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The Continuous Prisoner's Dilemma: II. Linear Reactive Strategies with Noise

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We present a general model for the Continuous Prisoner's Dilemma and study the effect of errors. We find that cooperative strategies that can resist invasion by defectors are *optimistic* (make high initial offers), *generous* (always offer more cooperation than the partner did in the previous round) and *uncompromising* (offer full cooperation only if the partner does). A necessary condition for the emergence of cooperation in the continuous Prisoner's Dilemma with noise is $b(1-p) > c$, where b and c denote, respectively, the benefit and cost of cooperation, while p is the error rate. This relation can be reformulated as an error threshold: cooperation can only emerge if the probability of making a mistake is below a critical value. We note, however, that cooperation in the continuous Prisoner's Dilemma with noise does not seem to be evolutionarily stable: while it is possible to find cooperative strategies that resist invasion by defectors, such cooperators are generally invaded by more cooperative strategies which eventually yield to defectors. Thus, the long-term evolution of the continuous Prisoner's Dilemma is either characterized by unending cycles or by stable polymorphisms of cooperators and defectors.

1. Introduction

Being "human" can apply to a spectrum of behaviors, but often this phrase refers simply to the unavoidable probability of making mistakes. In this paper, we incorporate continuous variability and inconsistency into the classic mathematical model of cooperation, the Prisoner's Dilemma (Rapoport & Chammah, 1965; Trivers, 1971; Smale, 1980; Axelrod & Hamilton, 1981).

Recent papers have investigated the possibility of extending this classical game by allowing a variable degree of cooperation, with payoffs scaled accordingly (Verhoeff, 1993; Doebeli & Knowlton, 1998; Roberts & Sherratt, 1998; Killingback *et al*., 1999; see also Smale, 1980; Frean, 1996). We have presented a general model for the Continuous Prisoner's Dilemma (Wahl & Nowak, 1999) which describes a continuous three-dimensional strategy space, and have studied the evolutionary outcome when a wide range of strategies play a game of alternating moves (Frean, 1994; Nowak & Sigmund, 1994) against each other. Here we study the effects of "noise" on this general model, that is, we assume that players will occasionally misinterpret an opponent's move, and study the outcome of the game using both evolutionary game theory (Maynard Smith, 1982) and adaptive dynamics (Nowak & Sigmund, 1990; Metz *et al*., 1996; Hofbauer & Sigmund, 1998). In the discrete Prisoner's Dilemma, this type of stochasticity

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may reveal crucial differences between strategies which are otherwise neutral with respect to each other (Nowak & Sigmund, 1990, 1992).

2. The Continuous Prisoner's Dilemma

We have proposed a general model of the Iterated Prisoner's Dilemma, in which both the costs and benefits of cooperation vary continuously (Wahl & Nowak, 1999). In brief, player 1 moves x in a given round (where x is in the interval [0, 1]), entailing cost $-cx$ to player 1, and benefit bx to player 2, with $b > c$.

We consider linear reactive strategies $y = S(x)$, where y is the response to an opponent's previous move x. Each strategy S is defined by a slope, k, an intercept, d, and a starting move x_0. Where $kx + d > 1$ we set $y = 1$, and likewise where $kx + d < 0$, we set $y = 0$. This subset of all S can be pictured as the set of straight lines which have a non-empty intersection with the unit square. We use the notation S_{k,d,x_0} to describe a given strategy (abbreviated to $S_{k,d}$ to describe a class of strategies which differ only in x_0).

Clearly, the strategy $S_{0,1,1}$ or $y = 1$ corresponds to indiscriminate cooperation (denoted *AllC*), while $S_{0,0,0}$ or $y = 0$ corresponds to indiscriminate defection (denoted *AllD*). The strategy $S_{1,0,1}$, or $y = x$ with the starting move $x_0 = 1$, is analagous to Tit-for-Tat in the discrete case; this strategy lies on the line of identity and is denoted I.

2.1. STRATEGY FAMILIES

The space of all possible strategies is a three-dimensional polyhydron in k, d and x_0. We subdivide this space based on the qualitative features of the strategies, as illustrated in Fig. 1 of the companion paper (Wahl & Nowak, 1999). Strategy families, denoted P or N, have positive or negative slopes, respectively, and repeated rounds of a game between two members of this family move the play towards the value given by the superscript.

P^1 is the set of all cooperators, i.e. the set of strategies for which $S(x) \geq x$ for all x. These strategies lie entirely on or above the line of identity, and repeated rounds between two cooperators move the play closer to one. We define defectors analogously as those strategies which lie completely below the line of identity, for which $S(x) < x$ for all x; the set of defectors is the family P^0.

2.2. THE ERROR DISTRIBUTION

It is clear that a large number of interesting strategies, for instance all those for which $S(1) = 1$ and $x_0 = 1$, are effectively identical to each other in the game without errors. This is because successive moves between two such players are always $S(1) = 1$, regardless of the value of $S(x)$ over the remainder of the interval [0, 1). These apparently equivalent strategies, however, may be markedly different in their response during an error-prone game.

We model the continuous Prisoner's Dilemma with errors in the following way. Let p represent the probability that an error occurs. With probability p, a previous move is misinterpreted, and instead of responding to x with move $y = S(x)$, a player will respond to $y = S(u)$, where u is a random variable. Note that this is slightly different from modelling y as a random variable, since in the latter case players could make "mistakes" that are inconsistent with their own strategies (see the Discussion section).

In this paper, we have treated the case when u is distributed uniformly over [0, 1]. In this case, the true value of the previous move, x, has no bearing on the distribution of $y = S(u)$. Another possible model would be the case when u is normally distributed around a mean value of x.

2.3. THE PAYOFF FUNCTION

We define a payoff function, $F(S, S')$, which corresponds to the mean payoff per round that strategy S receives when playing against S'. The payoff is clearly a function of the slopes, intercepts and starting moves of the two strategies, of the cost c and benefit b, and of the total number of rounds in the game. In this paper, we model games in which there is a constant probability of an additional round between two players; we let $\bar{n}$ denote the average number of rounds per game, and the probability of a further move after each round of the game is then given by $(1 - 1/\bar{n})$.

Because the payoff will also depend on whether S or S' moves first, we define the payoff function as the average payoff between these two cases. As a limiting case, we sometimes consider the payoff of an infinitely iterated game (payoff averaged over n rounds as $n \to \infty$). For example, in the infinite game without errors, $F(AllC, AllC) = (b - c)$, and likewise $F(AllD, AllD) = 0$. We also find that $F(I, I) = (b - c)$, because the starting move for I is defined to be 1. For other strategies which lie on the identity line, the payoff when $S_{1,0,x_0}$ plays $S_{1,0,x_0'}$ will be equal to $(1/2)(b - c)(x_0 + x_0')$.

