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Partner choice versus punishment in human Prisoner's Dilemmas

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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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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.

2.3. Switching partners

There were three experimental conditions which varied in whether participants could switch partners. We conducted 4 sessions in the Pay-to-Switch condition (N = 48), 4 sessions in the Sit-Out-to-Switch condition (N = 48), and 5 sessions in the No-Switching condition (N = 60). The uneven number of sessions is because there were not enough participants signing up to equalize sessions across conditions.

A) In the Pay-to-Switch condition, participants could pay a direct cost of L$1 to withdraw from the interaction by leaving their current partner and partnering with someone else for the next round. This L$1 switching cost was the same as the cost of punishing a partner. A pair was broken up if either member wanted to leave, but only people who actively chose to leave would pay the L$1.

B) In the Sit-Out-to-Switch condition, participants could switch partners by opting to withdraw for one round by sitting out and earning L$0 that round, whereupon after they would be paired with someone new. Thus, this condition was similar to the Pay-to-Switch condition except that the cost of withdrawing resembled a search cost of finding a new partner. Sitting out for a round introduced an opportunity cost for switching: rather than earn L$1 for defecting on a defector in a round (the most likely outcome against a persistent defector), participants could forgo that L$1 in that round by sitting out in order to be paired with someone else. Thus, this opportunity cost was designed to be approximately equivalent to the direct cost of switching in the Pay-to-Switch condition, on average. Comparing this condition with the Pay-to-Switch condition allows us to test whether cooperation and punishment levels depend on whether the cost of switching is a direct cost or an opportunity cost. A pair was broken up if either member wanted to withdraw, whereupon both members would sit out a round before re-pairing (as would happen if it were a search cost).

C) In the No-Switching condition, participants could not intentionally leave partners. This condition is identical to the Sit-Out-to-Switch condition in that participants could withdraw from the interaction ("sit out") and earn L$0 for one round, except that they would be repaired with the same partner after sitting out. If either party chose to withdraw, then both members of the pair sat out that round. The opportunity cost of switching is the same in this condition as in the Sit-Out-to-Switch condition, so comparing these two conditions allows us to most directly test the effects of being able to switch partners on cooperation and punishment levels, while holding constant the cost of withdrawing.

All decisions about switching and sitting out (henceforth "withdrawing") were made at the same time as the decisions about punishment. Thus, from a participant's perspective, each round in which a participant was not sitting out went as follows: a) decide whether to cooperate ("Red") or defect ("Blue"); b) see the partner's decision and both people's earnings; c) decide whether to punish versus not punish, plus decide whether to withdraw or not; and d) find out results of partner's punishment and withdrawing decisions.

2.4. Guaranteeing the availability of new partners

Leaving an uncooperative partner is only worthwhile if there are better partners available to switch to. If any pair had chosen to split in the Pay-to-Switch and Sit-Out-to-Switch conditions then, to guarantee the availability of alternative partners, the computer program randomly chose one of the pairs who opted to stay together and broke up that pair (and told them so); with six pairs per 12-person session, that means that participants could expect a computer-caused split every six rounds on average. Participants were informed of these exogenous computer-caused splits in the instructions, but not their frequency. This computer-broken pair was added to the pool of available partners. Participants who (endogenously) chose to switch partners would be randomly paired with someone *else* from the pool of available partners, i.e. someone *other* than the person they had just abandoned. If no pairs had endogenously chosen to split that round, then the computer did not exogenously split any pairs because there was no need for new partners. Between the computer-caused splits and the active choices to switch, a change of partners occurred 16.2% of the time in Pay-to-Switch and 13.8% of the time in Sit-Out-to-Switch. Participants did not know the identity of whom they were interacting with (i.e. no code names or numbers), so they would not know if they ever returned to the same partner later in the experiment. To keep the anticipated length of interactions consistent across conditions, the No-Switching condition had two pairs randomly split every two rounds (instead of one every round) and their memberships switched, i.e. a change of partners in 16.7% (1/6) of rounds.

