

Stochastic Strategies in the Prisoner's Dilemma

MARTIN NOWAK*

*Institut für Mathematik der Universität Wien,
Strudlhofg. 4, A-1090 Wien, Austria*

Received March 1, 1989

A complete analysis of all strategies where the probability to cooperate depends only on the opponent's previous move is given for the infinitely iterated Prisoner's Dilemma. All Nash solutions are characterized. A necessary condition for evolutionary stability against invasion by selection pressure is found. A mutation selection model is discussed which enables us to quantify the possibility to succeed over less cooperative strategies by means of reciprocity. © 1990 Academic Press, Inc.

1. INTRODUCTION

The theory of evolution is based on the struggle for survival. It would seem that cooperation and kindness are destined for elimination by natural selection. But many biological examples prove this view to be incorrect.

To account for the existence of cooperative or even altruistic behaviour in nature, three kinds of possible explanations have been given: group selection, kin selection, and reciprocity.

This paper deals with the Prisoner's Dilemma, the well-known paradigm of game theory for the evolution of cooperation based on reciprocity. For a recent survey of the literature concerning this subject we refer to Axelrod and Dion (1988). Two individuals are faced with the possibilities to cooperate (C) or to defect (D). Assuming symmetric payoffs both get the reward R for mutual cooperation, while mutual defection yields the smaller value P (for punishment). If one player defects, while the other cooperates, the defector gains the highest payoff T (temptation to defect), while the cooperator only gets the lowest S (sucker's payoff). We assume $T > R > P > S$ and $R > (S + T)/2$ to make mutual cooperation more efficient than alternating C and D . In a single encounter the rational choice is defection, because assuming that the other player will defect, it is better to defect ($P > S$), and assuming that he will cooperate, it is still better to

* Current address: Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK.

defect ($T > R$). Hence both players will choose defection, although they could gain more by cooperation.

But a great variety of strategies is possible, if there is some probability $w > 0$ for the same two players to meet again (the so-called Iterated Prisoner's Dilemma, IPD).

In Axelrod's famous computer tournaments (Axelrod, 1984) for the IPD the simplest of all strategies Tit for Tat (TFT), submitted by A. Rapoport, established itself as champion. TFT is a strategy which cooperates on the first move and then does whatever the opponent has done on the preceding move.

After TFT has won in two computer contests against a great variety of different strategies, the question arises if it has succeeded in nature, too. Will TFT appear most abundant among the reciprocal mechanisms in natural systems? Some kind of TFT-like, reciprocal behaviour has been found by Milinsky (1987) in sticklebacks and by Lombardo (1987) in swallows.

For application in evolutionary biology Axelrod and Hamilton (1981) proposed an ecological approach, where the fitness of a strategy is related to its payoff. Successful strategies will reproduce faster and eliminate weaker ones. Of course the selection coefficients are frequency dependent, because the success of a particular strategy depends on the frequencies of its competitors.

Although TFT is not an evolutionarily stable strategy in the sense of Maynard Smith (1982)—for example, AllC can invade by random drift—it possesses a great amount of stability. It has been shown by Axelrod (1984) that no strategy can invade a homogenous population of TFT players by selection pressure if

$$w > \max \left\{ \frac{T-R}{T-P}, \frac{T-R}{R-S} \right\}.$$

But real biological situations are fraught with errors and, hence, the answer to the other player's preceding move is never an all or nothing decision. In the game between two TFT players a single misperception or error will result in a series of alternating C and D, thus cooperation will break down completely. A simple calculation shows that in the presence of any amount of noise two TFT players will get the same payoff as two random players (Molander, 1985). Therefore some theoretical investigation of stochastic strategies seems useful (as was claimed by May, 1987).

In previous papers (Nowak and Sigmund, 1989a, b) we have introduced stochastic strategies where the probability to cooperate depends only on the opponent's preceding move. The resulting payoff functions are highly nonlinear and therefore not easily amenable to a complete analysis. In this

paper we escape from this difficulty by investigating the important limiting case $w = 1$. Thus two players can be sure to meet again for another round, a situation which is optimal for the evolution of cooperative play based on reciprocity. We give a complete classification of the set of our strategies, in the sense that we characterize all strategies that can invade a homogeneous population of players all using the same strategy. Several Nash solutions are found. In addition we find tools to estimate the direction by which a system will proceed due to mutation-selection forces.

2. THE IPD AS MARKOV CHAIN

The IPD between two players using the strategies E and E' can be described as a Markov chain on the state space CC, CD, DC, DD of the players' choice in each round.

As mentioned in the Introduction we restrict our analysis to such strategies where the probability to cooperate depends only on the opponent's preceding move. We define the conditional probabilities p and q to cooperate, given that the other player's previous choice was a C or D , respectively. Let y be the probability to cooperate in the first move. Thus a strategy E is a vector (y, p, q) . This set of strategies includes TFT = $(1, 1, 0)$, AllC = $(1, 1, 1)$, and AllD = $(0, 0, 0)$.

