Evolution and Human Behavior 37 (2016) 263–271

Contents lists available at ScienceDirect

Evolution and Human Behavior

journal homepage: www.ehbonline.org

Original Article

Partner choice versus punishment in human Prisoner's Dilemmas

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ARTICLE INFO

Article history:
Initial receipt 28 June 2015
Final revision received 31 December 2015

Keywords:
Cooperation
Partner choice
Punishment
Partner control
Prisoner's Dilemma

ABSTRACT

Two factors that promote cooperation are partner choice and punishment of defectors, but which option do people actually prefer to use? Punishment is predicted to be more common when organisms cannot escape bad partners, whereas partner choice is useful when one can switch to a better partner. Here we use a modified iterated Prisoner's Dilemma to examine people's cooperation and punishment when partner choice was possible and when it was not. The results show that cooperation was higher when people could leave bad partners versus when they could not. When they could not switch partners, people preferred to actively punish defectors rather than withdraw. When they could switch, punishment and switching were equally preferred. Contrary to our predictions, punishment was higher when switching was possible, possibly because cooperators could then desert the defector they had just punished. Punishment did not increase defectors' subsequent cooperation. Our results support the importance of partner choice in promoting human cooperation and in changing the prevalence of punishment.

1. Introduction

At first glance, costly cooperation appears puzzling from an evolutionary and an economics perspective: why would an organism do something that benefits a non-relative if doing so were costly? Some forms of non-kin cooperation are immediately beneficial (e.g. Barclay & Van Vugt, 2015; Bshary & Bergmüller, 2008), but other forms involve at least a temporary cost. In these latter cases, one has to ask how these investments are ultimately repaid. Biologists have identified several broad mechanisms that select for costly cooperation with non-relatives (Bshary & Bronstein, 2011). These include reciprocal strategies that condition their cooperative investments on those of the partner (Trivers, 1971), paying to impose costs on cheating partners ('punishment') or terminating the current interaction to seek out alternative partners elsewhere ('partner choice').

Perhaps the simplest way to incentivize a partner to cooperate is to use a conditionally cooperative strategy, such as tit-for-tat (Axelrod, 1984), whereby individuals cooperate if partners also cooperate but defect otherwise. Such strategies are expected to be particularly effective in two-player interactions. There is some evidence to suggest that non-human animals might use tit-for-tat-like strategies to maintain cooperation between unrelated individuals (Raihani & Bshary, 2011 for an overview). For example, experimental work on pied flycatchers (*Ficedula hypoleuca*) has shown that individuals will 'help' neighbors by joining in when mobbing predators at the neighbors' nest. Crucially, however, groups withhold help from neighbors who did not help them in the past (Krams, Krama, Igaune, & Mänd, 2008). In humans, there is good evidence to suggest that people condition their own helping behavior on that of the partner(s) in previous interactions, helping when they were helped but withholding help otherwise (reviewed by Barclay, 2010).

Despite the simplicity and apparent efficacy of conditionally cooperative strategies, other studies have demonstrated that individuals will also actively incur costs to 'punish' bad behavior. Punishment might be most common where individuals have different strategic options, as is common in interspecific mutualisms (e.g. see Bshary & Grutter, 2002). For example, saber-tooth blennies sneak up on and bite passer-by reef fish, imposing costs on the fish they attack. Reef-fish, however, cannot reciprocally cheat in response to being bitten. Instead, bitten fish will chase ('punish') biting blennies, which deters the blenny from attacking that individual again in future (Bshary & Bshary, 2010). Similarly, in interactions between reef-fish 'clients' and bluestreak cleaner wrasse (*Labroides dimidiatus*), only the cleaner fish has the option to 'cheat' (by eating client mucus, rather than removing ectoparasites). Due to the asymmetric strategy set, bitten clients often aggressively chase cheating cleaners, which constitutes punishment since it deters the cleaner from cheating in subsequent interactions (Bshary & Grutter, 2005). Humans also incur time, energy, reputational, and monetary costs to harm social cheats, in pairs and in groups, in laboratory studies (e.g. Abbink, Irlenbusch, & Renner, 2000; Barclay, 2006; Fehr & Gächter, 2002; Ostrom, Walker, & Gardner, 1992; Raihani & Bshary, 2015; Yamagishi, 1986), in field experiments (Barr, 2001; Henrich et al., 2010), and in anthropological observations of everyday behavior (Cordell & McKean, 1992; Fessler, 2002; Price, 2005). In

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http://dx.doi.org/10.1016/j.evolhumbehav.2015.12.004
1090-5138/

some experimental settings, punishment has been shown to be effective at motivating targets to cooperate (e.g. Fehr & Gächter, 2002; Gächter, Renner, & Sefton, 2008; Herrmann, Thöni, & Gächter, 2008), while studies that allow retaliation tend to observe retaliation rather than cooperation (e.g. Bone, Wallace, Bshary, & Raihani, 2015; Dreber, Rand, Fudenberg, & Nowak, 2008; Nikiforakis, 2008; Nikiforakis & Engelmann, 2011).

While many studies of human behavior have focused on the impact of punishment on cooperation, more recent work has examined the evolution of cooperation via *partner choice*. Cooperators do well when they can reject partners who are unlikely to cooperate (e.g. Archetti et al., 2011; Enquist & Leimar, 1993), withdraw from interactions with uncooperative partners to seek out better partners elsewhere (e.g. Aktipis, 2004, 2011; Hayashi & Yamagishi, 1998; Enquist & Leimar, 1993; McNamara, Barta, Frohmage, & Houston, 2008; Sherratt & Roberts, 1998; Vanberg & Congleton, 1992), reduce their investment in relationships with poor cooperators (e.g. Barclay, 2011; Bull & Rice, 1991; Kiers et al., 2011; Sachs, Mueller, Wilcox, & Bull, 2004), or actively choose the best available partner (e.g. Barclay, 2004; Barclay & Willer, 2007; Eshel & Cavalli-Sforza, 1982; Page, Putterman, & Unel, 2005). Defectors do poorly under such circumstances because they suffer the costs of rejection and abandonment, including search costs for new partners, or only being able to pair with other defectors (if anyone at all). This can create market-like competition for the "best" partners (Barclay, 2004, 2011, 2013; 2016; Noë & Hammerstein, 1994, 1995; Roberts, 1998), resulting in "runaway" selection for very high levels of cooperation (McNamara et al., 2008; Nesse, 2007).