2.5. Assessing comprehension

All participants completed seven comprehension questions before starting the experiment. 21 out of 156 participants answered one comprehension question incorrectly, and 4 participants answered 2 or 3 questions incorrectly. These participants had to call the experimenter for clarification before receiving a code to enter into the computer to move on; the majority of errors were simply misreading the question. This was designed to ensure that all participants understood the procedure.

3. Analyses

We used the data to ask the following questions:

1. Did propensity to cooperate vary across the three experimental conditions?

   We calculated the proportion of rounds that each player cooperated by dividing the total number of times a player chose to cooperate by the total number of rounds they played (i.e. excluding rounds where players were sitting out). This variable was set as the response term in a general linear model (GLM), with 'condition' specified as a three-level categorical explanatory variable.

2. In response to a partner's defection, were players more likely to punish or to withdraw?

   We expected that players would be more likely to punish than to withdraw in the condition where no new partner was available (i.e. the No-Switching condition). We did not expect to find this pattern in the conditions where focal players had access to new partners (i.e. the Pay-to-Switch and the Sit-Out-to-Switch conditions). To test whether people were more likely to punish versus withdraw, we performed three Wilcoxon signed rank tests (one for each condition) comparing the proportion of rounds where the focal player punished a defecting partner with the proportion of rounds where that same player withdrew in response to a defecting partner. Data were excluded for players who never experienced a defecting partner (N = 15 players).

3. Did people's tendency to punish a defecting partner vary across conditions?

   We predicted that punishment would be used most often in the No-Switching condition, compared to the Pay-to-Switch and Sit-Out-to-Switch conditions. For each player, we calculated the proportion of rounds that (s)he punished a defecting partner, by setting the number of times (s)he punished a defecting partner as the response term in a GLM with binomial error distribution, and setting the total number of times (s)he ever experienced a defecting partner as the binomial total. 'Condition'

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was specified as a three-level categorical explanatory variable. As above, data for players who never experienced a defecting partner were excluded.

4. Did people's tendency to withdraw in response to a defecting partner vary across conditions?

   We predicted that withdrawing would be used least in the No-Switching condition, compared to the Pay-to-Switch and Sit-Out-to-Switch conditions. For each player, we set the number of times (s)he withdrew as the response term in a GLM with binomial error distribution, with the total number of times (s)he had ever experienced a defecting partner set as the binomial total. 'Condition' was specified as a three-level categorical explanatory variable. As above, data for players who never experienced a defecting partner were excluded.

5. Did people's tendency to defect in response to a defection vary across conditions?

   We asked how likely a focal player was to defect in round $n + 1$ if the partner defected in round n. For initial analyses, we restricted data to instances where the focal player cooperated in round n. We calculated the proportion of rounds (for each player) where they defected in round $n + 1$ (in response to the partner defecting in round n) and whether these tendencies to defect in round $n + 1$ differed from an expected probability of 0.5 (which would be expected if players were choosing to defect at random). We performed three Binomial tests, each testing tendency to defect in response to partner defecting for one of the three experimental conditions.

   Next we explored whether people's tendency to defect in response to a partner defecting varied according to experimental condition. We used a generalized linear mixed model (GLMM) with binomial error structure. The focal player's behavior in round $n + 1$ was set as the binary response term (1 = defect; 0 = cooperate) and we included whether the focal player cooperated in round n (1 = cooperated; 0 = defected) and the experimental condition (3-level categorical variable) as explanatory terms. Since we had repeated observations per focal player, we included focal player ID as a random term in the model. Data were restricted to instances where the partner defected in round n (N = 1827).

