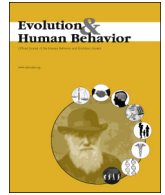




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Theoretical Contribution

Reputation based on punishment rather than generosity allows for evolution of cooperation in sizable groups

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ABSTRACT

Cooperation among unrelated individuals can arise if decisions to help others can be based on reputation. While working for dyadic interactions, reputation-use in social dilemmas involving many individuals (e.g. public goods games) becomes increasingly difficult as groups become larger and errors more frequent. Reputation is therefore believed to have played a minor role for the evolution of cooperation in collective action dilemmas such as those faced by early humans. Here, we show in computer simulations that a reputation system based on punitive actions can overcome these problems and, compared to reputation system based on generous actions, (i) is more likely to lead to the evolution of cooperation in sizable groups, (ii) more effectively sustains cooperation within larger groups, and (iii) is more robust to errors in reputation assessment. Punishment and punishment reputation could therefore have played crucial roles in the evolution of cooperation within larger groups of humans.

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1. Introduction

Explaining the rather high level of cooperation in humans is still a challenge for economists, social scientists, and evolutionary biologists, despite the variety of mechanisms that are known to promote cooperation (West, Griffin, & Gardner, 2007). These mechanisms can be categorized as conferring indirect fitness benefits (i.e. kin based, if individuals interact more often with related partners; Hamilton, 1964) or direct fitness benefits (if based on, for example, beneficial by-products; Kokko, Johnstone, & Clutton-Brock, 2001), the latter often being founded on enforcement mechanisms (West et al., 2007). Enforcing mechanisms require conditional behavioural strategies, e.g. punishing defectors or rewarding cooperators. On the one hand, cooperation can be enforced if individuals inflict sanctions on wrongdoers by punishing them (Sigmund, 2007) or by excluding them from the social group in order to avoid any future interactions with them (Guala, 2012; Sasaki & Uchida, 2013). On the other hand, cooperation can be based on reciprocity if individuals have a tendency to help those who have helped them in the past (i.e. direct reciprocity; Axelrod & Hamilton, 1981; Sigmund, 2010) or those who have helped others (i.e. indirect reciprocity; Alexander, 1987; Earley, 2010; Nowak & Sigmund, 2005; Sigmund, 2012). In the latter case, an individual's behaviour needs to be translated into a reputation by a set of rules that must be largely adopted within a social group.

One simple rule that has been used in previous analyses is that individuals earn a good reputation (good image score) by being cooperative, and a bad reputation (bad image score) when defecting (Nowak & Sigmund, 1998). It has been shown that image scoring could sustain cooperation even in the presence of more selfish strategies (e.g. see Leimar & Hammerstein, 2001) if reputation is not only binary (either “good” or “bad”) but comprises a third state “neutral” (Tanabe, Suzuki, & Masuda, 2013). Such a straightforward reputational mechanism enhances cooperation frequency and allows cooperative members of a group to recognise and trust each other (Nowak & Sigmund, 1998; Wedekind & Braithwaite, 2002; Wedekind & Milinski, 2000; Yoeli, Hoffman, Rand, & Nowak, 2013) and to benefit from choosing their partners (Fu, Hauert, Nowak, & Wang, 2008; Sylwester & Roberts, 2010), creating a biological market based on cooperativeness, i.e. competition among potential partners to be chosen for social interactions (Barclay, 2013).

Many conditional behavioural strategies are known to promote cooperation in dyadic interactions, but cooperation can easily break down in collective action problems, i.e. when more than two individuals are involved (Hardin, 1968). Cooperation frequency in both, direct and indirect reciprocity is predicted to decline rapidly with increasing group size (Boyd & Richerson, 1988; Fehr, 2004; Suzuki & Akiyama, 2005, 2007). Implementing positive incentives (rewards to co-operators) can stimulate cooperation in large groups but fails to stabilize it (Hauert, 2010; Sigmund, Hauert, & Nowak, 2001). Moreover, as group size grows, the probability of knowing everybody's reputation in a group decreases, and errors become more likely. The role of reputation-based cooperation in collective action dilemmas has therefore frequently been questioned (Fehr, 2004; Suzuki & Akiyama, 2005), and probably requires to be linked with reputation from other types of interactions (e.g.

