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A simple rule of direct reciprocity leads to the stable coexistence of cooperation and defection in the Prisoner's Dilemma game

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ABSTRACT

The long-term coexistence of cooperation and defection is a common phenomenon in nature and human society. However, none of the theoretical models based on the Prisoner's Dilemma (PD) game can provide a concise theoretical model to explain what leads to the stable coexistence of cooperation and defection in the long-term even though some rules for promoting cooperation have been summarized (Nowak, 2006, Science 314, 1560–1563). Here, based on the concept of direct reciprocity, we develop an elementary model to show why stable coexistence of cooperation and defection in the PD game is possible. The basic idea behind our theoretical model is that all players in a PD game prefer a cooperator as an opponent, and our results show that considering strategies allowing opting out against defection provide a general and concise way of understanding the fundamental importance of direct reciprocity in driving the evolution of cooperation.

1. Introduction

Five rules for promoting cooperation based on kin selection (Hamilton, 1964), direct and indirect reciprocity (Trivers, 1971; Axelrod and Hamilton, 1981; Axelrod, 1984; Nowak and Sigmund, 2005), graph selection (Nowak and May, 1992; Ohtsuki et al., 2006) and group selection (Traulsen and Nowak, 2006) have been summarized (Nowak, 2006b). The one-third law based on the stochastic evolutionary game in a finite population also shows how the emergence of cooperation can be favored by natural selection (Nowak et al., 2004). Although these theoretical results have been successful in explaining the evolution of cooperation, none of them provides a simple mechanism that can lead to stable coexistence of cooperation and defection in the long-term even though this phenomenon is common in nature and human society (Dugatkin, 1997).

Cooperation means that a donor pays a cost, c, for a recipient to get a benefit, b, where $b > c$ (Nowak, 2006a; Sigmund, 2010). In the corresponding one-shot Prisoner's Dilemma (PD) game, defection is the only Nash equilibrium (NE) (Nowak, 2006a; Sigmund, 2010). On the other hand, for the repeated PD game with two strategies TFT (tit-for-tat) and AllD (always defect), TFT is a NE if the expected number of iterated interactions between a pair of individuals is larger than the critical value $b/(b-c)$ (Axelrod and Hamilton, 1981; Axelrod, 1984; Nowak, 2006a, 2006b; Sigmund, 2010). However, the stable coexistence of TFT and AllD is impossible in the TFT-AllD game. Clearly, the success of TFT is mainly due to the increased chance of interactions between cooperators (Axelrod, 1984; Axelrod and Dion, 1988). That is, TFT provides a mechanism whereby cooperators preferentially interact among themselves. Similarly, assortative matching among cooperators has been used to explain why altruism can emerge (Eshel and Cavalli-Sforza, 1982; Cavalli-Sforza and Feldman, 1983; Fletcher and Doebeli, 2006; Taylor and Nowak, 2006; Pacheco et al., 2008), although the evolutionary origin of the non-uniform interaction rates among cooperators has not been explained (Taylor and Nowak, 2006; Pacheco et al., 2008). For the repeated PD game, one of the key assumptions is that the interaction between a pair of individuals will be repeated for several rounds, but that the expected number of iterated rounds is fixed (Axelrod, 1984; Axelrod and Dion, 1988; Nowak, 2006a; Sigmund, 2010). In particular, no player in a repeated PD game is able to unilaterally stop the interaction with his/her opponent. However, based on individual self-interest in the PD game, both cooperators and defectors prefer an opponent who cooperates (or only

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cooperators are always welcome). Thus, if players are able to unilaterally terminate the interactions with their opponents, then a simple rule will be followed by all individuals: I would like to keep my opponent if he/she is a cooperator; and if my opponent is a defector, I will immediately stop the interaction with him/her and seek a new partner instead. Clearly, this simple rule reflects the basic characteristics of direct reciprocity. Recently, an interesting study based on the concept of conditional dissociation, i.e. the option to leave an interacting partner in response to his/her behavior, found that a strategy called "out-for-tat" (OFT) may be important for the coexistence of cooperation and defection (Hayashi, 1993; Schuessler, 1989; Aktipis, 2004; Fujiwara-Greve and Okuno-Fujiwara, 2009; Izquierdo et al., 2010, 2014). In this study, strategy OFT means that an individual will respond to defection by merely leaving, i.e. OFT will not tolerate defection but, unlike TFT, it does not seek revenge. Although this study shows a possibility for the coexistence of cooperation and defection because of OFT, it is still not clear what the dynamical mechanism of the coexistence is. To reveal the fundamental evolutionary force driving the coexistence of cooperation and defection, based only on the concept of direct reciprocity (Trivers, 1971; Axelrod and Hamilton, 1981; Axelrod, 1984), we develop a concise theoretical model to show how opting out against defection improves the coexistence of cooperation and defection in PD game settings.