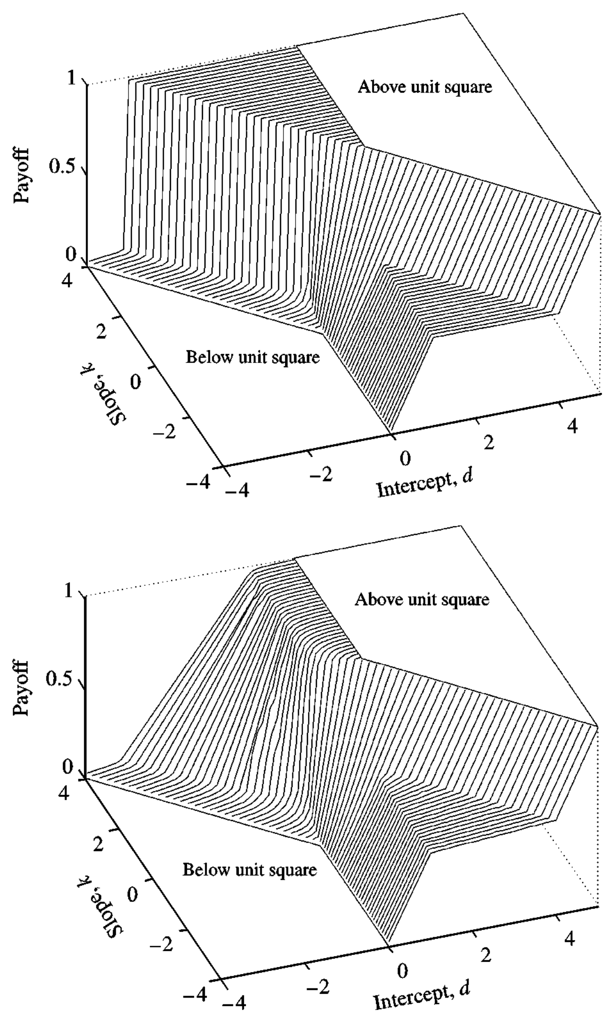

FIG. 1. Payoff against self without and with errors. The payoff $F(S, S)$ is shown for a game of 20 rounds on average, with $b = 2$, $c = 1$ and $p = 0$ (upper panel) or $p = 0.1$ (lower panel). We set $x_0 = 1$ for all strategies. The positions of strategy families are depicted in Fig. 1 in the companion paper (Wahl & Nowak, 1999). Note that the high payoff received by the family of cooperators, P^1, is maintained in the game with errors, while the payoff for family P^{01} is greatly reduced. The payoff surface in P^1 is flat in the game without errors but has a gradient in the lower panel (more cooperative strategies do slightly better).

Figure 1 shows the payoff function for each strategy family, for the game without errors (upper panel) or with errors (lower panel; $p = 0.1$). The surface plots the payoff each strategy receives when playing a game of 20 rounds on average ($\bar{n} = 20$) against itself, for the case of the most generous starting move, $x_0 = 1$. We find that cooperators (family P^1) continue to achieve high payoffs in the error-prone game, and that errors are most devastating for family P^{01}. Note that within P^1 the payoff surface is flat (strategies are neutral with respect to each other) in the game without errors, but there is a slight gradient in the payoff surface for the error-prone game (more cooperative strategies do slightly better).

3. Payoffs between Strategies—Analytical Results

We can derive the payoff function between several strategy families analytically. Note that we have not determined an analytical expression for the payoff between two *arbitrary* linear reactive strategies, but in the following sections, we treat a limited number of salient cases.

In the limiting case of an infinite game with errors, $F(AllC, AllC)$ is clearly equal to $(b - c)$, and likewise $F(AllD, AllD) = 0$; the responses of these strategies are unaffected by errors. Thus, *AllD* is able to invade and take over *AllC*, regardless of the error rate. The payoff for strategy I vs. itself, however, will be affected by stochasticity. Each error will move the play to a new value uniformly distributed across [0, 1] and the mean payoff $F(I, I)$ will equal $(1/2)(b - c)$.

3.1. *I* VS. *AllC*

When *AllC* plays I, *AllC* will always pay the total cost, c, but will receive the complete benefit, b, for only a fraction of the moves given by $1 - p$. Occasionally, for a fraction of the moves given by p, a random error will occur, and I will play u instead of 1. The mean value of u for this fraction of the moves will be 1/2. Thus, we find that the total payoff *AllC* receives when playing I in the infinite game with errors is given by

$$F(AllC, I) = -c + (1-p)b + \left(\frac{1}{2}\right)pb$$

$$= -c + b\left(1 - \frac{p}{2}\right). \quad (1)$$

It follows that

$$F(I, AllC) = b - (1-p)c - \left(\frac{1}{2}\right)pc$$

$$= b - c\left(1 - \frac{p}{2}\right). \quad (2)$$

From these values it is clear that $F(I, AllC) > F(AllC, AllC)$, and so I is always able to invade a population of indiscriminate cooperators. *AllC* is resistant against takeover by I, however, if $F(I, I) < F(AllC, I)$, that is under the condition

$$\frac{1}{2}(b-c) < -c + b\left(1 - \frac{p}{2}\right) \quad (3)$$

which reduces to

$$b(1-p) > c. \quad (4)$$

Thus, in the infinite game with errors, I is not able to take over a population of indiscriminate cooperators if the benefit, times a quality factor given by the probability of interpreting a move correctly, is greater than the cost. We should also note that when condition (4) is met, *AllC* can invade a population of I, but $F(AllC, AllC)$ is always less than $F(I, AllC)$, so that *AllC* can never dominate I. We can rewrite inequality (4) in terms of an "error threshold":

$$p < 1 - \frac{c}{b}. \quad (5)$$

While the error rate, p, is below this threshold, *AllC* is not dominated by I.

If the population is mixed between *AllC* and I, and the frequency of I in the total population is g, the growth rate of I will be proportional to $gF(I, I) + (1-g)F(I, AllC)$, while the growth rate of *AllC* will be proportional to $gF(AllC, I) + (1-g)F(AllC, AllC)$. For the growth of I to equal the growth of *AllC*, we find

$$g = \frac{cp}{(b-c)(1-p)}. \quad (6)$$

Thus, when the error rate is close to zero, the frequency of I in the equilibrium between *AllC* and I approaches zero, but as the error rate increases, the frequency of I increases, and reaches 100% when p is equal to $1 - c/b$. To summarize, we find that I and *AllC* are in equilibrium only if condition (4) is met and $p < 1 - c/b$, otherwise I dominates *AllC*.

3.2. *I* VS. *AllD*

We can likewise examine the possible outcomes when I plays *AllD*. For the limiting case of an infinite game with errors, we find that $F(AllD, I) = bp/2$ and $F(I, AllD) = -cp/2$. Since $F(AllD, AllD) = 0 > -cp/2$, we see that a single player with strategy I can never invade a population of defectors. If, however, the frequency of I in the total population is h, and the population is mixed between *AllD* and I, then the growth rate of I will exceed the growth of *AllD* when

$$h\left(\frac{1}{2}\right)(b-c) - (1-h)\left(\frac{1}{2}\right)cp > h\left(\frac{1}{2}\right)bp, \quad (7)$$

which reduces to

$$h > \frac{cp}{(b-c)(1-p)}. \quad (8)$$

We note that h can only be greater than this threshold if the right-hand side of inequality (8) is less than 1, which reduces to $b(1-p) > c$, or condition (4). This implies that I can invade a population of defectors only if condition (4) is met *and* the starting frequency of I exceeds the threshold given by inequality (8). We note that when $p = 0$, I invades *AllD*, and that I cannot invade *AllD* if $p > 1 - c/b$.

Conversely, I is stable against invasion by *AllD* under the condition that $F(I, I) > F(D, I)$, which is (again) the condition $b(1-p) > c$. It is clear, however, that when *AllD* is able to invade it will dominate. Thus, under the same condition that *AllC* resists take over by I, I resists invasion by *AllD*.

3.3. PAYOFFS FOR $P^1_{k,1-k}$

Results for the continuous Prisoner's Dilemma without errors (Wahl & Nowak, 1999) indicate that a large fraction of successful strategies may be cooperative, especially if the benefits of co-operation are high. With $b = 5$ and $c = 1$, we found that 48% of all generations had payoffs greater than 90% of the maximum payoff, $(b - c)$. We also noted that over 30% of the members of family P^1 lay in a narrow band along the boundary of P^1 and M, a region of apparent Nash equilibria.

We denote the set of cooperative strategies along this boundary $P^1_{k,1-k}$, since $d = 1 - k$ for this sub-family, and we note that for these strategies $0 < k < 1$. We are interested in the evolutionary dynamics surrounding $P^1_{k,1-k}$, and have derived the payoff for the error-prone game between this sub-family and a number of other strategies of interest, for the limiting case of an infinite game.