6. How did players respond to being punished?

   We asked whether players who were punished for defecting in round n were more likely to choose cooperate in round $n + 1$. We investigated the effect of being punished on subsequent propensity to cooperate separately in each condition, using three GLMMs. Cooperate in round $n + 1$ was set as the binary response term for each model (0 = continued to defect; 1 = cooperate). We also included the following explanatory terms in each model: 'partner cooperated' (=0 if partner defected in round n), 'partner punished' (=0 if partner did not punish in round n); 'withdrew' (=0 if partner did not withdraw in round n). Player ID was included as a random term to control for the effects of repeated observations from the same individuals. Data were restricted to instances where the focal player defected in round n, yielding a sample size of 557 decisions for the 'Pay-to-Switch' condition, 367 decisions for the "Sit-Out-to-Switch' condition and 825 decisions for the 'No-Switching' condition. Note that for the conditions where partners chose to skip the round following round n, round $n + 1$ refers to the next active round (i.e. $n + 2$).

4. Statistical approach

All data were analyzed using R version 3.0.3 (www.r-project.org). We determined the relative importance of the explanatory terms included in each model using an information-theoretic approach with model averaging as described in Grueber, Nakagawa, Laws, and Jamieson (2011). This approach involves generating a series of candidate models, with each model representing a biological hypothesis. Rather than testing a null hypothesis, the relative degree of support for each model from the candidate set is calculated (Burnham & Anderson, 2002). First, we specified a global model which included all the explanatory and random terms. Before model analysis, the input variables were standardized to a mean of 0 and standard deviation of 0.5 according to Gelman (2008). This allows the standardization of predictor variables to a common scale, meaning that the relative strength of parameter estimates can be interpreted. We used the package MuMIn (Bartoń, 2009) to derive and compare submodels from the initial global model. Models were compared to one another using Akaike's Information Criterion corrected for small sample sizes (AICc) (Bartoń, 2009). A subset of "top models" was defined by taking the best model (the model with the lowest AICc value) and any models within 2AICc units of the best model (following Burnham & Anderson, 2002). Using this subset of 'top' models, we computed the average (standardized) parameter estimates for each term included in the subset of models, as well as the relative importance of the term. Importance is calculated by summing the Akaike weights of all models where the term in question is included in the model. Akaike weights represent the probability of a given model being the true model (compared to other candidate models in the set) (Burnham & Anderson, 2002). Importance can therefore be thought of as the probability that the term in question is a component of the best model (Symonds & Moussalli, 2011). In the results section, we only present the standardized parameter estimates from the top models (those that were within 2 AICc units of the best model). All data and R code are available as supplementary materials.

5. Results

1. *Did propensity to cooperate vary across the conditions?*

   Mean cooperation levels were relatively high in this study: players chose to cooperate on an average proportion (±SEM) of 0.69 ± 0.02 rounds. Cooperation varied across the three conditions, with individuals in the Pay-to-Switch condition cooperating on 0.70 ± 0.04 of rounds; individuals in the Sit-Out-to-Switch cooperating on 0.76 ± 0.04 of rounds and individuals in the No-Switching condition cooperating on 0.63 ± 0.04 of rounds (Fig. 1). The output from the GLM showed that cooperation in the No-Switching condition was lower than in the Sit-Out-to-Switch condition (standardized effect size of Sit-Out-to-Switch relative to No-Switching: 0.13, 95% CI: 0.02, 0.25) and lower (albeit not quite significantly so) than the Pay-to-Switch condition (standardized effect size of Pay-to-Switch versus No-Switching: 0.08, 95% CI: −0.04, 0.19, Tables 1 and 2). Re-ordering the factor levels showed that cooperation levels in the Pay-to-Switch and Sit-Out-to-Switch conditions were not statistically distinguishable (see Tables S1 and S2 online supplementary material). We therefore collapsed the factor levels such that we had two experimental