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alternate dyadic interactions). Nevertheless, humans often show high levels of cooperation in collective action dilemmas.

Here, we test whether a reputation mechanism based on punitive actions can support the evolution of cooperation in groups of unrelated individuals. Punishment can increase cooperation levels if there are opportunities to punish defectors, that is, decreasing a defector's immediate payoff at a personal immediate cost (Fehr & Gächter, 2002; Raihani, Grutter, & Bshary, 2010; Raihani, Thornton, & Bshary, 2012; Sigmund, 2007). Until recently, such costly punishment has been perceived as an evolutionary puzzle because punishers accept costs to harm others while third parties benefit from the increased cooperation levels (Dreber, Rand, Fudenberg, & Nowak, 2008; Fehr & Gächter, 2002; Rankin, dos Santos, & Wedekind, 2009; Sigmund, 2007; Wu et al., 2009). However, if punishers can build up a punishment reputation that affects later decisions of others, punishment can lead to long-term benefits that compensate or even outweigh the immediate costs of punishment (dos Santos, Rankin, & Wedekind, 2011, 2013; Hilbe & Sigmund, 2010; Hilbe & Traulsen, 2012). This holds for dyadic interactions, but it is unclear whether punishment reputation also facilitates the emergence of cooperation in groups larger than 2. We therefore compare the evolution of two types of reputational mechanisms in the same public goods game (PGG) followed by punishment, namely a reputation of being generous and a punishment reputation. In a separate third scenario, we consider a PGG followed by a rewarding stage and reputation based on rewards.

Our analyses confirm that a reputational mechanism based on generosity is unlikely to lead to cooperation in larger groups because such mechanisms are sensitive to memory constraints, to errors in reputation assessment, and even to low frequencies of defection. Adding reward to cooperators allowed for the emergence of cooperation but turned out to be unstable since a population of rewarders can be quickly invaded by non-rewarders, as predicted from previous analyses (Hauert, 2010; Sigmund et al., 2001). We find that a reputational mechanism based on punitive actions largely solves these problems, i.e. it resists higher error rates in reputation assessment and frequently allows for the evolution of stable cooperation within larger groups.

2. Model

We model a population of finite size N , with individuals playing on average m interactions per generation over which they can build up a reputation. For each interaction, one group of size n is randomly formed while the rest of the population observes the interaction. The total number of interactions per generation is fixed and equal to mN/n , hence individuals play m interactions on average. Since strategies cannot condition their behaviour on the number of interactions, no end game effects are possible. An interaction always comprises two stages: a public goods game followed by a punishment stage. In the first stage, all group members play a public goods game where they can contribute or not to a public good by investing an amount c . Their decision to contribute is based on their coplayers' reputation (see below). The sum of all contributions is multiplied by a factor r (with $1 < r < n$) and then equally divided among all group members. As in previous models (Suzuki & Akiyama, 2005), we exclusively investigated cases where r is a function of group size such that the incentive to cooperate remains similar as group size grows. In the second stage, individuals have the opportunity to impose fines on each defector within their group by paying an amount α for the defector to lose β , with $\alpha < \beta$. The punishment decision is binary such that deciding to punish implies punishing all defectors irrespective of their number, and punishers have to pay α for each defector. At the end of a generation, individuals from the current generation are selected with replacement in proportion to their payoff to be the parent of a new offspring (the absolute value of the minimum possible payoff + 1 is added to all individuals in order to avoid negative or zero payoffs). This process is repeated until the offspring population reaches N . A parent transmits culturally its strategy $\{(x, y, z)\}$; see below) to its offspring (analogous

to genetic transmission; Cavalli-Sforza, 1981). Transmission errors (mutations) occur at rate μ and lead to the replacement of an offspring's strategy at random by another one. Hence all strategies (i.e. all combinations of x, y, z) have an equal probability of arising through mutation.