When $P^1_{k,1-k}$ plays *AllD*, the benefit to $P^1_{k,1-k}$ is always 0, and the cost is $1 - k$ for a fraction of the moves given by $1 - p$. When an error occurs, strategy $P^1_{k,1-k}$ will mistakenly play $P^1_{k,1-k}(u)$. Since u is uniformly distributed, the mean value of $P^1_{k,1-k}(u)$ is just the mean value of $P^1_{k,1-k}(x)$ for $x \in [0, 1]$, or $1 - (k/2)$ (this is simply the area under the strategy in the unit square). This gives

$$F(P^1_{k,1-k}, AllD) = -c\left(1 - k + \frac{kp}{2}\right) \qquad (9)$$

and similarly

$$F(AllD, P^1_{k,1-k}) = b\left(1 - k + \frac{kp}{2}\right). \qquad (10)$$

By similar arguments, we can derive the mean payoff when $P^1_{k,1-k}$ plays *AllC*, finding

$$F(P^1_{k,1-k}, AllC) = b - c\left(1 - \frac{kp}{2}\right) \qquad (11)$$

and

$$F(AllC, P^1_{k,1-k}) = -c + b\left(1 - \frac{kp}{2}\right). \qquad (12)$$

To understand the system further, we derive the payoff when $P^1_{k,1-k}$ plays itself. This works out to be (see Appendix A)

$$F(P^1_{k,1-k}, P^1_{k,1-k}) = (b-c)\frac{1-k+(kp/2)}{1-k+kp}. \qquad (13)$$

For the game between $P^1_{k,1-k}$ and I we find (see Appendix B)

$$F(P^1_{k,1-k}, I) = \frac{(b-c)(kp^2+2k-2)+p(2ck-3bk+b)}{2(k(1-p)^2-1)} \qquad (14)$$

and

$$F(I, P^1_{k,1-k}) = \frac{(b-c)(kp^2+2k-2)+p(-2bk+3ck-c)}{2(k(1-p)^2-1)}. \qquad (15)$$

These results are summarized in the payoff matrix shown in Table 1.

3.3.1. $P^1_{k,1-k}$ *vs. AllD*

By comparing $F(P^1_{k,1-k}, P^1_{k,1-k})$ and $F(AllD, P^1_{k,1-k})$, we find that $P^{k,1-k}$ is stable against invasion by *AllD* under the condition

$$bk(1-p) > c. \qquad (16)$$

When $k = 1$, this condition is identical to inequality (4), and we also note that for $0 < k < 1$, inequality (4) is necessary for condition (16) to be met. Inequality (16) can also be written in terms of an error threshold

$$p < 1 - \frac{c}{bk}. \qquad (17)$$

This condition gives a lower limit on k, and intuitively it can be understood that if the strategy gives too much in response to total defection

TABLE 1

Partial payoff matrix for family $P^1_{k,1-k}$, for the infinite game with errors. Entries give the mean payoff received by the strategy noted in each row, when playing against the strategy noted in each column

	AllD	*AllC*	*I*	$P^1_{k,1-k}$
AllD	0	b	$\frac{1}{2}bp$	$b\left(1-k+\frac{kp}{2}\right)$
AllC	$-c$	$b-c$	$b\left(1-\frac{p}{2}\right)-c$	$b\left(1-\frac{kp}{2}\right)-c$
I	$-\frac{1}{2}cp$	$b-c\left(1-\frac{p}{2}\right)$	$\frac{1}{2}(b-c)$	$\frac{(b-c)(kp^2-2k-2)+p(-2bk+3ck-c)}{2(k(1-p)^2-1)}$
$P^1_{k,1-k}$	$-c\left(1-k+\frac{kp}{2}\right)$	$b-c\left(1-\frac{kp}{2}\right)$	$\frac{(b-c)(kp^2+2k-2)+p(2ck-3bk+b)}{2(k(1-p)^2-1)}$	$\frac{(b-c)(1-k+(kp/2))}{1-k+kp}$

($d=1-k$ is large), it is vulnerable to invasion by *AllD*. We can also see that if *AllD* invades, it dominates. Once again we find [inequality (16)] that the relevant factor is whether the weighted benefit outscales the cost of cooperation.

Conversely, we can solve for the starting frequency, f, that would be required for a small number of players with strategy $P^1_{k,1-k}$ to invade and take over a population of *AllD*. Comparing the growth rates of $P^1_{k,1-k}$ and *AllD* in a mixed population of the two, we find

$$f > \frac{c(1-k(1-p))}{(b-c)k(1-p)}. \tag{18}$$

Again we see that *AllD* is stable against invasion by $P^1_{k,1-k}$ for $k < c/(b(1-p))$ [condition (16)] and that *AllD* can be invaded by smaller starting frequencies of $P^1_{k,1-k}$ as k approaches 1.

3.3.2. $P^1_{k,1-k}$ *vs.* I

Comparing $F(P^1_{k,1-k}, P^1_{k,1-k})$ and $F(I, P^1_{k,1-k})$, we find that when condition (16) is *not* met, I can invade a population of $P^1_{k,1-k}$, but I can never take over $P^1_{k,1-k}$. Conversely, we find that $P^1_{k,1-k}$ is always able to invade I, and can take over I when condition (16) is met. Thus, $P^1_{k,1-k}$ invades and takes over I when the error rate is sufficienty low, while at higher error rates, an equilibrium between I and $P^1_{k,1-k}$ is possible. The frequency of $P^1_{k,1-k}$ in this equilibrium is given by

$$f = \frac{(1-k+kp)((b-c)(3k+1)+pb(k-1))}{(b-c)((1-p)(1-7k^2)+6k+2kp)}. \tag{19}$$

When $k=0$, this frequency reduces to $1-g$ where g is defined in eqn (6); the situation is effectively *AllC* vs. I in this limiting case.

3.3.3. $P^1_{k,1-k}$ *vs. AllC*

We likewise find that *AllC* can only invade a population of $P^1_{k,1-k}$ under the condition

$$bk(1-p) > c. \tag{20}$$

Since *AllC* is never stable against invasion by $P^1_{k,1-k}$, $P^1_{k,1-k}$ will form an equilibrium when condition (20) is met, otherwise $P^1_{k,1-k}$ will dominate *AllC*.

3.4. OTHER STRATEGY SUBFAMILIES

We have derived analytical expressions for the payoff between *AllD*, *AllC*, I and two other strategy subfamilies. The cooperative strategies, denoted $P^1_{k,0}$, are those strategies that intersect $(0,0)$ on the unit square $(1<k<\infty)$, while the family $P^1_{1,d}$ describes strategies that are parallel to, but above, the line of identity $(0<d<1)$. For the family $P^1_{k,0}$, we find that *AllD* can never invade a population of $P^1_{k,0}$, while both I and

TABLE 2
Partial payoff matrix for family $P^1_{k,0}$, infinite game with errors

	AllD	*AllC*	*I*	$P^1_{k,0}$
AllD	0	b	$\frac{1}{2}bp$	$bp\left(1-\frac{1}{2k}\right)$
AllC	$-c$	$b-c$	$b\left(1-\frac{p}{2}\right)-c$	$b\left(1-\frac{p}{2k}\right)-c$
I	$-\frac{1}{2}cp$	$b-c\left(1-\frac{p}{2}\right)$	$\frac{1}{2}(b-c)$	$\frac{2(b-c)(1-k+(p^2/2))+p(-kc+3c-2b)}{2((1-p)^2-k)}$
$P^1_{k,0}$	$-cp\left(1-\frac{1}{2k}\right)$	$b-c\left(1-\frac{p}{2k}\right)$	$\frac{2(b-c)(1-k+(p^2/2))+p(kb-3b+2c)}{2((1-p)^2-k)}$	$(b-c)\frac{k-1+(p/2)}{k-1+p}$

AllC can invade under the condition

$$b(1-p) > ck. \quad (21)$$

Strategy *AllC* does not dominate $P^1_{k,0}$, but I dominates $P^1_{k,0}$ when

$$b(1-p) > c. \quad (22)$$

The analytical results for payoffs between $P^1_{k,0}$, *AllD*, *AllC* and I are shown in Table 2. Figure 2 illustrates the payoff each of these strategies receive when playing $P^1_{k,0}$; simulated (open circles) and analytical (solid lines) results show excellent agreement.