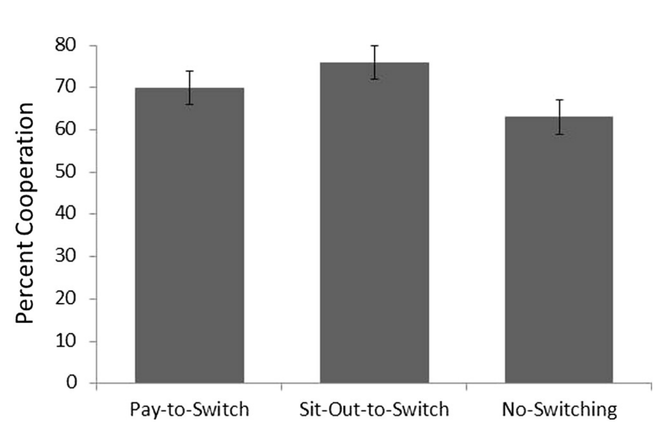

Fig. 1. Percent of rounds (± s.e.m.) where participants cooperated.

Table 1
GLM to investigate the effect of condition on average cooperation levels. The table shows the top models (models within 2AICc units of the best model), with AICc values and Akaike weights (w^i). The best model is highlighted.

Model Rank	Parameters	df	AICc	w^i
1	**Condition**	**4**	**74.8**	**0.64**
2	Null	2	75.9	0.36

conditions, one where players could not get a new partner (i.e. the No-Switching condition) and one where players could get a new partner (i.e. the Pay-to-Switch and Sit-Out-to-Switch conditions combined). A Wilcoxon rank-sum test comparing the proportion of rounds each player cooperated according to whether they were in the "new partner possible" versus the No-Switching conditions revealed that players cooperated more when in the "new partner possible" condition (mean proportion rounds players cooperated = 0.73 ± 0.03) than in the "No-Switching" condition (0.63 ± 0.04, Wilcoxon rank-sum test, W = 3578.5, p = 0.01; Bonferroni P = 0.02).

2. *In response to a partner's defection, were players more likely to punish versus withdraw?*

   As predicted, participants in the No-Switching condition were more likely to punish a defecting partner (mean proportion of rounds where defector was punished ± SEM: 0.13 ± 0.03) than to withdraw (0.07 ± 0.02) (Wilcoxon signed rank test, V = 379, N = 58, p = 0.03; Fig. 2). This within-condition pattern was not replicated in the Pay-to-Switch condition (punished: 0.19 ± 0.05, switched: 0.19 ± 0.03; Wilcoxon signed rank test, V = 135.5, N = 44, p = 0.69) or in the Sit-Out-To-Switch condition (punished: 0.26 ± 0.06, switched: 0.26 ± 0.05, Wilcoxon signed rank test, V = 149.5, N = 39, p = 1), indicating no preference for punishment over withdrawing (and switching) in those conditions.

3. *Did people's tendency to punish a defecting partner vary across conditions?*

   Contrary to predictions, punishment use was lowest in the 'No-Switching' condition, compared to both the 'Pay-to-Switch' condition (standardized effect = 0.71, 95% CI: 0.38, 1.06) and to the 'Sit-Out-to-Switch' condition (standardized effect = 0.88, 95% CI: 0.51, 1.25) (Table 3). Re-ordering factor levels revealed no difference in punishment use between the 'Pay-to-Switch' and 'Sit-Out-to-Switch' conditions (Table S2).

4. *Did people's tendency to withdraw from a defecting partner vary across conditions?*

   As predicted, players were least likely to withdraw in response to a defecting partner in the 'No-Switching' condition, compared with either the 'Pay-to-Switch' condition (standardized effect = 1.33, 95% CI: 0.93, 1.74) or the 'Sit-Out-to-Switch' condition (standardized effect = 1.56, 95% CI: 1.14, 2.00) (Table 4). Re-ordering factor levels revealed no difference in tendency to withdraw between the 'Pay-to-Switch' and 'Sit-Out-to-Switch' conditions (Table S3).