For $E = (y, p, q)$ and $E' = (y', p', q')$ the transition probability matrix of the Markov process can be written as the stochastic matrix

$$M = \begin{pmatrix} pp' & p(1-p') & (1-p)p' & (1-p)(1-p') \\ qp' & q(1-p') & (1-q)p' & (1-q)(1-p') \\ pq' & p(1-q') & (1-p)q' & (1-p)(1-q') \\ qq' & q(1-q') & (1-q)q' & (1-q)(1-q') \end{pmatrix}.$$

The initial distribution of the process is given by

$$\pi_0 = (yy', y(1-y'), (1-y)y', (1-y)(1-y'))$$

which converges exponentially to the stationary distribution π , if the matrix M is mixing. π is the (unique) normalized, left-hand eigenvector with eigenvalue 1 and is dominating, in the sense of the largest absolute value,

$$\pi = \pi M.$$

The probability distribution in the n th round is given by $\pi_n = M^n \pi_0$. We note that in each round the cooperation of the first and second player is independent. This will also hold for the stationary distribution.

In order to obtain π it is easier to solve

$$\pi = \pi M^2,$$

where

$$M^2 = \begin{pmatrix} \alpha\alpha' & \alpha(1-\alpha') & (1-\alpha)\alpha' & (1-\alpha)(1-\alpha') \\ \alpha\beta' & \alpha(1-\beta') & (1-\alpha)\beta' & (1-\alpha)(1-\beta') \\ \beta\alpha' & \beta(1-\alpha') & (1-\beta)\alpha' & (1-\beta)(1-\alpha') \\ \beta\beta' & \beta(1-\beta') & (1-\beta)\beta' & (1-\beta)(1-\beta') \end{pmatrix}$$

with

$$\alpha = pp' + q(1-p')$$

$$\beta = pq' + q(1-q')$$

$$\alpha' = p'p + q'(1-p)$$

$$\beta' = p'q + q'(1-q).$$

Clearly α (α') and β (β') represent the conditional probabilities for E (E') to cooperate given that the own last but one move was a C or D . M^2 can be written as the Kronecker product of two matrices

$$M^2 = \begin{pmatrix} \alpha & 1-\alpha \\ \beta & 1-\beta \end{pmatrix} \times \begin{pmatrix} \alpha' & 1-\alpha' \\ \beta' & 1-\beta' \end{pmatrix},$$

and the eigenvector π is the Kronecker product of the corresponding eigenvectors of the two matrices

$$\begin{aligned} \pi &= (\beta, 1-\alpha) \times (\beta', 1-\alpha') \\ &= (\beta\beta', \beta(1-\alpha'), (1-\alpha)\beta', (1-\alpha)(1-\alpha')) \end{aligned} \quad (1)$$

which yields after normalization

$$\pi = (ss', s(1-s'), (1-s)s', (1-s)(1-s')), \quad (2)$$

where s and s' are the probabilities for E and E' to cooperate in the stationary distribution. Clearly both s and s' are functions of E and E' , and we can write

$$s = s(E, E')$$

$$s' = s(E', E).$$

Comparing Eqs. (1) and (2) yields

$$s = \frac{q'r + q}{1 - rr'}$$

$$s' = \frac{qr' + q'}{1 - rr'}$$

with

$$r = p - q$$

$$r' = p' - q'.$$

Of course, the initial probabilities y and y' do not alter the stationary values s and s' as long as the matrix M is mixing or $|rr'| < 1$. Therefore the parameters y and y' can be neglected, if we exclude games between reciprocal strategies $p = 1, q = 0$ and paradoxical strategies $p = 0, q = 1$. But instead of describing a strategy E by the parameters p and q , we choose the coordinates r and q to simplify the resulting expressions. Therefore our set of strategies is given by the parallelogram

$$\Sigma = \{E = (r, q) \mid q \in [0, 1], r \in [-q, 1 - q]\}.$$

Let us formulate our calculation as a

THEOREM. *If $|rr'| < 1$ then the matrix M is mixing. In this case the probability that $E = (r, q)$ cooperates in the n th round with $E' = (r', q')$ converges to*

$$s(E, E') = \frac{q'r + q}{1 - rr'}.$$

Similarly, the probability for E' to cooperate with E converges to $s(E', E) = (qr' + q')/(1 - rr')$. We note that

$$s = s'r + q$$

$$s' = sr' + q'.$$

Hence all strategies E with constant probability s to cooperate in the game with E' are lying on the straight line $q = s - s'r$. Note that along this line the probability $s' = s(E', E)$ is constant, too. For every given number $s \in [0, 1]$ the strategy E with $p = q = s$ achieves precisely $s(E, E') = s$. We

also note that in the game of E' with itself the probability to cooperate is converging to

$$s(E', E') = \frac{q'r' + q'}{1 - r'r'} = \frac{q'}{1 - r'}.$$

A useful result follows immediately

THEOREM (Equal cooperativity). *Provided $r, r' \in (-1, 1)$, the following conditions are equivalent:*

$$s(E, E') = s(E', E)$$

$$s(E, E') = s(E', E')$$

$$s(E, E) = s(E', E').$$

Hence the only “mutual” level of cooperativity is that of the strategy against itself.

Remark. The conditions of the theorem correspond to the linear equation in r and q

$$(1 - r')q = q'(1 - r)$$

which defines a line through $E' = (r', q')$ and the reciprocal strategy $(r, q) = (1, 0)$. Hence there exist for every given E' an infinite number of strategies E that fulfill the conditions of the theorem.