For the family $P^1_{1,d}$ the analysis is more complex, but again we find similar general features: these cooperators can be invaded by *AllD* when d is greater than some threshold, and once invaded the population is taken over by *AllD*; a (different, in this case) threshold value determines whether I can invade the population; a third threshold determines whether *AllC* can invade; and both I and *AllC* are unable to dominate.

4. Adaptive Dynamics

These analytical results suggest that equilibrium states are possible between *AllC*, I and a range of cooperative strategies between the two. Within this cooperative space, a number of strategies are certainly vulnerable to exploitation by *AllD* and presumably by more sophisticated defectors. We are interested in the evolutionary dynamics of this system: does a population of such strategies evolve towards cooperation in the long run? And if so, does it become vulnerable to takeover by defectors?

4.1. THE EVOLUTION OF x_0

We begin by analysing adaptive changes in x_0, that is, we determine which starting move is "best" for a given strategy. To do this, we start with an initial strategy S_{k,d,x_0} and consider a strategy S', identical to S except for a small perturbation in the starting move, $x'_0 = x_0 + \delta x$. If $F(S', S) > F(S, S)$ and $F(S', S') > F(S, S')$, it is clear that S' will invade and takeover a population of S: we let x'_0 replace x_0 and continue.

The results of these simulations are shown in Fig. 3. Here we let S and S' play 5000 games against each other, where each game has on average 20 rounds and $p = 0.05$. These surfaces plot the steady-state values of x_0 ($\hat{x}_0$) when x_0 is originally set to be 0 or 1 in the simulation.

We note that $\hat{x}_0 = 1$ is robust for much of the strategy space, and in particular we find a region in the upper corner of strategy family M for which x_0 evolves to one, regardless of its initial value. The steady-state value of x_0 for $k < 0$ was zero, regardless of its initial value. These results were identical to those observed for the game without noise (Wahl & Nowak, 1999), the only difference being the number of games (5000)

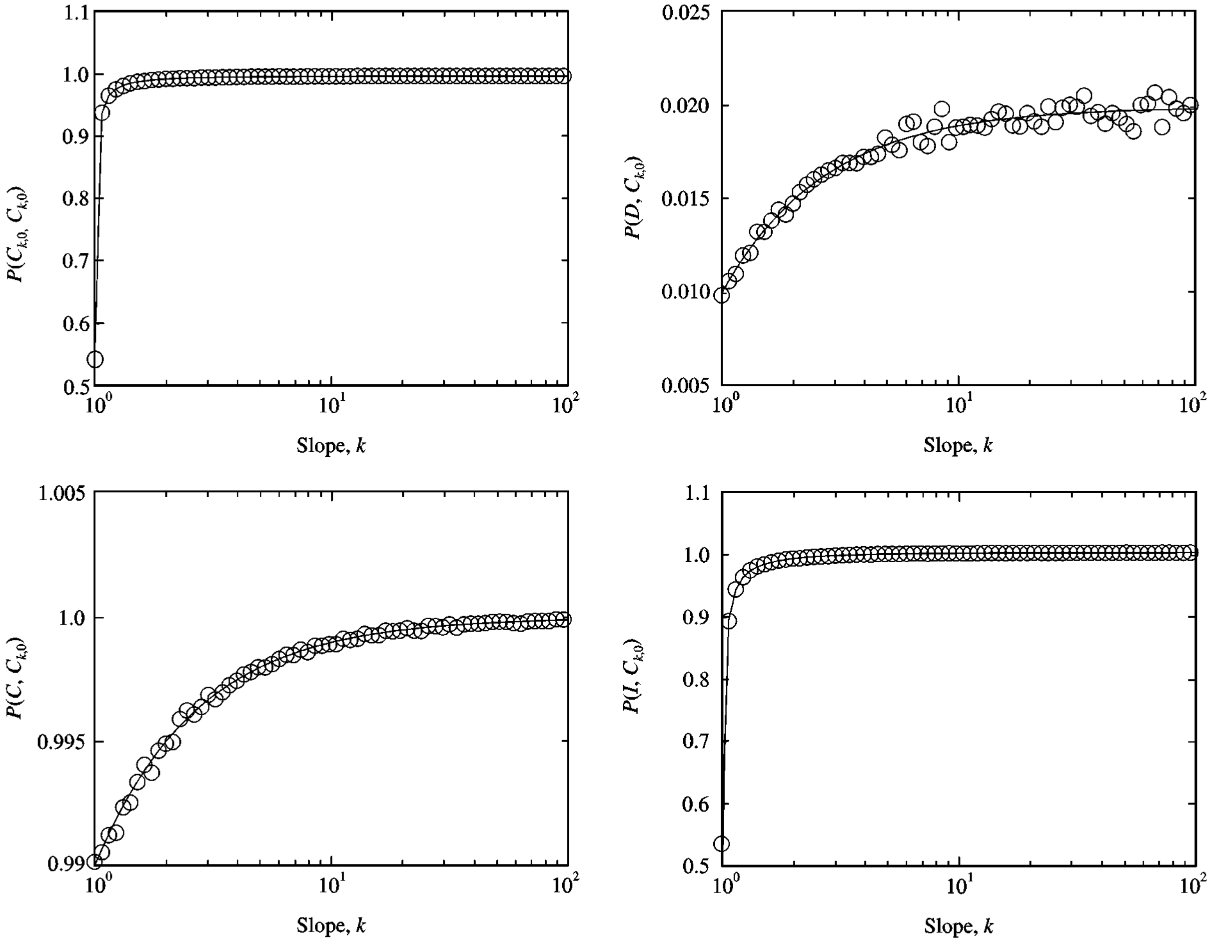

FIG. 2. Payoff vs. slope, k, for strategy family $P^1_{k,0}$. The payoffs which $P^1_{k,0}$, *AllD*, *AllC* and I receive when playing $P^1_{k,0}$ are shown, for $b = 2$, $c = 1$, $p = 0.1$ and $1 < k < 100$. Payoffs for an infinitely iterated game were simulated by playing single 100 000 round games between $P^1_{k,0}$ and *AllD*, *AllC* or I for each value of k (○). These compare well with analytical predictions (——); equations are provided in Table 2.

needed in simulating the error-prone game to ensure a smooth $\hat{x}_0$ surface.

4.2. THE EVOLUTION OF k, d AND x_0

We repeated these simulations, allowing k, d and x_0 to vary simultaneously. For each strategy S_{k,d,x_0}, we considered strategies distributed in a sphere around that strategy, and accepted the parameter values of the strategy S' with the highest payoff against S_{k,d,x_0}, under the condition that strategy S' is able to invade and take over a population of S.