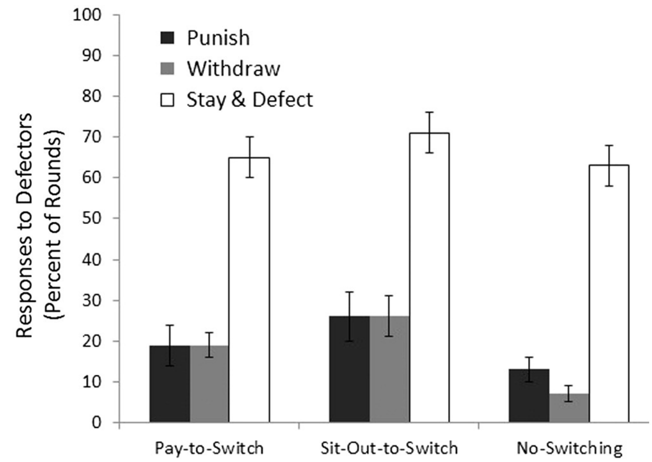

Fig. 2. Percent of rounds (± s.e.m.) where participants punished in response to a defector, withdrew in response to a defector, or defected upon a defector, in the Pay-to-Switch condition (dark bars), Sit-Out-to-Switch condition (gray bars), and No-Switching condition (light bars). Numbers do not add up to 100% because some responses are not mutually exclusive.

5. *Did people's tendency to stay with and defect on a defecting partner vary across conditions?*

   In all three conditions, players who cooperated in round *n* typically responded to defection from a partner by defecting in round $n + 1$ (proportion rounds where focal player switched to defection: Pay-to-Switch: 0.65 ± 0.05; Sit-Out-to-Switch: 0.71 ± 0.05; No-Switching: 0.63 ± 0.05; Binomial tests p = 0.009, p = 0.0003 and p = 0.007 respectively). We then compared whether the tendency to defect in response to a partner's defection varied across conditions. Condition was not included in the top model, indicating no effect of condition on people's tendency to respond to defection with defection (Table 5). The only term included in the top model set was 'focal player cooperated in round n', which had a positive but non-significant effect on people's tendency to defect in round n + 1 in response to a defector (standardized effect = 0.11, 95% CI: −0.16, 0.38, Table 6).

6. *How did players respond to being punished?*

   In each condition, the main factor determining whether the focal player would cooperate in round $n + 1$, if they had defected in round *n*, was whether the partner cooperated in round *n* (Tables 7, 8). Thus, players seemed to use a conditionally cooperative strategy in each condition. Although being punished was included as a term in the top models for all three analyses, in each case the confidence intervals associated with the term spanned zero, indicating that being punished was not affecting the focal player's decision to cooperate in any case.

Table 2
Estimates, unconditional standard errors, confidence intervals and relative importance for parameters included in the top models from Table 1. Effect sizes have been standardized on two SD following Gelman (2008). Standard errors are unconditional, meaning that they incorporate model selection uncertainty (Grueber et al., 2011). Condition is a 3-level categorical variable ('Pay-to-Switch', 'Sit-Out-to-Switch' and 'No-Switching'). No-switching is the reference level. Estimates from the same model when the reference level for Condition is Sit-Out-to-Switch are presented in Supplementary Information (Table S1).

Parameter	Estimate	Unconditional SE	Confidence Interval	Relative Importance
Intercept	0.69	0.02	(0.64, 0.74)	
Condition (Pay-to-Switch)	0.08	0.06	(−0.04, 0.19)	0.64
Condition (Sit-Out-to-Switch)	0.13	0.06	(0.02, 0.25)	0.64

Table 3
Estimates, unconditional standard errors, confidence intervals and relative importance for parameters included in model investigating the effect of 'Condition' on tendency to punish a defecting partner. Only one top model was supplied. Condition is a 3-level categorical variable ('Pay-to-Switch', 'Sit-Out-to-Switch' and 'No-switching'). No-switching is the reference level. Estimates from the same model when the reference level for Condition is Sit-Out-to-Switch are presented in Supplementary Information (Table S2).