It seems worth mentioning that the conditions of the theorem correspond also to a linear equation in p and q

$$(1 - p')q = q'(1 - p)$$

which means that strategies with the same quotient $q/(1 - p)$ do as well. Both q and $1 - p$ are quantities that describe the probability to act just opposite of the other player's previous move.

Remark. The following inequalities are equivalent: (if $r, r' \in (-1, 1)$)

$$s(E, E') > s(E', E)$$

$$s(E, E') > s(E', E')$$

$$s(E, E) > s(E', E')$$

$$(1 - r')q > q'(1 - r).$$

This remark enables us to compare the levels of cooperativity of different

strategies: We say that E is less cooperative than E' if it achieves in the game against itself a lower probability to cooperate in the stationary distribution than E' against itself, hence $s(E, E) < s(E', E')$.

For $rr' = 1$ the transition matrix M is not irreducible. There are two possibilities:

$$(i) \quad r = r' = 1.$$

In the game between two "reciprocal" players $E = (y, 1, 0)$ and $E' = (y', 1, 0)$ the probability for E to cooperate is given by the sequence y, y', y, y', \dots of period 2.

$$(ii) \quad r = r' = -1.$$

In the game between two "paradoxical" players $E = (y, 0, 1)$ and $E' = (y', 0, 1)$ player E cooperates with probability $y, 1 - y', y, 1 - y', \dots$.

For $rr' = -1$ the transition matrix M is irreducible but not mixing. This is

$$(iii) \quad r = 1, r' = -1 \text{ (or vice versa)}.$$

The game between a reciprocal strategy $E = (y, 1, 0)$ and a paradoxical strategy $E' = (y', 0, 1)$ is represented by a Markov chain with period 4. E and E' cooperate with probabilities $y, y', 1 - y, 1 - y', y, \dots$ and $y', 1 - y, 1 - y', y, y', \dots$, respectively.

So far we have dealt with general properties of the IPD between two stochastic strategies, where the probability to cooperate in the next move depends only on the opponent's previous move. In particular the probability w for continuing the game has played no role so far.

Now we are going to introduce the payoff function according to the rules mentioned in the Introduction. We restrict our analysis to the infinitely iterated Prisoner's Dilemma, hence $w = 1$.

If $|rr'| < 1$ the payoff for E against E' is simply defined as the expected payoff in the stationary distribution, since this is the limit of the payoff in the n th round:

$$\begin{aligned} A(E, E') &= Rss' + Ss(1 - s') + T(1 - s)s' + P(1 - s)(1 - s') \\ &= G_1ss' + G_2s + G_3s' + P. \end{aligned} \quad (3)$$

We have used the following abbreviations:

$$G_1 = R - S - T + P$$

$$G_2 = S - P < 0$$

$$G_3 = T - P > 0.$$

As a consequence of the theorem on "equal cooperativity" we mention

COROLLARY. *If $r, r' \in (-1, 1)$, then $s(E, E') = s(E', E)$ is equivalent to $A(E, E) = A(E, E') = A(E', E) = A(E', E')$.*

If $|rr'| = 1$, then the expected payoff is obtained by averaging over a period:

(i) if $r = r' = 1$

$$\begin{aligned} A(E, E') &= Ryy' + \frac{S+T}{2} (y(1-y') + y'(1-y)) + P(1-y)(1-y') \\ &= (R-S-T+P)yy' + \frac{S+T-2P}{2} (y+y') + P \end{aligned} \quad (4)$$

which is symmetric in y and y' ;

(ii) if $r = r' = -1$

$$A(E, E') = \frac{R+P}{2} (yy' + (1-y)(1-y')) + Sy(1-y') + T(1-y)y'; \quad (5)$$

(iii) if $r = 1, r' = -1$

$$A(E, E') = A(E', E) = \frac{R+S+T+P}{4}.$$

3. CLASSIFICATION OF THE STRATEGIES

The goal of this section is to analyse the relations

$$A(E, E') > A(E', E')$$

and

$$A(E, E') = A(E', E')$$

for all pairs of strategies E and E' , because then our set of strategies can be classified in the sense that we find all strategies that can invade a given strategy.

(i) First let $r' \in (-1, 1)$, hence we exclude for E' the reciprocal and the paradoxical strategy. Let

$$F(E, E') := A(E, E') - A(E', E').$$

Setting $F=0$ is equivalent to

$$G_1(ss' - s_0^2) + G_2(s - s_0) + G_3(s' - s_0) = 0.$$

Since $s' = r's + q'$, this is a quadratic equation in s :

$$G_1(r's^2 + q's - s_0^2) + G_2(s - s_0) + G_3(r's + q' - s_0) = 0. \quad (6)$$

One checks immediately that

$$s = s_0 = \frac{q'}{1 - r'}$$

is a solution. If $G_1 r' \neq 0$ there exists another solution of (6), i.e., of

$$\begin{aligned} G_1 r' s^2 + (G_1 q' + G_2 + G_3 r')s + G_3 q' \\ - s_0(G_1 s_0 + G_2 + G_3) = 0 \end{aligned} \quad (7)$$

which is immediately obtained as

$$s = s_1 := -\frac{G_1 q' + (1 - r')(G_2 + G_3 r')}{G_1 r'(1 - r')}. \quad (8)$$

