is approached in damped oscillations (*A*). For $u = 0.002$ (*B*) and $u = 0.001$ (*C*) we observe periodic oscillations in the overall level of cooperation (with period 2 and 4, respectively). This period doubling continues, and for $u = 0.0004$ (*D*) the oscillations become aperiodic. For still smaller mutation, $u = 0.00001$, we return to stable oscillations (*E*). For $u = 0.000001$ there are long periods of defection interrupted by sudden outbreaks of cooperation (*F*). The average time from one peak in cooperation to the next is about 75 generations for $u = 0.002$, 0.001, or 0.0004; 500 generations for $u = 0.00001$; and 2300 generations for $u = 0.000001$. Without mutation (i.e., $u = 0$) the system converges to one of the two evolutionarily stable strategies, AllD or GRIM, depending on the initial conditions. Note that a very small amount of mutation leads to the coexistence of strategies. For this effect see also refs. 30–32. This example shows how recurrent invasions can change the classical picture of evolutionary game dynamics, and replace the steady approach to an evolutionarily stable strategy by complex oscillations and chaos. Here the error frequency for the strategies in the IPD is $\varepsilon = 0.01$.

reverts to C again. With initial state C, rule (1, 0, 0, 1) cooperates whenever both players choose the same action in the previous round. It fares poorly against AllD, since it reverts each second round to C. For this reason, it has been called "simpleton" by Rapoport and Chammah (25). We think that this appellation is not entirely deserved; following Kraines and Kraines (26), we prefer to call it PAVLOV, since it responds to positive and negative conditioning (switching its behavior whenever one round's payoff is lower than R) and embodies a learning mechanism of basic interest in social psychology (27–29). There are 16 deterministic rules altogether, which we number from 0 to 15 (the ith quadruple being the binary expression for i). The strategy corresponding to rule i will be denoted by S_i. Thus S_0 is AllD, S_9 is PAVLOV, S_{10} is TFT, and S_{15} is AllC. The S_i strategies are exactly the 16 corner points of the four-dimensional strategy space formed by all (p_1, p_2, p_3, p_4) strategies.

We shall now take uncertainty into account by replacing 1 by $1 - \varepsilon$ and 0 by ε in the quadruples. The small probability ε describes the frequency of errors. If $\varepsilon > 0$ the first round no longer matters. The total payoff can be defined as the limit of the mean payoff per round. The game between the two players, $S = (p_1, p_2, p_3, p_4)$ and $S' = (p_1', p_2', p_3', p_4')$, is a Markov process given by the transition probability matrix

$$\begin{bmatrix} p_1p_1' & p_1(1-p_1') & (1-p_1)p_1' & (1-p_1)(1-p_1') \\ p_2p_3' & p_2(1-p_3') & (1-p_2)p_3' & (1-p_2)(1-p_3') \\ p_3p_2' & p_3(1-p_2') & (1-p_3)p_2' & (1-p_3)(1-p_2') \\ p_4p_4' & p_4(1-p_4') & (1-p_4)p_4' & (1-p_4)(1-p_4') \end{bmatrix}$$

The stationary distribution (s_1, s_2, s_3, s_4) is the lefthand eigenvector corresponding to the eigenvalue 1. The payoff for strategy S is then given by $Rs_1 + Ss_2 + Ts_3 + Ps_4$. By this change, the payoff for a TFT player against another drops from 3 to 2.25; against GRIM, it drops from 3 to about 1, etc. On the other hand, a pair of PAVLOV players handle accidental mistakes quite well: they both play D for one round and then revert to C. Against GRIM or TFT, PAVLOV suffers from errors, however. Among the 16 S_i strategies AllD and GRIM are the only evolutionarily stable strategies. There are three strategies that receive a payoff very close to full cooperation ($R = 3$) when playing against themselves: these are AllC, (1, 1, 1, 0), and PAVLOV.