Parameter	Estimate	Unconditional SE	Confidence Interval	Relative Importance
Intercept	−2.01	0.07	(−2.16, −1.87)	
Condition (Pay-to-Switch)	0.71	0.17	(0.38, 1.06)	1
Condition (Sit-Out-to-Switch)	0.88	0.19	(0.51, 1.25)	1

Table 4
Estimates, unconditional standard errors, confidence intervals and relative importance for parameters included in model investigating the effect of 'Condition' on tendency to withdraw in response to a defecting partner. Only one top model was supplied. Condition is a 3-level categorical variable ('Pay-to-Switch', 'Sit-Out-to-Switch' and 'No-switching'). 'No-switching is the reference level. Estimates from the same model when the reference level for Condition' is 'Pay-to-Switch' are presented in Supplementary Information (Table S3).

Parameter	Estimate	Unconditional SE	Confidence Interval	Relative Importance
Intercept	−2.26	0.09	(−2.44, −2.09)	
Condition (Pay-to-Switch)	1.33	0.21	(0.93, 1.74)	1
Condition (Sit-Out-to-Switch)	1.56	0.22	(1.14, 2.00)	1

Having one's partner withdraw was not included in any of the top models for the 'Pay-to-Switch' condition (Tables 7, 8), indicating that it did not affect the focal player's decision to cooperate in round $n+1$. A partner withdrawing was included in the top model set for the 'Sit-Out-to-Switch' condition, but the confidence intervals associated with the term (−1.11, 0.37) indicated no effect of partner's withdrawal on subsequent cooperation. In the 'No-Switching' condition, focal players showed a slight tendency to cooperate more in the next active round if the partner chose to opt out of a round following round n (effect size = 0.79, CI = −0.04, 1.62).

6. Discussion

We tested whether, all else being equal, humans prefer to punish or to exercise partner choice when paired with a cheating partner in a prisoner's dilemma game. We also investigated how the option to leave uncooperative partners affected cooperation in this setting (Prediction 1). We found that cooperation was higher when participants could leave uncooperative partners than when they could not. This is consistent with past theoretical (e.g. Aktipis, 2004, 2011; Hayashi & Yamagishi, 1998; Enquist & Leimar, 1993; McNamara et al., 2008; Sherratt & Roberts, 1998) and empirical (e.g. Bednarik, Fehl, & Semmann, 2014; Fehl, van der Prost, & Semmann, 2011; Rand, Arbesman, & Christakis, 2011) work showing the beneficial effects of being able to break links with bad cooperators. In particular, participants cooperated more often in the Sit-Out-to-Switch condition than in the No-Switching condition, which were identical except that withdrawing would result in a new partner in the former condition but not in the latter.

As predicted, the possibility to leave uncooperative partners influenced participants' willingness to use costly punishment. When they could not leave partners (No-Switching), participants preferred to pay to directly punish defectors rather than to withdraw and sit out a round. This matches previous predictions and empirical findings (Bshary & Grutter, 2002; Raihani, Thornton, et al., 2012). This preference for punishment over withdrawing disappeared when withdrawing meant acquiring a new partner (Pay-to-Switch and Sit-Out-to-Switch), such that partners were equally likely to punish a defector as to leave a defector in those conditions. The cost of punishment was the same as the cost of leaving a partner (L$1), suggesting that people have no preference for punishment over switching when the costs are equal and when the cooperativeness of alternative partners is unknown a priori (as in our experiment). Further research could vary the costs of punishment or switching: all else being equal, we predict that people should prefer the cheaper of the two, unless other factors like local competition make it important to not become disadvantaged relative to any partner (Barclay & Stoller, 2014; Gardner & West, 2004). Similarly, we predict that people's preferences will depend on the likelihood of achieving a better partner by switching: people should not prefer switching if the available partners are no better than their current partner (McNamara et al., 2008), whereas they should prefer switching if they can actively choose a preferred partner (Barclay, 2013). Future work could also examine punishment within groups larger than two, to investigate whether our results generalize to larger groups.