We have $s_1 = 0$ for all strategies $E' = (r', q')$ such that

$$q' = \frac{G_3 r' + G_2}{-G_1} (1 - r') := f_1(r')$$

which implies that $F(\text{AllD}, E') = 0$. We have $s_1 = 1$ for $E' = (r', q')$ such that

$$q' = \frac{(G_1 + G_3)r' + G_2}{-G_1} (1 - r') = f_1 - r'(1 - r') := f_2(r')$$

which implies that $F(\text{AllC}, E') = 0$. For the second solution to represent a probability, one must have $0 \leq s_1 \leq 1$, which is equivalent to

$$f_1(r') \geq q' \geq f_2(r').$$

The two solutions coincide ($s_0 = s_1$) for $E' = (r', q')$ such that

$$q' = \frac{G_2 + G_3 r'}{-G_1} \frac{1 - r'}{1 + r'} = \frac{f_1}{1 + r'} := f(r')$$

which means that $F(E, E') = 0$ only if E achieves the same level of cooperativity: $s(E, E) = s_0$.

The graphs of the functions f , f_1 , and f_2 subdivide the strategy space Σ into four disjoint regions which are important for the classification.

Remark 1. For all $E = (r, q) \in \Sigma$, one has

$$q \leq f_2(r) \Rightarrow q \leq f(r) \Rightarrow q \leq f_1(r)$$

and, conversely,

$$q \geq f_1(r) \Rightarrow q \geq f(r) \Rightarrow q \geq f_2(r).$$

Remark 2. If $r' > 0$ then

$$f_1(r') < q' \Leftrightarrow s_1 < 0$$

$$f_1(r') = q' \Leftrightarrow s_1 = 0$$

$$f(r') < q' < f_1(r') \Leftrightarrow 0 < s_1 < s_0$$

$$q' = f(r') \Leftrightarrow s_1 = s_0$$

$$f_2(r') < q' < f(r') \Leftrightarrow s_0 < s_1 < 1$$

$$q' = f_2(r') \Leftrightarrow s_1 = 1$$

$$q' < f_2(r') \Leftrightarrow s_1 > 1.$$

Remark 3. If $r' < 0$, then $s_1 > 1$ for $G_1 < 0$ and $s_1 < 0$ for $G_1 > 0$.

First let us investigate the special case

1. $G_1 = 0$.

Here the analysis is very simple, because

$$F = (G_2 + G_3 r')(s - s_0)$$

which implicates the following

THEOREM. Let $G_1 = 0$ and $r' \in (-1, 1)$.

$$A(E, E') > A(E', E')$$

is equivalent to

$$s > s_0 \quad \text{if} \quad G_2 + G_3 r' > 0$$

$$s < s_0 \quad \text{if} \quad G_2 + G_3 r' < 0.$$

Moreover $A(E, E') = A(E', E')$, iff $s = s_0$ or $G_2 + G_3 r' = 0$.

2. $G_1 < 0$.

The factorization of F ,

$$F = \begin{cases} G_1 r' (s - s_0)(s - s_1) & \text{if } r' \neq 0 \\ (s - s_0)(G_1 s_0 + G_2) & \text{if } r' = 0, \end{cases} \quad (9)$$

yields the following result:

THEOREM. Let $G_1 < 0$ and $r' \in (-1, 1)$.

$$A(E, E') > A(E', E')$$

is equivalent to

- a) $s_0 < s$ if $q' < f_2(r')$.
- b) $s_0 < s < s_1$ if $f_2(r') \leq q' < f(r')$
- c) $s_1 < s < s_0$ if $f(r') < q' \leq f_1(r')$
- d) $s < s_0$ if $q' > f_1(r')$

If $q' = f(r)$ then $s \neq s_0$ implies $A(E, E') < A(E', E')$. Moreover $A(E, E') = A(E', E')$ iff $s = s_0$ or $s = s_1$.

(For an illustration of the theorem see Fig. 1.)

3. $G_1 > 0$

The analysis of (9) for $G_1 > 0$ yields

THEOREM. Let $G_1 > 0$ and $r' \in (-1, 1)$.

$$A(E, E') > A(E', E')$$

is equivalent to

- a) $s > s_0$ if $f_1(r') \leq q'$.
- b) $s > s_0$ or $s < s_1$ if $f(r') < q' < f_1(r')$
- c) $s < s_0$ or $s > s_1$ if $f_2(r') < q' < f(r')$
- d) $s < s_0$ if $q' \leq f_2(r')$
- e) $s < s_0$ or $s > s_0$ if $q' = f(r')$

Moreover $A(E, E') = A(E', E')$ iff $s = s_0$ or $s = s_1$.

(See Fig. 2.)

So far we have dealt with the (general) case $r' \in (-1, 1)$.