Figure 4 illustrates an example of evolution through strategy space, where a given starting strategy has been followed for 20 000 successful mutations. The circle on each graph shows the value of x_0 for the strategy illustrated. We seeded the simulation with a highly cooperative strategy ($k = 0.6$, $d = 0.7$ and $x_0 = 1$), and set $p = 0.05$. This cooperative strategy is remarkably stable; although d, k and x_0 vary widely over the subsequent 18 000 mutations, the strategy remains entirely cooperative, $S(x) \geqslant x$ for all x. Between mutations 18 000 and 18 600, however, the strategy rapidly mutates towards *AllD*. The detailed illustration of this evolution reveals that between mutations 18 100 and 18 200, k decreases, such that $k + d$ is no longer greater than one. The strategy crosses the boundary from family P^1 to

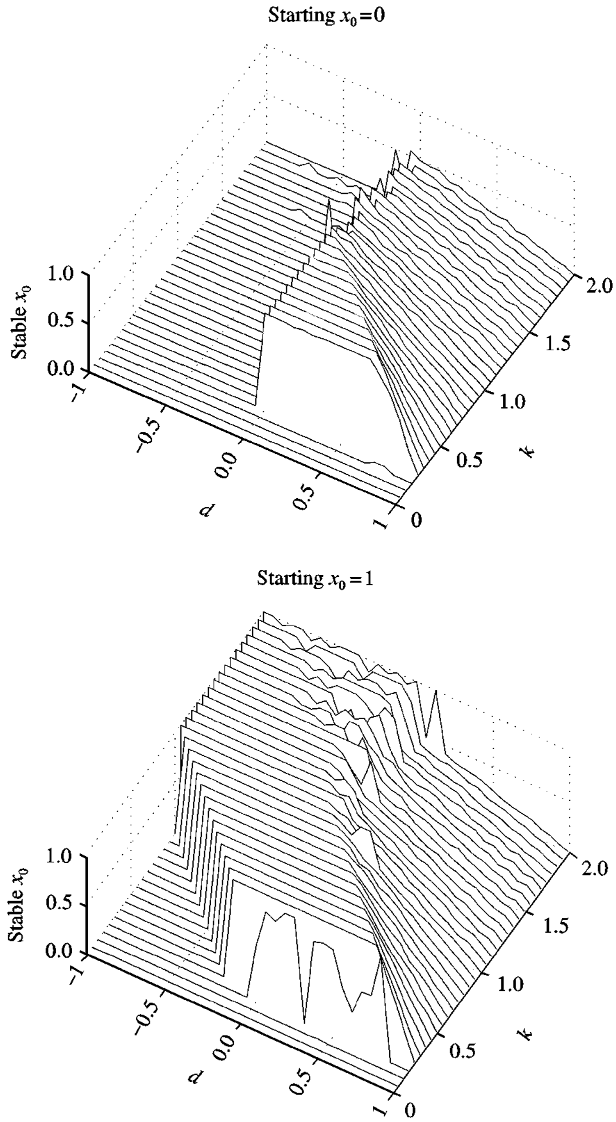

FIG. 3. Steady-state values of x_0. The surfaces show the steady-state values of x_0 ($\hat{x}_0$) when both k and d are fixed. In these simulations, strategy S_{k,d,x_0} played 5000 games against S_{k,d,x'_0} where $x'_0 = x_0 + \delta x$; here $b = 5$, $c = 1$ and $p = 0.05$. We set δx to 0.05 or -0.05 when x_0 was initially set to 0 or 1, respectively. Games which were 20 rounds long on average ($\bar{n} = 20$) were modelled by simulating 100 rounds and weighting the payoff in round i by the probability that a game would last to round i, $(1 - (1/\bar{n}))^{i-1}$. We note that $\hat{x}_0 = 1$ is robust for a significant fraction of the strategy space.

family M. Once the strategy is a member of family M (with low k), x_0, k and d all evolve to zero; the steady state is *AllD*.

To examine the evolutionary trajectories through strategy space more generally, we seeded strategies at uniform intervals in k, d and x_0, and followed the evolution of each strategy for a small number of mutations. Figure 5 shows one plane through the results of this simulation, the d–k plane at the level $x_0 = 1$. Open circles show the initial positions of the strategies investigated. Lines indicate the direction of the evolution through strategy space. Where open circles appear without visible evolutionary trajectories in this plane, the trajectory is into the page; x_0 evolves towards smaller values in regions P^{01}, P^1 and N^{01}.

This figure reveals a fairly complex set of trajectories on the $x_0 = 1$ plane. For the majority of strategies within P^0 and M, and for all strategies in N^1, N^{01} and N^0, strategies evolve towards the lower left boundary of the space, or towards indiscriminate defection. For sections of P^0 and M where k is sufficiently large, however, and for all of P^{01}, strategies evolve towards the upper left; they become more cooperative. This evolution, however, takes the strategy towards a region of P^1 where x_0 evolves towards lower values, and from there (as illustrated in Fig. 4), the strategy evolves back into family M where there is a strong gradient towards *AllD*.

In the error-free game (Wahl & Nowak, 1999), we observed a cooperative subfamily of apparent Nash equilibria along the boundary of families M and P^1 when $x_0 = 1$. These strategies, denoted $P^1_{k,1-k}$, fare better than near neighbors in family M when $k > c/b$, and are neutral with neighbors in P^1 in the game without errors.

Figure 5 indicates that strategies in this subfamily are not Nash equilibria in the error-prone game, but evolve away from the boundary of M and P^1. Appendix C shows that when $k > c/b$ strategies along this boundary can be invaded by other members of family P^1; for smaller values of k, strategies along this boundary can be invaded by members of family M.

5. Stochastic Adaptive Dynamics in the Error-prone Game

To analyse the overall behavior of this system, we use a modification of adaptive dynamics, in which a stochastic element is introduced to capture the effects of random drift (Wahl & Nowak, 1999). We begin with a single strategy, S, and allow it to evolve by small random changes in k,