2. Definitions and assumptions

Consider a simplified PD game with payoff matrix $\begin{pmatrix} b-c & -c \\ b & 0 \end{pmatrix}$ (Nowak, 2006a; Sigmund, 2010). Unlike the classic repeated game, we assume that the interaction between a pair of individuals can be continued but each player can unilaterally break off the interaction with his/her opponent at any time according to his/her own volition. This means that all individuals (including both cooperators and defectors) will respond to defection by merely leaving (i.e. all individuals use OFT) (Izquierdo et al., 2010, 2014). On the other hand, we continue to assume as in the classic repeated game that the expected number of rounds between a pair of individuals is limited even if these two individuals would like to continue their interaction (Axelrod, 1984; Axelrod and Dion, 1988; Nowak, 2006a; Sigmund, 2010). Specifically, we assume that the interaction between a pair of individuals will be terminated after each round with probability ρ, where ρ is independent of these individuals' strategies. Thus, the probability that an interaction pair CC (where C represents cooperation) will remain in the next round is $1-\rho$, implying that the expected length of their interaction is $1/\rho$. On the other hand, the interaction pairs CD (where D denotes defection) and DD will never continue to the next round, becoming single individuals immediately. At the end of each round, all single individuals form new interaction pairs through random mating in the next round.

Let P_{CC}, P_{CD} and P_{DD} denote the frequencies of interaction pairs CC, CD and DD, respectively, with $P_{CC}+P_{CD}+P_{DD}=1$. Then, the frequency of C at time t, denoted by x, can be given by $x=P_{CC}+P_{CD}/2$, and the frequency of D is $1-x=P_{CD}/2+P_{DD}$. Notice that, for a given population size N, the expected change of the frequency of cooperation from x to $x\pm 1/N$ in the time interval $(t,\, t+1/N)$ can be logically expressed as

$$\begin{aligned}\langle \Delta x\rangle &\equiv \langle x(t+1/N)-x(t)\rangle = Pr\{\Delta x=1/N\}(x(t)+1/N)+Pr\{\Delta x\\ &=-1/N\}(x(t)-1/N)+[1-Pr\{\Delta x=1/N\}-Pr\{\Delta x=-1/N\}]x(t)\\ &-x(t)=\frac{1}{N}[Pr\{\Delta x=1/N\}-Pr\{\Delta x=-1/N\}]\end{aligned} \tag{1}$$

where $Pr\{\Delta x=\pm 1/N\}$ denotes the probability that Δx equals exactly $\pm 1/N$. On the hand, notice also that the expected changes of numbers of interaction pairs CC, CD and DD are

$$N\left[(1-\rho)P_{CC}+\left(\frac{2\rho P_{CC}+P_{CD}}{2(\rho P_{CC}+P_{CD}+P_{DD})}\right)^2\cdot(\rho P_{CC}+P_{CD}+P_{CC})-P_{CC}\right],$$
$$N\left[\frac{(2\rho P_{CC}+P_{DD})(P_{CD}+P_{DD})}{2(\rho P_{CC}+P_{CD}+P_{DD})^2}\cdot(\rho P_{CC}+P_{CD}+P_{DD})-P_{CD}\right],$$
$$N\left[\left(\frac{P_{CD}+2P_{DD}}{2(\rho P_{CC}+P_{CD}+P_{DD})}\right)^2\cdot(\rho P_{CC}+P_{CD}+P_{DD})-P_{DD}\right]$$

respectively. Thus, the expected changes of P_{CC}, P_{CD} and P_{DD}, which are defined as $\Delta P_* = P_*(t+1/N)-P_*(t)$ for $*=CC$, CD and DD, are easily given by