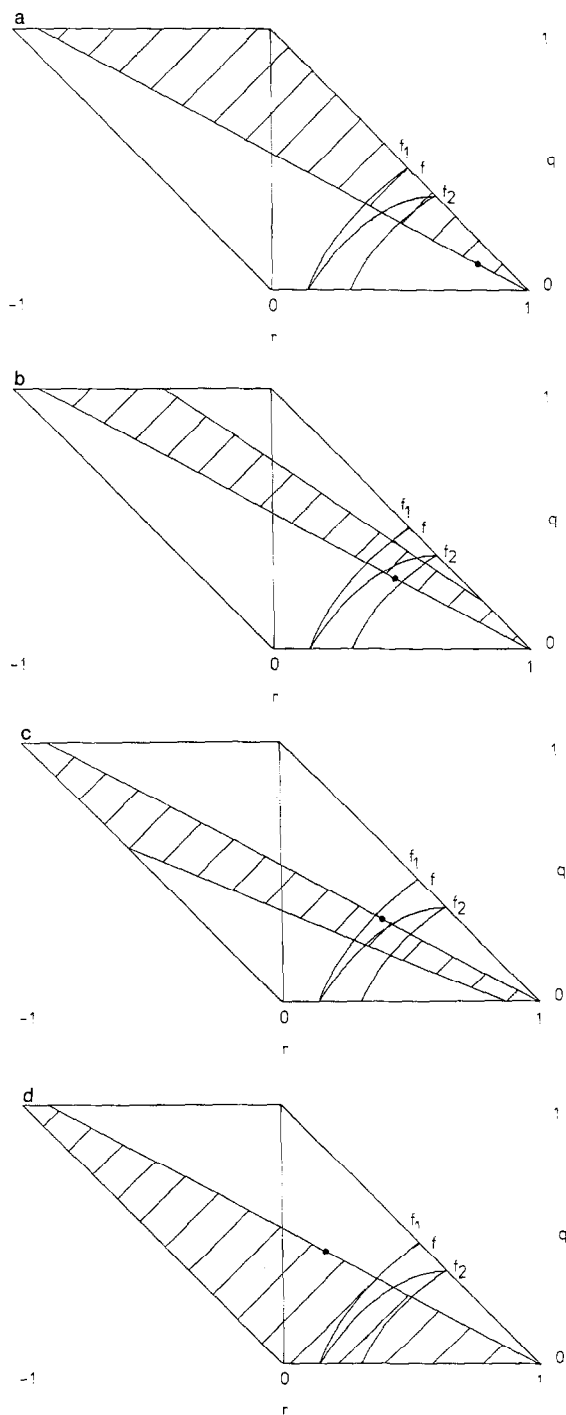


FIG. 1. (a-d) Illustration of the theorem for $G_1 < 0$. The strategy $E' = (r', q')$ is represented by the dot. Strategies E lying in the dashed region fulfill $A(E, E') > A(E', E')$.

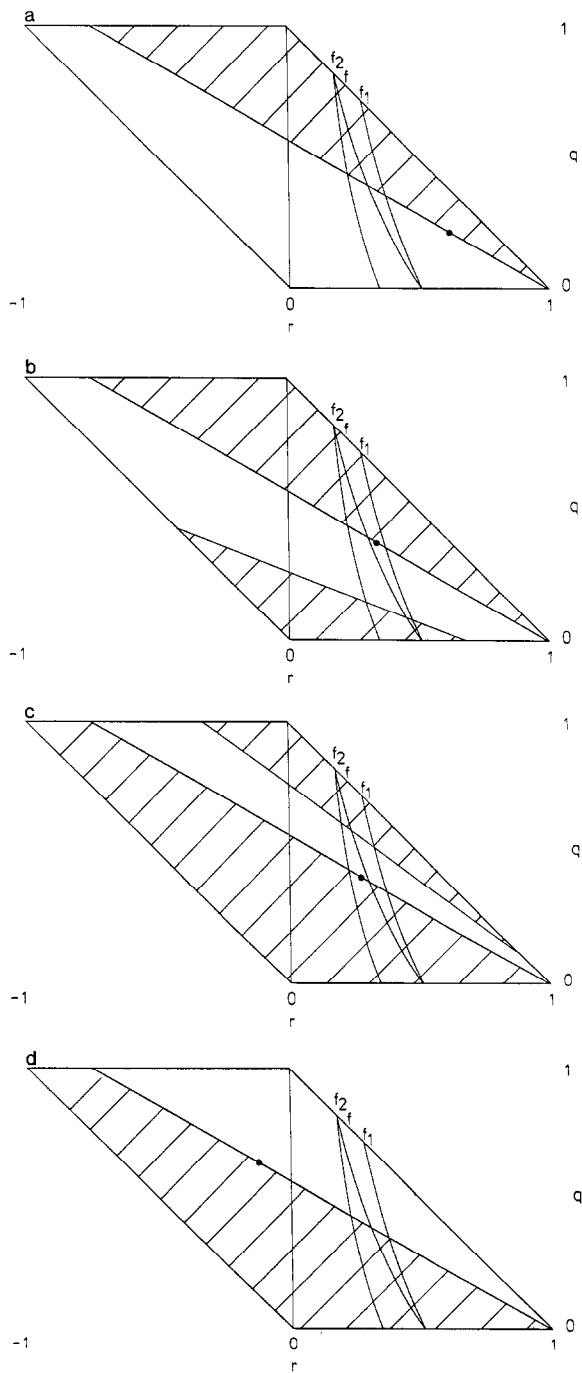


FIG. 2. (a-d) Illustration of the theorem for $G_1 > 0$. The strategy $E' = (r', q')$ is represented by the dot. Strategies E lying in the dashed region fulfill $A(E, E') > A(E', E')$.