We now consider a large population of players using the strategies S_0 to S_{15}. By x_i, we denote the frequency of S_i in a given generation. In each generation all the strategies play the infinitely iterated PD among one another (subject to a small error frequency, ε). It is easy to compute the average payoff f_i for an S_i player (which depends on the composition of the population). The evolutionary dynamics map the frequencies x_i after one generation into x_i' according to the following rule: first selection provides each S_i strategist with a number of offspring proportional to its expected payoff f_i (the higher the payoff, the more offspring). To this is added a tiny number of invaders, u, which may be caused by mutation. This yields a deterministic recurrence equation for the frequencies of the strategies:

$$x_i' = \left(\frac{x_i f_i}{\sum x_i f_i} + u\right)/(1 + nu), \qquad i = 1, \ldots, n.$$

Here n denotes the total number of strategies in the population.

This modification of the usual game dynamics allows for recurrent and simultaneous invasion attempts. The resulting dynamics can exhibit complicated periodic and even chaotic orbits (see Figs. 1 and 2). The most interesting dynamics occur around $u = 0.0004$. Here the strategies S_4, S_6, S_7, and S_{12} are driven almost to extinction, but the other strategies and the total payoff for the population display violent oscillations (with large amplitudes for strategies S_0, S_1, S_8, S_9, S_{10}, and S_{11}). The minima of their frequencies are very close to 0, except for the TFT-like strategy S_{10}, which is best protected against extinction and is in this sense the "safest bet." But whenever the proportion of TFT players is large, they are superseded by the more generous strategy S_{11} [whose transition rule (1, 0, 1, 1) forgives a defection by the other player if it was matched by a defection of its own] and PAVLOV (S_9). The S_{11} and PAVLOV population, in turn, is invaded by the parasitic S_1 (which cooperates only if its defection has met with instant chastisement). This paves the way for the strategies close to AllD (S_0) and to GRIM (S_8), which in turn leads to the resurgence of TFT. This is the main cycle in the selective mechanics, but the other strategies introduce the twists leading to chaos. Figs. 1 and 2 show the dynamics for the error frequency $\varepsilon = 0.01$, but other values of ε give essentially the same results; for example, $\varepsilon = 0.001$, $\varepsilon = 0.0001$, and even the limiting case, $\varepsilon \rightarrow 0$. Thus the observed complicated dynamics is not a consequence of using highly erroneous strategies, it can also be observed for arbitrary small values of ε. (But note that for $\varepsilon = 0$ the first moves become important in some interactions. These additional complications will be analyzed in a more technical paper.) For large error frequencies—e.g., $\varepsilon = 0.1$—the interesting dynamics disappear and the population is dominated by defecting strategies.

Chaos and irregular oscillations seem to be robust features of the IPD. Not all the 16 S_i strategies are necessary to display chaotic behavior. Smaller systems can be chaotic as well. (The smallest chaotic system that we found consists of the 10 S_i strategies AllD, S_1, S_3, S_5, GRIM, PAVLOV, TFT, S_{11}, S_{13}, and S_{14}.) Chaos can also be found if one includes a number of other stochastic strategies, given by some arbitrary probabilities (p_1, p_2, p_3, p_4). Complicated dynamics can also be observed within the subset of simpler strategies which are specified by the opponent's last move (33).

This erratic evolution can be strongly biased toward cooperation if one includes GTFT. We have studied the evolutionary dynamics of a population which consists of the 16 S_i strategies and GTFT. For larger mutation rates, GTFT makes the oscillations more regular (allowing only period 2) and increases slightly the overall level of cooperation. For small mutation rates, we even find a stable equilibrium dominated by GTFT. For $u = 0.000001$, for example, the equilibrium frequency of GTFT is 0.98 and the overall level of cooper-