We first investigate two reputation mechanisms in this public goods game followed by punishment. The only difference between these two conditions is the information used by the players, which allows us to isolate the effect of information. In one case, reputation is based only on cooperative and non-cooperative actions (i.e. generosity scoring). In the other case, reputation is only based on punitive and non-punitive actions (i.e. punishment scoring). Under both reputation systems, an individual's reputation can only be in one of 3 different states: $\{-1, 0, +1\}$. Under generosity scoring, only cooperative and uncooperative actions during the PGG stage of an interaction can affect reputation: an individual's reputation, starting at 0, shifts to +1 after a contribution to the public good and shifts to -1 after a defection. For example, the reputation of a defector (-1) will directly switch to +1 if she cooperates. Therefore, only the previous interaction influences a player's reputation (no difference in cooperation rate was found with a system under which reputation would first switch to 0 and potentially later to +1 in the case of a cooperative act, or from +1 to 0 and then -1 in the case of two consecutive defections). Under punishment scoring, only punitive and non-punitive actions during the punishment stage of an interaction can affect reputation. Here, an individual's reputation starts at 0, shifts to +1 after punishing defectors, and shifts to -1 after not punishing defectors.

We further investigate a third reputation system based on rewards (i.e. reward scoring). In this condition, the punishment stage is replaced by a rewarding stage: individuals can reward those who contributed to the public good by paying a cost α for the other to get β . Here, reputation is only based on whether an individual has rewarded or not contributors to the PGG: an individual's reputation starts at 0, shifts to +1 after rewarding cooperators, and shifts to -1 after not rewarding cooperators.

Each interaction is public, and everybody knows everybody's reputation, i.e. who contributed to the public good (under generosity scoring) or punished defectors (under punishment scoring) in their last interaction. We implemented errors (e.g. based on memory constraints) in reputation assessment. In each interaction, a focal individual has a probability ε for each of her $n-1$ group members of forgetting their reputation. If this happens, the focal individual acts as if their reputation was 0. Consequently, the probability that a focal individual knows the reputation of all her $n-1$ group members is $(1-\varepsilon)^{n-1}$.

Individuals are defined by 3 traits: x, y and z . The first two, x and y , determine an individual's behaviour in the public good game according to the following action rule: contribute an amount c to the public good if there are in the group at least $x \in \{1, 2, \dots, n-1\}$ players with reputation equal to $y \in \{-1, 0, +1\}$. For example, an individual with $x = 5$ and $y = +1$ will contribute to the public good if there are at least 5 other group members with reputation +1. For the punishment stage, the trait $z \in \{0, 1\}$ determines an individual's punishment strategy (i.e. never punish/punish defectors). We also added unconditional defectors (ALLD) and cooperators (ALLC) which could both either not punish (i.e. ALLD-0; ALLC-0) or punish (i.e. ALLD-1; ALLC-1). These strategies were added in this way and not simply by letting x range from 0 to n , because the latter option would have created a surplus of unconditional strategies (i.e. individuals with $x = 0$ but with different y would all be ALLC, similarly individuals with $x = n$ but with different y would all be ALLD).

All simulation runs started with a population of ALLD-0. If not stated otherwise, we use $N = 500$, $m = 5$, $c = 1$, $\mu = 0.002$, $\varepsilon = 0$, and 20,000 generations in all our simulations. Table 1 lists all symbols used in the model. Average cooperation frequencies are calculated across 10 replicates for generations 15,000 to 20,000.

We have performed additional simulations with larger population sizes ($N = 2500, 5000, 10000$) subdivided into (25, 50, 100, respectively) social groups of 100 individuals in order to reduce the effect of drift.

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