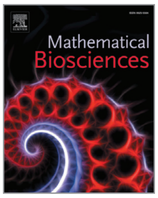
Mathematical Biosciences 279 (2016) 63–70

Contents lists available at ScienceDirect

Mathematical Biosciences

journal homepage: www.elsevier.com/locate/mbs



Payoff non-linearity sways the effect of mistakes on the evolution of reciprocity

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ARTICLE INFO

Article history:
Received 25 March 2016
Revised 4 July 2016
Accepted 10 July 2016
Available online 15 July 2016

Keywords:
Prisoner's dilemma
Cooperation
Reciprocity
Mistakes
Payoff linearity
Synergetic effect

ABSTRACT

The existence of cooperation is considered to require explanation, and reciprocity is a potential explanatory mechanism. Animals sometimes fail to cooperate even when they attempt to do so, and a reciprocator has an Achilles' heel: it is vulnerable to error (the interaction between two reciprocators can lead to an endless vendetta.). However, the strategy favored by natural selection is determined also by its interaction with other strategies. The relationship between two reciprocators leading to a collapse of cooperation through error does not straightforwardly imply that mistakes make the conditions under which reciprocity evolves stringent. Hence, mistakes may facilitate the evolution of reciprocity. However, it has been shown through the analysis of the interaction between reciprocators and unconditional defectors that the existence of mistakes makes the conditions for reciprocators stable against invasion by an unconditional defector more stringent, which indicates that mistakes discourage the evolution of reciprocity. However, this result is based on the assumption that the effects of cooperation are additive (payoff is linear), while the game played by real animals does not always display this feature. In such cases, the result may be swayed. In this paper, we remove this assumption, reexamining whether mistakes disturb the evolution of reciprocity. Using the analysis of an evolutionarily stable strategy (ESS), we show that when extra fitness costs are present in cases where mutual cooperation is established, mistakes can facilitate the evolution of reciprocity; whereas, when the effect of cooperation is additive, mistakes always disturb the evolution of reciprocity, as has been shown previously.

1. Introduction

The existence of cooperation is mysterious. This mystery has been a crucial topic in evolutionary biology for a long time [13,26,28,40]. Mechanisms explaining the existence of cooperation have been proposed [13,28,29,37,40]. One potential explanatory mechanism for the evolution of cooperation is direct reciprocity [3,5,8,16,19–21,23,31,40], and direct reciprocity has been long regarded as a major hypothesis (but see also Kurokawa, unpublished data).

Animals are error-prone, and even when they attempt to cooperate, they sometimes fail to do so, with some probability [25]. It has been proposed that the strategy of tit-for-tat (direct reciprocity) has an Achilles' heel: it is vulnerable to error [3–7,17,27,30,32]. If a tit-for-tat (TFT) player erroneously defects against another TFT-player, this will lead to an endless vendetta. Several strategies to overcome this problem have been proposed. One of them is a strategy called generous tit-for-tat: always cooperate if the opponent has cooperated in the previous round, but defect only with a certain probability if the opponent has defected [27,31]. Generous TFT is a stochastic error-proof strategy [28]. Another is the strategy called win-stay, lose-shift: cooperate if and only if the focal player and the opponent player used the same move in the previous round [11,18,32]. Win-stay, lose-shift is a deterministic error-proof strategy [28]. These strategies are error-proof: mistaken defections are corrected, and mutual cooperation is resumed. Thus, it is considered that TFT is vulnerable, and other strategies are necessary for survival in a world in which there are mistakes.

However, this argument only considers the interaction between the same two strategies, while the strategy that is favored by natural selection must also be determined by its interaction with other strategies.

Let us consider a population consisting of TFT players and unconditional defectors. In this case, making a mistake has not only a demerit (i.e., the reciprocating players' mistaken defection can lead to an endless vendetta) but also a merit (i.e., the reciprocator can avoid cooperating with an unconditional defector opponent in the first move by mistake) for reciprocators. Thus, mistakes may facilitate the evolution of TFT.

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http://dx.doi.org/10.1016/j.mbs.2016.07.004
0025-5564/© 2016 Published by Elsevier Inc.

Table 1
Payoff matrix of the prisoner's dilemma game.

		When playing against	
		Cooperator	Defector
Payoff to	Cooperator	$b-c+d$	$-c$
Payoff to	Defector	b	0

However, this expectation is not supported by the results of theoretical studies using mathematical models. Therefore, the existence of mistakes makes the condition for reciprocators being stable against invasion by unconditional defectors more stringent, indicating that mistakes discourage the evolution of reciprocity [19].

However, this result is based on the assumption that the effects of cooperation are additive (payoff is linear), while the payoff obtained in the game played by real animals is sometimes nonlinear [1,2,33,36,39]. When mutual cooperation is established, in some cases, benefits of extra fitness emerge, and in other cases, extra fitness costs emerge [36]. When the payoff is not linear, does the result that mistakes in behaviors disturb the evolution of reciprocity still holds true?