Which strategy will organisms use to maintain cooperation—punishment or partner choice? When organisms cannot leave, avoid or reduce time spent with an uncooperative partner, then we should expect them to use mechanisms like reciprocating defection with defection, or punishment (Bshary & Bronstein, 2011; Bshary & Bshary, 2010; Raihani, Thornton, & Bshary, 2012). A preference for punishment might also be expected where the punisher can impose costs on the target that are sufficient to outweigh the temptation to defect (e.g. Gneezy & Rustichini, 2000). This may be most likely where asymmetries in power between the punisher and the target increase the impact of punishment and reduce the likelihood of retaliation (e.g. Clutton-Brock & Parker, 1995; Fischer et al., 2015; Raihani, Grutter, & Bshary, 2010; Raihani, Grutter, & Bshary, 2012; but see Bone et al., 2015). Conversely, when individuals have higher paying outside options (Cant, 2011) (e.g. withdrawing from an interaction with a current partner and seeking interaction elsewhere) then punishment and conditionally cooperative strategies should be less common and individuals might instead exercise partner choice (Raihani, Thornton, et al., 2012). This prediction is borne out by empirical work on the interspecific mutualism between cleaner fish and their clients. Clients that have a small home range, and therefore can only access one or a few cleaning stations, are more likely to respond to a cheating cleaner fish with aggressive punishment (Bshary & Grutter, 2002). Conversely, clients that have a larger home range with access to several cleaning stations exhibit choosy behavior: if they experience cheating they leave the interaction and visit a different cleaning station for the next cleaning service (Bshary & Schäffer, 2002). Individuals might also be expected to prefer switching partners over punishing when alternative partners are readily available (i.e. search time to find a new partner is not prohibitive) and there is sufficient population variability in cooperative tendency that the choosy individual can improve upon the current (defecting) partner by switching (McNamara & Leimar, 2010).

Here we use a modified iterated prisoner's dilemma game to investigate whether – when costs are equal – humans prefer to use punishment or partner choice in response to a defecting partner; and what the consequences of each strategy are for maintaining cooperation. As in the standard prisoner's dilemma game, participants can cooperate or defect each round. They then additionally have the option of paying to punish the partner. We examine people's cooperation and their willingness to actively punish defectors when they can leave partners compared to when they cannot leave partners. We used the two-person Prisoner's Dilemma rather than N-person Public Goods Game because the former allowed us to directly compare the choice (and consequences) of punishing versus leaving one single person instead of leaving an entire group. Specifically, we tested the following six predictions:

1) Cooperation will be more common when participants can switch partners;
2) When faced with a defector, participants who cannot switch partners will be more likely to punish than to withdraw, whereas participants who can switch partners will have no preference for punishing versus switching;
3) Participants will be more likely to punish defectors if they cannot switch partners than if they can switch;
4) Participants will be more likely to withdraw from an interaction if doing so will result in a new partner;
5) Participants will be more likely to defect on a defector if they cannot switch partners than if they can switch;
6) Defectors who are punished will subsequently become more cooperative.

2. Methods

2.1. Participants, earnings, and anonymity

We used posters to recruit 63 males and 93 females from the University of Guelph (mean age 21.6 years ± s.d. 5.0 years, range 17–48). Twelve people participated in each session. Participants earned lab dollars (henceforth L$) which were converted to Canadian dollars after the experiment at the pre-announced rate of 5:1. Earnings averaged CAN$21.58 (± s.d. CAN$4.59). Partitions prevented visual contact between participants, and communication was not permitted. All decisions were made via computers using the z-tree software (Fischbacher, 2007), so no one (including the experimenter) knew any individual decisions. All payoffs were confidential: the experimenter placed each person's total earnings in an envelope on that person's desk, without knowing what decisions or outcomes had caused those earnings. All participants received full and truthful information about the experiment. These methods were approved by the Research Ethics Board at the University of Guelph.

2.2. Procedure

2.2.1. Prisoner's Dilemma with punishment

Participants started with an initial endowment of L$20 and played a modified Prisoner's Dilemma for 40 rounds (the number of rounds was unknown to participants). In each round, participants were paired with someone else, and each could cooperate or defect (called "Red" and "Blue", respectively, to avoid framing effects; see Supplementary Material for instructions). Participants who cooperated earned L$3 if their partner also cooperated and L$0 if their partner defected. Participants who defected earned L$5 if their partner cooperated and L$1 if their partner defected. Thus, defection was the individual payoff-maximizing strategy in any given round, but the payoff for mutual cooperation (L$3) was higher than the payoff for mutual defection (L$1). As such, if both parties followed their self-interest by defecting they would produce a collectively worse outcome than if they both cooperated. The decision to cooperate or defect was made simultaneously by each player. After finding out whether one's partner cooperated or defected and what each partner earned, participants could pay to punish that partner, i.e. spend L$1 to make the partner lose L$3 (the words "reduce earnings" were used instead of "punishment", see online supplementary information for experimental instructions). This money was not gained by the punisher; punishment resulted in a loss to both parties. Bankruptcies did not happen because of the L$20 endowment everyone started with.