(ii) Next let E' be the reciprocal strategy, hence $r' = 1$ and $q' = 0$. In this case we have to consider the probability y' , too. We have to distinguish whether or not E is itself a reciprocal strategy.

$$(1) \quad E = (y, r, q) = (y, 1, 0).$$

The payoff is given by Eq. (4). Of course $A(E, E') = A(E', E)$. A straightforward calculation shows that $A(E, E') > A(E', E')$ iff $y > y'$.

$$(2) \quad E = (y, r, q) \text{ with } r \in [-1, 1).$$

Here we have $A(E, E') = A(E', E) = A(E, E)$, with the last equality valid only if $r > -1$. We find that $A(E, E') > A(E', E')$ iff $s(E, E') > y'$. Thus the stationary probability of E cooperating with E' must exceed y' . Note that $s(E, E') = q/(1-r)$ in this case.

(iii) Last E' should represent the paradoxical strategy $r' = -1$, $q' = 1$. We have to distinguish three cases:

$$(1) \quad E = (y, r, q) = (y, -1, 1).$$

By analysing Eq. (5), one can show that $A(E, E') > A(E', E')$ iff $y < y'$.

$$(2) \quad E = (y, r, q) = (y, 1, 0).$$

Of course, $A(E, E') = (R + S + T + P)/4$ and $A(E', E') = (R + P)/2 - G_1 y'(1 - y')$. If $G_1 = 0$ then $A(E, E') = A(E', E')$. For $G_1 \neq 0$ a simple calculation shows: If $y' = \frac{1}{2}$ then $A(E, E') > A(E', E')$. If $y' \neq \frac{1}{2}$ then $A(E, E') - A(E', E')$ has the same sign as $-G_1$.

$$(3) \quad E = (y, r, q) \text{ with } r \in (-1, 1).$$

It can be shown: $A(E, E') - A(E, E')$ has the same sign as $1 - k(r + q) - q (= 1 - kp - q)$ with $k = (-b + \sqrt{b^2 - 4ac})/2a$, where

$$a = T - A(E', E') > 0$$

$$b = R + P - 2A(E', E') = 2G_1 y'(1 - y')$$

$$c = S - A(E', E') < 0.$$

(If $G_1 = 0$ then $k = 1$.)

4. CONSEQUENCES

In the last chapter we have classified all combinations of inequalities $A(E, E') > A(E', E')$ for E and E' . Therefore the whole class of game dynamical behaviour for two strategies has been investigated. We can find all examples for stable dimorphisms

$$A(E, E') > A(E', E')$$

$$A(E', E) > A(E, E),$$

bistability

$$A(E, E') < A(E', E')$$

$$A(E', E) < A(E, E),$$

domination

$$A(E, E') \geq A(E', E')$$

$$A(E', E) \leq A(E, E),$$

where at least one of the relations must be a strict inequality and neutrality

$$A(E, E') = A(E', E')$$

$$A(E', E) = A(E, E).$$

We note that Feldman and Thomas (1987) have also found stable polymorphisms if the probability w is part of the strategy.

We mention the existence of stone-paper-scissors cycles: E dominates E' , which dominates E'' , which dominates E . A prominent examples is the cycle AllD, AllC, and the reciprocal strategy with $0 < y < 1$.

For a further discussion we need some definitions from evolutionary game theory.

DEFINITION. (1) E' is a strict Nash solution iff $A(E', E') > A(E, E')$ for all $E \neq E'$.

(2) E' is an evolutionary stable strategy (ESS), iff

$$A(E', E') > A(E, E')$$

or

$$A(E', E') = A(E, E')$$

$$A(E', E) > A(E, E)$$

for all $E \neq E'$.

(3) E' cannot be invaded by selection pressure, iff

$$A(E', E') > A(E, E')$$

or

$$A(E', E') = A(E, E')$$

$$A(E', E) \geq A(E, E)$$

for all E . Hence E' can be invaded only by random drift.

(4) E' is a Nash solution iff $A(E', E') \geq A(E, E')$ for all E .

A strategy that is stable against invasion by selection pressure cannot be dominated, but there may exist strategies E that dominate a Nash solution E' , namely, $A(E', E') = A(E, E')$ and $A(E', E) < A(E, E)$.

Remark. (1) \Rightarrow (2) \Rightarrow (3) \Rightarrow (4).

(A strict Nash solution is evolutionary stable. An ESS cannot be invaded by selection pressure. Strategies that cannot be invaded by selection pressure must represent Nash solutions.)

The results of Section 3 implicate the following remarks for our set of strategies:

Remark 1. There is no ESS, because for every E' there exist strategies that obtain exactly the same payoff, i.e., $A(E, E) = A(E, E') = A(E', E) = A(E', E')$.

Remark 2. The reciprocal strategy $E = (y, 1, 0)$ cannot be invaded by selection pressure iff $y = 1$. The reciprocal strategy is not even a Nash solution iff $y < 1$.