When dealing with the evolution of cooperation, the consideration of the case where extra fitness costs are present is reasonable; this is because a cooperator will then give less cooperation, on average, to other cooperators because some of them have already died (because they cooperated) or because it is more likely that they will die in the future thereby squandering their gains [9,36]. Hence, let us consider the case where extra fitness costs are present. When two reciprocal players meet, they can avoid the extra fitness costs experienced when mutual cooperation is established through the collapse of mutual cooperation in the existence of mistakes. Thus, in the case where extra fitness costs are present, making a mistake can boost the evolution of reciprocity, and hence making mistakes might facilitate its evolution.

The rest of this paper is structured as follows. Section 2 describes the model and defines the strategies. Section 3 considers the case wherein payoff is linear and introduces a previous study briefly. Section 4 considers the case wherein extra fitness costs are present and examines whether mistakes can facilitate the evolution of reciprocity, using an evolutionarily stable strategy (ESS) analysis. Section 5 summarizes the results obtained in this paper and interprets the results. In addition, we report the results of the case wherein extra fitness benefits are present, and we suggest directions for future study. We also consider the case where a strategy of anti-reciprocation (attempt at cooperation where the opponent has defected and attempt at defection when the opponent has cooperated) invades a population following TFT.

2. Model

Consider the repeated prisoner's dilemma game in which individuals either cooperate or defect in each round. A cooperator will pay an opponent b at a personal cost of c, and $b > c > 0$ holds true. And when mutual cooperation is established, each of the two players gets extra d [36]. In this case, a cooperator gets $b-c+d$ when interacting with a cooperator. A cooperator gets $-c$ when interacting with a defector. A defector gets b when interacting with a cooperator. A defector gets 0 when interacting with a defector (Table 1). The prisoner's dilemma demands $-(b-c)/2 < d < c$. When $d=0$ is satisfied, payoff is linear. We assume that individuals are paired randomly and that the population is not age structured (see, e.g., [24] for a study considering an age-structured population). The probability of individuals' interacting more than t times in a given pair is w^t. Here, w is a constant discounting factor that is greater than 0 and less than 1. In this case, it is straightforward that the expected number of interactions is $1/(1-w)$.

Here, we consider the case where mistakes in behavior, such as an individual intending to cooperate but sometimes failing to do so, occur [25]. Let μ, $0 \le \mu \le 1$, be the probability that a player makes mistakes (i.e., an individual who intends to cooperate fails to and defects). When $\mu = 1$ holds true, players never cooperate, and the case does not qualify for investigation. Hence, we consider the case wherein $\mu < 1$ is met.

Following earlier studies [5], we consider two strategies: always defect (ALLD) and tit-for-tat (TFT). In the ALLD strategy, the player defects no matter what the opponent does. An actor following the TFT strategy attempts to cooperate with probability 1 but fails to do so with probability μ when the round is the first or is following one in which the opponent has cooperated on the last move. In contrast, an actor following the TFT strategy defects with probability 1 when the round is the following round and the opponent has defected in the last move.

3. Previous studies [19]

In this section, we consider the case where payoffs are linear. This case can be regarded as a special case of Kurokawa [19]. From Kurokawa [19], we know that the condition under which a TFT strategy is an ESS against the encroachment of an ALLD strategy is given as

$$\frac{c}{b} < w(1-\mu). \tag{1}$$

The right-hand side of (1) decreases as μ increases implying that the existence of mistakes interferes with the evolution of reciprocity. In the next section, we consider the case where an extra fitness cost is present and examine whether payoff non-linearity can sway this result or not.

4. Analysis wherein the extra fitness cost is present ($d < 0$)

In this section, we consider a case where an extra fitness cost is present. We define x as the expected total payoff for an individual playing TFT for a game in a pair of two players following TFT strategies and y as the expected total payoff for an individual playing TFT in a pair consisting of one player following the TFT strategy and one following the ALLD strategy. In this case, we have (see Appendices A and B respectively for the derivation)

$$x = d\frac{(1-\mu)^2}{1-w(1-\mu)^2} + (b-c)\frac{(1-\mu)}{1-w(1-\mu)}. \tag{2}$$

$$y = b(1-\mu). \tag{3}$$

We can then determine the conditions under which a TFT strategy is an ESS against the encroachment of an ALLD strategy; we can show that the ESS conditions hold if and only if $x > y$. Using (2) and (3), this inequality becomes (4).

$$d > \frac{\left(1-w(1-\mu)^2\right)}{(1-\mu)(1-w(1-\mu))}(c-bw(1-\mu)). \tag{4}$$

Substituting $d=0$ into (4), (4) reduces to (1). In the following, we obtain the conditions under which mistakes can facilitate the evolution of reciprocity. If reciprocity is unstable against invasion by unconditional defectors when there are no mistakes and there is a parameter (μ) for which reciprocity is stable against invasion by unconditional defectors, we can safely conclude that mistakes can facilitate the evolution of reciprocity. Here, we define $f(\mu)$ as the right-side hand of (4), and we have

$$f(\mu) = \frac{\left(1-w(1-\mu)^2\right)}{(1-\mu)(1-w(1-\mu))}(c-bw(1-\mu)) \tag{5}$$