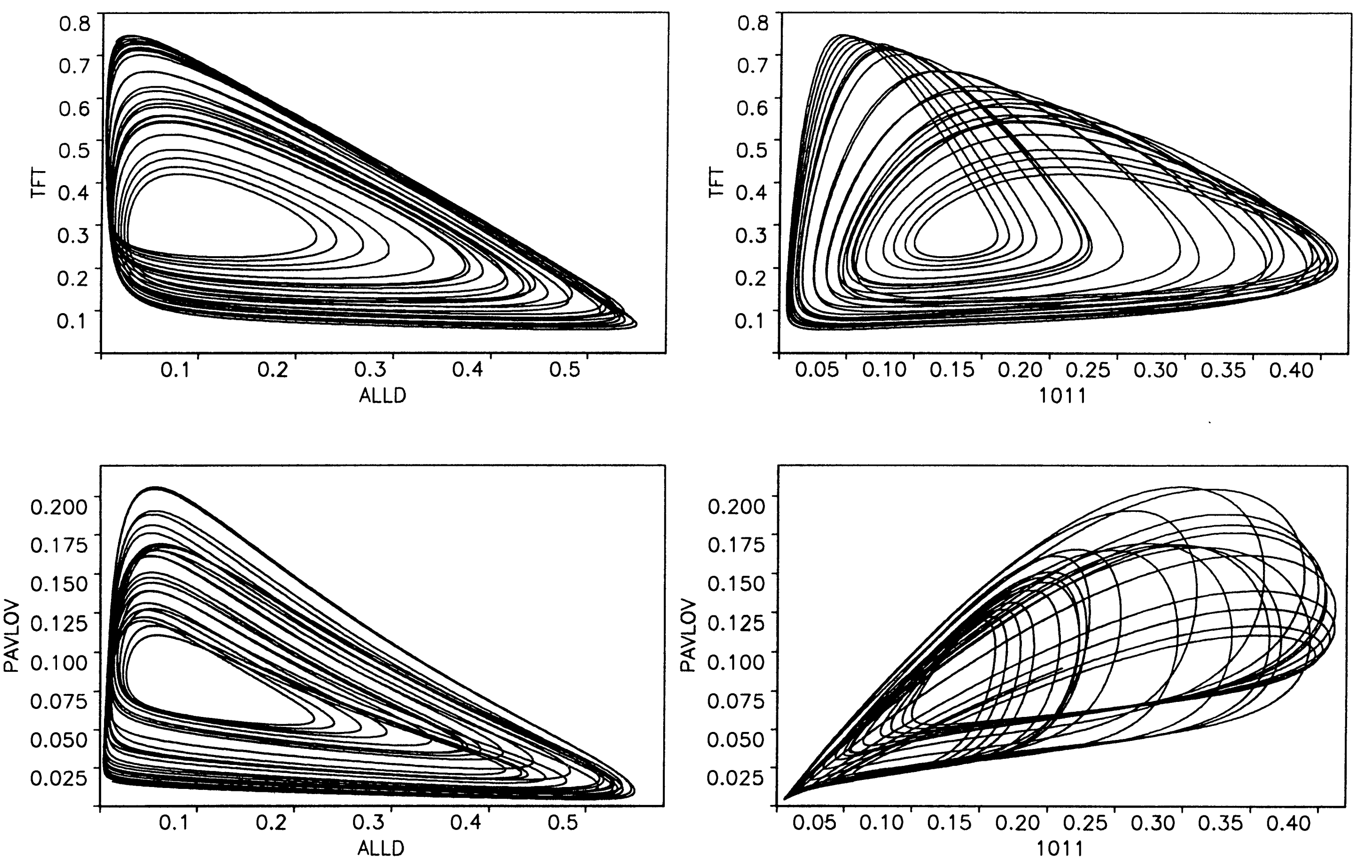

FIG. 2. The evolutionary dynamics of the 16 S_i strategies lead to chaos. Four two-dimensional projections of the chaotic attractor are shown: TFT versus AllD, TFT versus (1, 0, 1, 1), PAVLOV versus AllD, and PAVLOV versus (1, 0, 1, 1). Invasion rate $u = 0.0004$; error frequency $\varepsilon = 0.01$.

ation is 2.96 (rather than 1.15 in the system without GTFT). This success of GTFT is surprising, because AllD and GRIM are still the only evolutionarily stable strategies, and GTFT can be invaded by AllC, (1, 0, 1, 1), (0, 1, 1, 1), and the alternating strategy (0, 0, 1, 1). It seems that very small repeated invasion attempts can twist this system from defection to cooperation. For $u = 0$, we observe convergence to either AllD or GRIM.

Chaos and unpredictability may play important roles in the evolution of cooperation. Simple strategies in the IPD can lead to very complicated evolutionary dynamics.

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