However, we can find strategies that represent Nash solutions independent of y :

Remark 3. $E = (r, q)$ cannot be invaded by selection pressure, if $r = 1 - q$ and

(1) $G_1 < 0 : 0 < q \leq (2R - S - T)/(R - S)$ [$q = (2R - S - T)/(R - S)$ is the intersection between $q = f(r)$ and $q = 1 - r$]

(2) $G_1 = 0 : 0 < q < (R - P)/(T - P) (= (2R - S - T)/(R - S))$

(3) $G_1 > 0 : 0 < q < (R - P)/(T - P)$ [$q = (R - P)/(T - P)$ is the intersection between $q = f_1(r)$ and $q = 1 - r$].

Thus a necessary condition for stability against invasion by selection pressure is $p = 1$ (equivalent to $r = 1 - q$). If the probability q exceeds the given values, then less cooperative strategies can invade. This result should be compared with Molander's (1985) level of generosity.

Remark 4. $E = (r, q)$ represents a Nash solution, if $q = 0$ and

(1) $G_1 < 0 : 0 \leq r \leq (P - S)/(T - P)$ [$r = (P - S)/(T - P)$ is the zero of $f(r)$]

(2) $G_1 = 0 : 0 \leq r \leq (P - S)/(T - P) (= (P - S)/(R - S))$

(3) $G_1 > 0 : 0 \leq r \leq (P - S)/(R - S)$. [$r = (P - S)/(R - S)$ is the zero of $f_2(r)$]

or $q > 0$ and

(1) $G_1 < 0 : q = f(r), r < 1$

(2) $G_1 = 0 : G_2 + G_3 r = 0$ (hence $r = (P - S)/(T - P)$).

In each case the Nash solutions with $q = 0$ are dominated only by reciprocal strategies with $y > 0$. For $G_1 < 0$ strategies $E(r, q)$ with $q = f(r)$ and $r < 1$ are dominated only by reciprocal strategies with $y > q/(1 - r)$. For $G_1 = 0$ a particular strategy $E' = (r', q')$ with $r' = (P - S)/(T - P)$ is dominated both by reciprocal strategies with $y > q'/(1 - r')$ and by all strategies $E = (r, q)$ that fulfill

$$r > \frac{P - S}{T - P} \quad \text{and} \quad q(1 - r') > q'(1 - r)$$

or

$$r < \frac{P - S}{T - P} \quad \text{and} \quad q(1 - r') < q'(1 - r).$$

If $G_1 > 0$ there are no Nash solutions in the interior of Σ .

The picture is different, if we consider some limits to precision (the presence of "noise" in biological systems); i.e., we choose $p \in [\varepsilon_1, 1 - \varepsilon_2]$ and $q \in [\varepsilon_3, 1 - \varepsilon_4]$ with ε_i small and positive. The parallelogram Σ is modified to

$$\Sigma^* = \{E = (r, q) \mid q \in [\varepsilon_3, 1 - \varepsilon_4], r \in [\varepsilon_1 - q, 1 - q - \varepsilon_2]\}.$$

Our analysis implicates for the set Σ^* :

Remark 1. The stochastic AllD version $E(\varepsilon_1 - \varepsilon_3, \varepsilon_3)$ is the only strict Nash solution.

Remark 2. The stochastic TFT strategy $E = (1 - \varepsilon_2 - \varepsilon_3, \varepsilon_3)$ (y is unimportant) is dominated by all strategies with $q > (\varepsilon_3/(\varepsilon_2 + \varepsilon_3))(1 - r)$.

Remark 3. $E = (r, q)$ cannot be invaded by selection pressure, if $G_1 < 0$ and $q = f(r)$.

Remark 4. Nash solutions are found for $G_1 = 0$ and $r = (P - S)/(T - P)$. Except for stochastic AllD, no Nash solutions exist for $G_1 > 0$.

If we restrict ourselves to the set of all deterministic strategies, i.e., $p, q \in \{0, 1\}$, it turns out that all strategies can be dominated except for TFT (Aumann, 1981). This result does not carry over to the "mixed" strategies $E \in \Sigma$, because the payoff $A(E, E')$ is nonlinear in the parameters p and q . However, in both cases TFT is stable against invasion by selection pressure and ALLD represents a Nash solution (but is dominated by TFT).

We note the existence of strategies $E \in \Sigma$ that are stable against invasion by less cooperative strategies. Let us define the subset

$$\Sigma_s := \begin{cases} \{E = (r, q) \mid q < f(r)\} & \text{if } G_1 < 0 \\ \{E = (r, q) \mid G_2 + G_3 r > 0\} & \text{if } G_1 = 0 \\ \{E = (r, q) \mid q > f_1(r)\} & \text{if } G_1 > 0. \end{cases}$$

All strategies $E \in \Sigma_s$ cannot be invaded by strategies E' with $s(E', E') < s(E, E)$.