$$\begin{aligned}\langle \Delta P_{CC}\rangle &= (1-\rho)P_{CC}+\frac{(2\rho P_{CC}+P_{CD})^2}{4(1-(1-\rho)P_{CC})}-P_{CC}\,,\\ \langle \Delta P_{CD}\rangle &= \frac{(2\rho P_{CC}+P_{CD})(P_{CD}+2P_{DD})}{2(1-(1-\rho)P_{CC})}-P_{CD}\,,\\ \langle \Delta P_{DD}\rangle &= \frac{(P_{CD}+2P_{DD})^2}{4(1-(1-\rho)P_{CC})}-P_{DD}\end{aligned} \tag{2}$$

respectively. Thus, for large N, the changes of P_{CC}, P_{CD} and P_{DD} should be considered to be the fast variables comparing to the change of x since $\lim_{N\to\infty}\langle\Delta x\rangle=0$ but $\langle\Delta P_{CC}\rangle$, $\langle\Delta P_{CD}\rangle$ and $\langle\Delta P_{DD}\rangle$ are independent of N. Then, in analogy to the Hardy-Weinberg equilibrium in population genetics (Hofbauer and Sigmund, 1998), it is reasonable to assume that the interaction pairs CC, CD and DD are at a "temporal equilibrium" at any time t because of the random meeting between a pair of individuals. From the solutions of equations $\langle\Delta P_{CC}\rangle=0$, $\langle\Delta P_{CD}\rangle=0$ and $\langle\Delta P_{DD}\rangle=0$, the temporal equilibrium satisfies $P_{CD}^2=4\rho P_{CC}P_{DD}$ (or $((1-\rho)/\rho)P_{CD}^2+2P_{CD}-4x(1-x)=0$ since $P_{CC}+P_{CD}+P_{DD}=1$ and $x=P_{CC}+P_{CD}/2$). This implies that, at any time t, P_{CD} can be expressed as

$$P_{CD}=-\frac{\rho}{1-\rho}+\sqrt{\left(\frac{\rho}{1-\rho}\right)^2+\frac{4x(1-x)\rho}{1-\rho}} \tag{3}$$

for all possible $0<x<1$ and $0<\rho<1$.

3. Stability analysis of the deterministic model

Based on the definitions and assumptions in Section 2, it is easy to see that, at any time t, a cooperator has an opponent displaying cooperation (respectively, defection) with probability $2P_{CC}/(2P_{CC}+P_{CD})$ ($P_{CD}/(P_{CD}+2P_{CC})$, respectively). Similarly, a defector has an opponent displaying cooperation (respectively, defection) with probability $P_{CD}/(P_{CD}+2P_{DD})$ ($2P_{DD}/(P_{CD}+2P_{DD})$, respectively). This implies that the expected payoffs of C and D, denoted by π_C and π_D, respectively, can be expressed as

$$\begin{aligned}\pi_C &= \frac{2P_{CC}}{2P_{CC}+P_{CD}}(b-c)-\frac{P_{CD}}{2P_{CC}+P_{CD}}c=\frac{2x-P_{CD}}{2x}b-c\\ \pi_D &= \frac{P_{CD}}{P_{CD}+2P_{DD}}b=\frac{P_{CD}}{2(1-x)}b\end{aligned} \tag{4}$$

Obviously, if the population size is assumed to be large enough, then the time evolution of x obeys a simple differential equation

$$\frac{dx}{dt}=x(1-x)(\pi_C-\pi_D)=x(1-x)(b-c)-\frac{bP_{CD}}{2} \tag{5}$$

where P_{CD} is assumed to be at the temporal equilibrium (see Eq. (3)) (Hofbauer and Sigmund, 1998).

For the above differential equation, Eq. (5), it is easy to see that the boundary x=0 must be at least locally asymptotically stable since $d(dx/dt)/dx|_{x=0}=-c$, and that the boundary x=1 must be unstable since $d(dx/dt)/dx|_{x=1}=c$. On the other hand, it is also easy to see that the interior equilibrium of Eq. (5) is the solution of equation $\pi_C-\pi_D=0$, i.e.