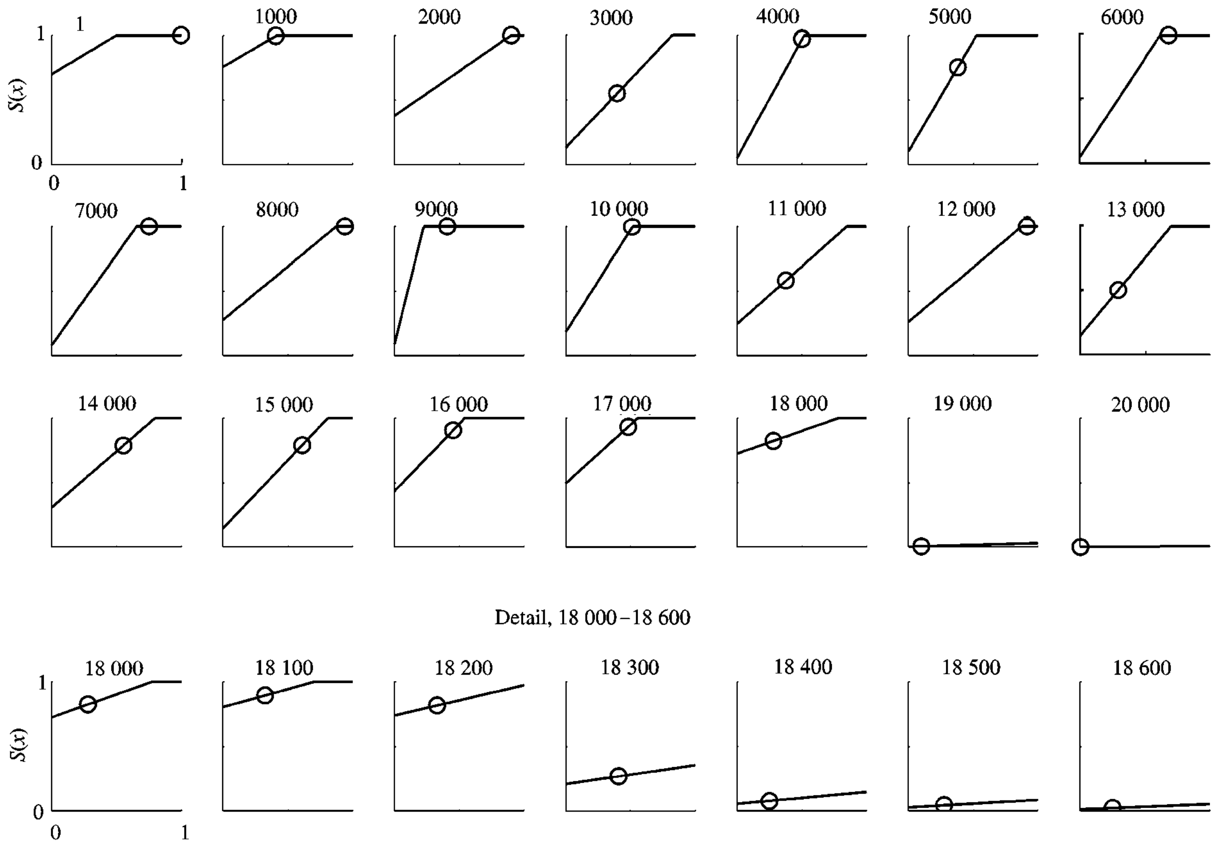

FIG. 4. Strategy evolution. The evolution of a single cooperative strategy is shown; all three parameters of the starting strategy ($k = 0.6$, $d = 0.7$, $x_0 = 1$) were allowed to evolve. Each panel plots the value of $S(x)$ for $0 \leqslant x \leqslant 1$; the circle on each graph shows the value of x_0 for the strategy illustrated. The top left panel plots the starting strategy and subsequent panels show the strategy after 1000–20 000 successful mutations. We used $b = 2$, $c = 1$, $p = 0.05$ and $\bar{n} = 20$ for these simulations. This strategy remains cooperative for 18 000 mutations, but eventually evolves towards *AllD*, a transition that occurs very quickly between mutations 18 200 and 18 600 (see detail).

d or x_0 to a new strategy S'. We let S' replace S if

$$F(S', S) > F(S, S) \tag{23}$$

and

$$F(S', S') > F(S, S'). \tag{24}$$

This assumes that the frequency of advantageous mutations is low compared to the rate at which fixation occurs, and is the standard transition rule of adaptive dynamics (Nowak & Sigmund, 1990; Metz *et al*., 1996; Hofbauer & Sigmund, 1998). To this standard rule, we add three "stochastic" rules (Wahl & Nowak, 1999), which allow us to model fixation by a putative invader due to three effects: the chance extinction of one of two strategies at equilibrium; the chance extinction of one of two strategies which are neutral with respect to each other; and the chance fluctuation of the frequency of the putative invader past an invasion barrier.

Finally, we periodically introduce new mutants by choosing k, d and x_0 from random distributions, rather than constraining S' to be a near neighbor of S. These mutant strategies are then accepted or rejected according to the same rules. Note that if S' does not invade S, we rewrite S in the sequence of successful strategies, and generate a new S'.

These transition rules allow us to "explore" the strategy space adaptively, by forming a discrete sequence of successful strategies. In the final adaptive sequence, the number of strategies

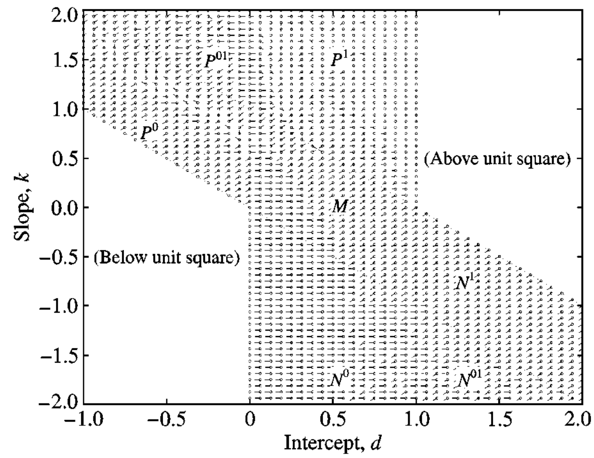

FIG. 5. Strategy trajectories, $x_0 = 1$. Strategies were seeded at uniform intervals in k, d and x_0 and were allowed to evolve through two successful mutations; all three parameters of the starting strategies were allowed to evolve. For this figure we used $b = 2$, $c = 1$, and $p = 0.05$; strategies played 5000 games against each other with an average of 20 rounds per game. The figure illustrates the d–k plane at the level $x_0 = 1$. Open circles show the initial positions of the strategies investigated, and these are connected by solid lines to the final position of the strategy after two mutations. Where open circles appear without visible evolutionary trajectories in this plane, the trajectory is into the page; x_0 evolves towards smaller values in these regions. For the majority of strategies within P^0 and M, and for all strategies in N^1, N^{01} and N^0, strategies evolve towards the lower left boundary of the space, or towards indiscriminate defection. For sections of P^0 and M where k is sufficiently large, however, strategies evolve towards the upper left; they become more cooperative, but eventually reach a region on P^1 where x_0 evolves to smaller values.

which lie in each region of the space reflects how "successful" strategies in that region are, or how unlikely it is for strategies of this type to be invaded or to drift to zero frequency. This feature allows us to use the final sequence to build a probability distribution in strategy space, reflecting the success and overall robustness of every type of strategy.

Using this method, we simulated the long-term evolution of the system, starting with strategy I and producing 100 000 new strategies successively. Each strategy played a single game against each putative successor, with $b = 5$ and $c = 1$. We simulated the game with an average of 20 rounds ($\bar{n} = 20$) by weighting the payoff in round i by the probability that a game would last to round i, $(1 - 1/\bar{n})^{i-1}$.

The results of this simulation are illustrated in Fig. 6. This figure shows the distribution, over the d–k plane, of 100 000 successive strategies. The figure illustrates that each of the seven strategy families are represented in this sequence; strategies from any of these families may be "successful". A clear peak in the distribution appears along the boundaries of the space near $k = d = 0$; strategies near this point are almost entirely defective. We observe a second cluster of strategies along the M–P^1 boundary above $k = c/b = 0.2$; these strategies are cooperators. In the error-free game, this is a region of apparent Nash equilibria (Wahl & Nowak, 1999).

A significant fraction of the strategies in this sequence are cooperative: 18% are members of strategy family P^1, and 20% have payoffs against themselves which are greater than $0.9(b - c)$, or more than 90% the maximum possible payoff in a game against an identical strategy; 21% of the strategies in the sequence are members of family P^0, the defectors. The remaining strategies are divided between strategy families as follows: 10% P^{01}; 13% M; 24% N^0; 7% N^{01}; 7% N^1.

The lower panel in the figure shows a frequency histogram of the payoff each strategy in the sequence receives against itself (solid line). Again we see that the number of cooperators in this sequence of strategies (area under the rightmost peak) is slightly less than the number of defectors (leftmost peak). The correlation coefficient between $F(S, S)$ and x_0 was 0.60 in this sequence. The correlation between the payoff and k was 0.07; between the payoff and d, -0.06. The dotted line shows the payoff distribution for a sequence of strategies generated as described above but with $b = 10$. Under this condition, cooperation is more favorable and cooperators (P^1) actually outnumber the defectors (P^0) 2 : 1.

6. Discussion

In the continuous Prisoner's Dilemma *without* errors, we found that the value of the initial offer, x_0, was a critical factor in determining the long-term success and payoff of a strategy (Wahl & Nowak, 1999). We observe similar behavior in the game with errors, finding that the value of the inital offer is a strong predictor of the payoff a strategy receives against itself. In addition, evolutionary successful strategies evolve towards values of x_0 that elicit complete cooperation in a partner in a single move, rather than building up trust gradually.

Given a strategy $y = S(x)$, we modelled errors by setting $y = S(u)$, where u is a random variable. This method assumes that errors occur in the interpretation of an opponent's move. Another way to incorporate errors would be to allow errors in implementation, such that $y = u \in [S(0), S(1)]$ (implementation is consistent with S) or $y = u \in [0, 1]$ (implementation is independent of S). These methods are not equivalent for most strategies. We note that the noise model used here is an extreme case, where the player has *no* information about the opponent's move. To model a less extreme case, each of the implementations described above could be modified such that the distribution of u is a function of either the opponent's previous move, x, or the correctly implemented response, $S(x)$. The behavior of natural systems should lie somewhere between the predictions of the error-free model and the behavior predicted when the noise is completely unrelated to the signal.