The results in Sections 2 and 3 enable us to give a description of the evolutionary behaviour of a population of PD-players if the population is homogeneous at the beginning and mutations are so rare that selection leads to an equilibrium after each mutation. We start with a homogeneous population of players all using the same strategy $E_0 = (r_0, q_0)$. We neglect the probability y . After some time a mutant is generated that uses a slightly different strategy $E_1 = (r_1, q_1)$ with $p_1 = p_0 + \delta_p$ and $q_1 = q_0 + \delta_q$. Let us define two subsets of Σ :

$$\Sigma_r := \begin{cases} \{E = (r, q) \mid q < f(r)\} & \text{if } G_1 < 0 \\ \{E = (r, q) \mid G_2 + G_3 r > 0\} & \text{if } G_1 = 0 \\ \{E = (r, q) \mid q > f(r)\} & \text{if } G_1 > 0 \end{cases}$$

and

$$\Sigma_{nr} := \begin{cases} \{E = (r, q) \mid q > f(r)\} & \text{if } G_1 < 0 \\ \{E = (r, q) \mid G_2 + G_3 r < 0\} & \text{if } G_1 = 0 \\ \{E = (r, q) \mid q < f(r)\} & \text{if } G_1 > 0. \end{cases}$$

(Σ_r contains a neighbourhood of the reciprocal strategy.) If we choose the δ 's sufficiently small, such that E_0 and E_1 are in the same subset, then there are only two possibilities: either E_0 dominates E_1 or vice versa. If E_0 dominates, then E_1 cannot invade. The process is repeated with another trial for E_1 , until a mutant E_1 appears that dominates E_0 . Then E_1 can invade and E_0 will be eliminated by selection. Next mutants E_2 of E_1 are generated and selected in the same way, thereby producing a sequence E_i of strategies that represent a "path of evolution" for this mutation selection process. The sequence E_i fulfills the following properties:

If $E_0 \in \Sigma_r$, then $s_i := s(E_i, E_i)$ is increasing, because E_{i+1} dominates E_i ($\in \Sigma_r$), if $s(E_{i+1}, E_i) > s(E_i, E_i)$ which is equivalent to $s_{i+1} > s_i$.

On the other hand, if $E_0 \in \Sigma_{nr}$ then s_i is decreasing.

The qualitative interpretation goes as follow: If we start within the subset Σ_{nr} , then less cooperative strategies can invade. Thus cooperation will steadily decrease. If we start within the subset Σ_r , then invading strategies must possess higher probabilities to cooperate. The amount of cooperation has to increase along the path of evolution. Less cooperative strategies are eliminated by selection. Evolution optimizes the readiness to cooperate. In a following paper (Nowak and Sigmund, 1990) this mutation selection process is investigated as a dynamical system on Σ . There it is shown that TFT is not the outcome of this mutation selection process.

Last we should mention that an interesting evolutionary behaviour can be found if we assume that the parameter q is fixed at $q = q_0$ and mutations can only occur in p . If $G_1 < 0$ and $q_0 < (2R - S - T)/(R - S)$ there exists a unique value \hat{r} such that $q_0 = f(\hat{r})$. The strategy $\hat{E} = (\hat{r}, q_0)$ is a strict Nash solution (and therefore an ESS) in the sense that $A(\hat{E}, \hat{E}) > A(E, \hat{E})$ for all $E = (r, q_0) \neq \hat{E}$. However, there is no way for \hat{E} to become established in the first place, because only those mutants that drive the value r away from \hat{r} can invade: If $r_0 > \hat{r}$ then $E_0 = (r_0, q_0) \in \Sigma_r$. In this case the evolutionary sequence E_i has the property that s_i and hence r_i will increase. If $r_0 < \hat{r}$ then $E_0 \in \Sigma_{nr}$ and r_i has to decrease. In this sense \hat{E} is an "inaccessible" ESS (Nowak, 1990).

5. CONCLUSIONS

Biological interactions, in contrast to interactions between computer programs, teem with uncertainties. Therefore the analysis of stochastic strategies seems to be necessary for biological interpretations of the Prisoner's Dilemma. This paper gives a complete classification of all strategies where the probability of cooperation depends only on the other player's preceding move. The theorems characterize all strategies that are capable of invading a given strategy. Therefore we can find all Nash solutions. It is interesting that $p = 1$ (never D after C) is a necessary condition for stability against invasion by selection pressure. Thus all strategies with $p < 1$ can be dominated.

Within our set of strategies a region Σ_r is found, where cooperation increases due to mutation-selection forces. A homogenous population of players adopting a strategy $E \in \Sigma_r$ cannot be invaded by less cooperative strategies. Thus the possibility of succeeding over less cooperative strategies by means of reciprocity within the IPD has been quantified. If we consider any limits to precision the resulting stochastic TFT version (which

represents the "biologically relevant" TFT) is not even a Nash solution. In an error-prone world, TFT loses much of its success, since a single mistake between two TFT players leads to an endless sequence of mutual recriminations. A certain level of generosity (i.e., a tendency to cooperate even after a defection by the opponent) is much more appropriate. In the presence of "noise," it is sometimes best to forget a bad turn ($q > 0$) but never a good one ($p \rightarrow 1$).

ACKNOWLEDGMENTS

The author is indebted to Karl Sigmund for his generous help. Support from the Austrian Forschungsförderungsfond, Projects P6866 and 6864C, is gratefully acknowledged.

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