In the continuous game with errors, we observe a general pattern of interaction between classic strategy types that is analagous to patterns observed in the discrete error-prone game. When the benefits of cooperation are sufficiently high, we find that *AllD* dominates *AllC*, that *I* (analagous to Tit-for-Tat in the discrete game) and *AllC* are in equilibrium with each other, and that *I* and *AllD* form a bistable equilibrium. For other cooperative strategy families which we investigated, we found in general that strategies behave similarly to either *I* or *AllC*, making transitions between the two behavior patterns along boundaries in the k–d plane.

Along one such boundary, we observed a set of cooperative strategies which are Nash equilibria in the game without errors (Wahl & Nowak, 1999). In the error-prone game, however, we find

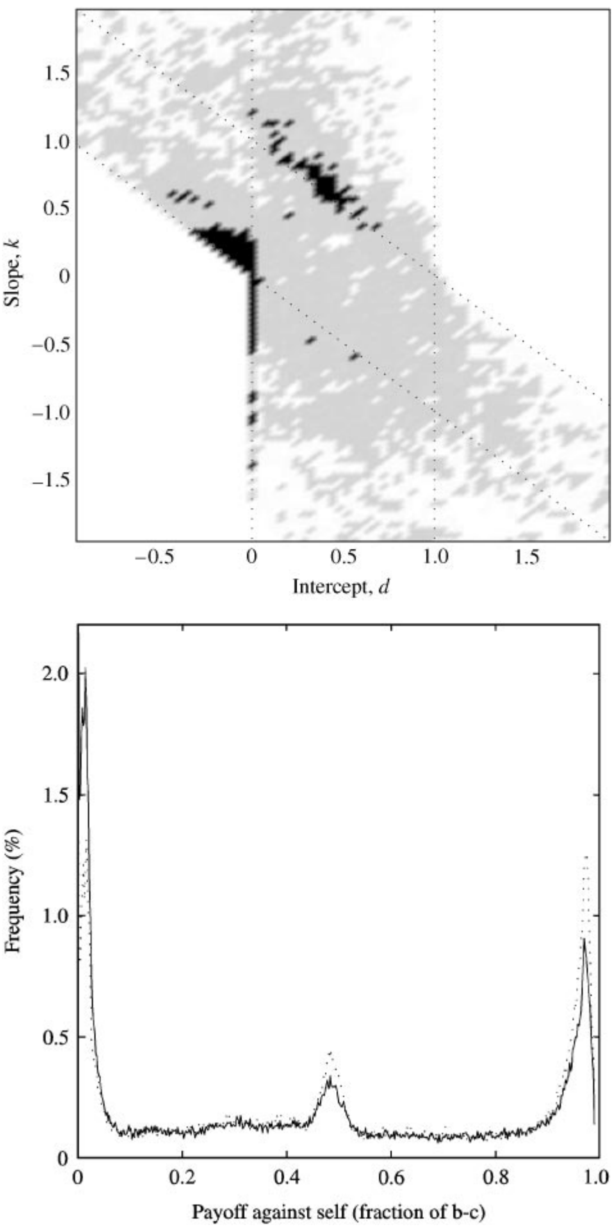

FIG. 6. Distribution of strategies determined by stochastic adaptive dynamics. A sequence of 100 000 successive strategies was generated by stochastic adaptive dynamics, for an initial strategy I ($b = 5$, $c = 1$, $p = 0.1$ and $\bar{n} = 20$). The distribution of these strategies is illustrated on the d–k plane (top panel). The plane was divided into pixels (width = height = 0.02), and the number of strategies in each pixel was determined from the sequence. The results were mapped to a three-level grey scale and then smoothed by Gouraud shading. The figure illustrates that successful strategies are more often defective (towards the lower left corner of the figure) than cooperative (upper right), but we see a cluster of cooperative strategies along the boundary of M and P^1. The lower panel shows a histogram the payoff each strategy in the sequence receives against itself (solid line). The distribution has three peaks; the number of strategies in the peak corresponding to cooperators (rightmost peak, high payoff) is slightly less than the number of defectors (leftmost peak, low payoff). The dotted line shows the payoff distribution for a sequence of strategies generated with $b = 10$; in this case the cooperators outnumber the defectors.

that this subfamily of cooperators is no longer neutral with respect to slightly more cooperative strategies. Near neighbors of this subfamily are able to invade, and the system evolves towards greater cooperation, often reaching a state which is vulnerable to invasion by defectors.

Despite this eventuality, however, cooperative strategies persist for long stretches of our adaptive simulations, as illustrated in Fig. 4. When the cost-to-benefit ratio is sufficiently low, cooperators outnumber defectors in the overall strategy distribution, and likewise the frequency of essentially cooperative strategies (payoff against self is high) is greater than the frequency of essentially defective strategies. Even when $b - c = 1$, a cooperative peak in the distribution persists.

This peak occurs along the boundary of strategy families M and P^1, where strategies are *optimistic* (make high initial offers) and *generous* (always cooperate a little more than their partner did in the previous round), but *uncompromising* (only cooperate fully if their partner does). The most successful cooperative strategies in our model offer intermediate to high values of x_0, differing in this way from Raise-the-Stakes, as proposed by Roberts & Sherratt (1998). We note, however, that when our strategies meet an opponent who is initially reticent to cooperate, they respond with a low second move ($d < 1 - c/b$), and continue attempts to raise the stakes from there.

In our analytical treatment of the payoff function for the classic strategy types mentioned above, we repeatedly found that condition (4), determined the qualitative behavior of the system. This condition requires that the benefit of cooperation, scaled by a quality factor (the probability of interpreting a move correctly), is greater than the cost. When condition (4) is met, we find that I and *AllC* are in equilibrium, that a starting frequency of I can invade *AllD*, and that I is stable against invasion by *AllD*.

For the strategy family $P^1_{k,1-k}$, we found that condition (16) determines the qualitative behavior of the system. Here again the condition requires that the weighted benefits of cooperation outscale the costs. When this condition is met, we find that strategies in subfamily $P^1_{k,1-k}$ are stable against invasion by *AllD*, and that $P^1_{k,1-k}$ can invade *AllD* if seeded with a sufficiently large frequency. $P^1_{k,1-k}$ dominates I when this condition is met, and is in equilibrium with *AllC*. In summary, we find that $P^1_{k,1-k}$ dominates and behaves in qualitatively similar ways to I when condition (16) is met, and dominates and behaves similarly to *AllC* when condition (16) is not met. We found similar results for subfamily $P^1_{k,0}$; the defining inequality in this case is condition (21).

Each of conditions (4), (16) and (21) can be rearranged to predict an *error threshold*. We therefore find that as the error rate, p, increases, the system shifts qualitatively in a way that is equivalent to reducing the benefits of cooperation. Larger subsets of the cooperators become vulnerable to invasion by defectors as the game becomes increasingly error-prone. Given the different restrictions on k for conditions (16) and (21), we see that condition (4) is necessary for either of the other conditions to be fulfilled. Thus, the decisive feature in the continuous Prisoner's Dilemma with errors is whether the benefit, scaled by the probability of interpreting a move correctly, exceeds the cost. When this is true, cooperation is worth the risk.

Finally, our analysis suggests a fundamental pattern of cooperation and defection, illustrated in Fig. 7. Cooperative strategies (region 1) are

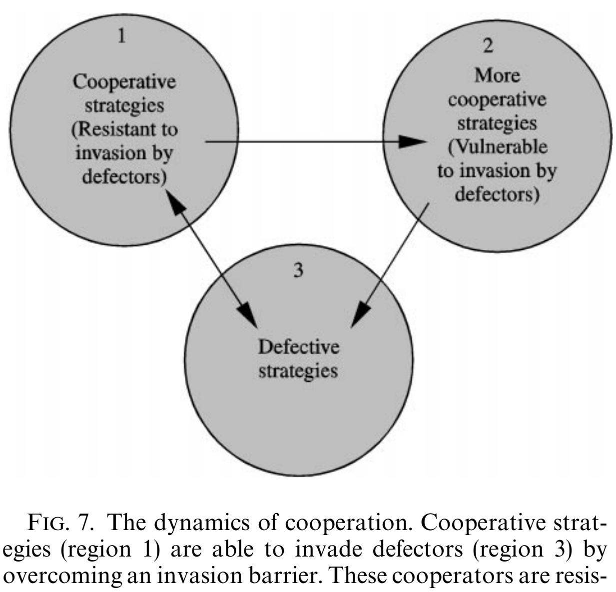

FIG. 7. The dynamics of cooperation. Cooperative strategies (region 1) are able to invade defectors (region 3) by overcoming an invasion barrier. These cooperators are resistant to invasion by less cooperative strategies, but can be invaded, through either selection or drift, by strategies that are more cooperative (region 2). The population of more cooperative strategies, however, is not resistant to invasion by defectors. This system will either cycle between the three regions of state space, or reach an interior stable equilibrium, a mix of the three strategy types.

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APPENDIX A

Derivation of $F(P^1_{k,1-k}, P^1_{k,1-k})$

We would like to derive the payoff that strategy $P^1_{k,1-k}$ receives when playing against itself, for the limiting case of an infinitely iterated game. At each step in this game, the probability that an error occurs is given by p.

Suppose an error has just occurred. The previous move was misinterpreted to be u, which was drawn from a uniform distribution on [0, 1]. The "zeroth" move, the move which is in error, is then $ku + d$ or $ku + 1 - k$. The first move after the error will be $k(ku + 1 - k) + 1 - k$ [which reduces to $k^2(u - 1) + 1$], and the subsequent i moves, until the next error occurs, will be $k^{i+1}(u - 1) + 1$.

Obviously, all the terms of this sequence of moves will not be played before another error occurs and we jump to a new value of u. The probability that $k^2(u - 1) + 1$ is played is one minus the probability that another error occurs at this point in the game, or $(1 - p)$. The probability that the ith move after the error is played, without another error occurring, is $(1 - p)^i$.

To get the mean payoff received for a given value of u, we sum the payoffs received for the ith move, weighted by the probability that the ith move occurs. This sum is divided by the average number of moves in the sequence, or $(1/p)$. We can then integrate the payoff received for a given u over every possibly value of u. Thus, we find that

$$F(P^1_{k,1-k}, P^1_{k,1-k}) = \int_{u=0}^{1} p(b-c) \sum_{i=0}^{\infty} \{(1-p)^i [k^{i+1}(u-1)+1]\} \delta u$$

$$= \frac{(b-c)}{1-k+kp} \int_{u=0}^{1} (1-k+kpu)\delta u$$

$$= (b-c) \frac{1-k+(kp/2)}{1-k+kp}.$$

APPENDIX B

Derivation of $F(P^1_{k,1-k}, I)$

When $P^1_{k,1-k}$ plays I, the sequence of moves after an error will differ, depending on which player makes the first move. When $P^1_{k,1-k}$ makes an error, the zeroth move is $ku+1-k$, to which the response by I is also $ku+1-k$. When I makes an error, the zeroth move is u, to which the response is $ku+1-k$. This results in two possible sequences of costs and benefits accrued by $P^1_{k,1-k}$, each of which must be weighted by the probability of each move occurring before the next error, and all of which must be integrated over possible values of u. We thus find

$$F(P^1_{k,1-k}, I) = \int_{u=0}^{1} p\left\{ b\sum_{i=0}^{\infty}(k^i(u-1)+1)(1-p)^{2i} + (b-c)\sum_{i=0}^{\infty}(k^{i+1}(u-1)+1)(1-p)^{2i+1} - c\sum_{i=0}^{\infty}(k^{i+1}(u-1)+1)(1-p)^{2i}\right\}\delta u$$

$$= \int_{u=0}^{1} \frac{u((b-c)kp^2+bp(-1-k)+2ckp)+(bp-b+c)(1-k)}{k(1-p)^2-1}\delta u$$

$$= \frac{(b-c)(kp^2+2k-2)+p(2ck-3bk+b)}{2(k(1-p)^2-1)}.$$

It is clear that the payoffs received by I during this sequence of moves will be the same as the costs paid by $P^1_{k,1-k}$, and vice versa. Thus we switch b and $-c$ to find

$$F(I, P^1_{k,1-k}) = \frac{(b-c)(kp^2+2k-2)+p(-2bk+3ck-c)}{2(k(1-p)^2-1)}.$$

APPENDIX C

Evolution of $P^1_{k,1-k}$

Consider the game between two strategies, S_{k,d,x_0} and S'. For simplicity, we assume that S' has the same slope and starting move as S, but has a different intercept, $d' = d + \delta$. We allow δ to be positive or negative. Note that $d = 1-k$ for strategies in the sub-family of interest.

Suppose an error occurs, which will move the play to a new value, x. Table A1 illustrates the first five moves after the error, for the game between S and itself, and for the two cases of the game between S and S' (depending on which strategy moves first).

We are interested in the conditions under which S will evolve towards S', that is, the conditions under which $F(S', S) > F(S, S)$. We can compare the costs and benefits in the game between S and itself with those incurred by S' when it plays S. Averaging between the two cases for the game between S and S', we see that the additional costs paid by S' will be a sequence which begins

$$\tfrac{1}{2}c\{0+\delta+(k^2\delta+\delta)+\cdots+\delta+(k^2\delta+\delta)+\cdots\}.$$

The additional benefits received by S' will be a sequence

$$\tfrac{1}{2}b\{0+k\delta+(k^3\delta+k\delta)+\cdots + k\delta+(k^3\delta+k\delta)+\cdots\}$$

We therefore find that

$$F(S', S) - F(S, S) \approx (bk-c)\sum_{i=0}^{m}\sum_{j=0}^{i}(k^{2j}\delta), \quad \text{(C.1)}$$

Equation (C.1) is an approximation for a number of reasons. First, we have ignored the weighting

TABLE A1

	Round 1	Round 2	Round 3
S	x	$k^2x + kd + d$	$k^4x + k^3d + k^2d + kd + d$
S	$kx + d$	$k^3x + k^2d + kd + d$	…
S	x	$k^2x + kd + k\delta + d$	$k^4x + k^3d + k^3\delta + k^2d + kd + k\delta + d$
S'	$kx + d + \delta$	$k^3x + k^2d + k^2\delta + kd + d + \delta$	…
S'	x	$k^2x + kd + d + \delta$	$k^4x + k^3d + k^2d + k^2\delta + kd + d + \delta$
S	$kx + d$	$k^3x + k^2d + kd + k\delta + d$	…

of successive moves by $(1 - p)^i$ for the case when the number of moves per game is not fixed. Second, we have ignored the fact that unlike the game between S and itself, the sequence of moves between S and S' after an error will eventually reach the limit when both players are cooperating fully. Finally, we have used m as the mean number of moves before the next error occurs, rather than weighting appropriately terminated sums.

Nonetheless, this simple model of the game between S and S' predicts that $F(S', S) > F(S, S)$ under the condition that the right-hand side of eqn (C.1) is greater than zero. Since we know that $k > 0$, this is true for positive values of δ under the condition $bk - c > 0$, and true for negative values of δ under the condition $bk - c < 0$. This implies that strategies along the boundary between families M and P^1 can be invaded by interior members of P^1 when $k > c/b$, and can be invaded by interior members of M when $k < c/b$. This describes the pattern of evolution observed in Fig. 5.