Contrary to our predictions, people were more likely to punish uncooperative partners whom they could leave. This is the opposite of what one would predict if punishment functions to control a current partner's behavior and induce cooperation. One possible explanation for this unexpected result is that participants were reluctant to face retaliatory punishment. People often retaliate against punishment received, and this can set off waves of mutual punishment (in economic games: Cinyabuguma, Page, & Putterman, 2006; Denant-Boemont, Masclet, & Noussair, 2007; Dreber et al., 2008; feuds and vendettas: Daly & Wilson, 1988). This retaliation could suppress the punishment of defectors (Nikiforakis, 2008; Nikiforakis & Engelmann, 2011). Our data tentatively suggest that participants punished more when they could escape retaliation: participants were more likely to withdraw after punishing if doing so would result in new partner (Pay-to-Switch: 43% ± 9% of rounds; Sit-Out-to-Switch: 53% ± 10% of rounds) than if it would not result in a new partner (No-Switching: 22% ± 7%, Wilcoxon rank sum test relative to Pay-to-Switch and Sit-Out-to-Switch, W = 609, N = 62, $p = 0.02$). This punish-and-leave strategy may seem maladaptive on the surface, but one's "irrational" willingness to punish – even with no future interactions – can be a powerful deterrent against exploitation if it allows committed punishers to acquire a punitive reputation and therefore suffer fewer transgressions (e.g. Daly & Wilson, 1988; dos Santos, Rankin, & Wedekind, 2011, 2013; Frank, 1988; Hilbe & Traulsen, 2012; Raihani & Bshary, 2015; Yamagishi et al., 2009). This may not be beneficial in artificial laboratory environments, but could easily be

Table 5
GLMM to investigate the effect of condition on focal players' tendency to defect in round $n+1$, if the partner defected in round n. 'Focal player cooperated' is a binary variable denoting whether the focal player cooperated in round n (1 = cooperated). The table shows the top models (models within 2AICc units of the best model), with AICc values and Akaike weights (w^i). The best model is highlighted.

Model Rank	Parameters	df	AICc	w^i
1	**Null**	**2**	**1926.7**	**0.67**
2	Focal player cooperated	3	1928.1	0.33

Table 6
Estimates, unconditional standard errors, confidence intervals and relative importance for parameters included Table 5.

Parameter	Estimate	Unconditional SE	Confidence Interval	Relative Importance
Intercept	0.76	0.15	(0.48, 1.05)	
Focal player cooperated	0.11	0.14	(−0.16, 0.38)	0.33

Table 7
GLMMs to investigate factors affecting focal players' decision to cooperate in round $n+1$, if the player defected in round n. The table shows the top models (models within 2AICc units of the best model), with AICc values and Akaike weights (w^i) associated with each experimental condition. In each case, the best model is highlighted.

Condition	Model Rank	Parameters	df	AICc	w^i
Pay-to-Switch	**1**	**Partner cooperated**	**3**	**613.5**	**0.73**
	2	Partner punished	4	615.4	0.27
Sit-Out-to-Switch	1	**Partner cooperated**	3	393.5	0.48
	2	Partner cooperated + withdrew	4	394.6	0.28
	3	Partner cooperated + Partner punished	4	394.9	0.24
No-switching	**1**	**Partner cooperated + Withdrew**	**4**	**844.3**	**0.40**
	2	Partner cooperated + Partner punished + Withdrew	5	845.2	0.26
	3	Partner cooperated + Partner punished	4	845.8	0.18
	4	Partner cooperated	3	846.1	0.16

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Table 8
Estimates, unconditional standard errors, confidence intervals and relative importance for parameters included in the top models presented in Table 5.

Condition	Parameter	Estimate	Unconditional SE	Confidence Interval	Relative Importance
Pay-to-Switch	Intercept	−0.64	0.22	(−1.07, −0.21)	
	Partner cooperated	0.58	0.22	(0.15, 1.00)	1
	Partner punished	0.08	0.30	(−0.51, 0.66)	0.27
Sit-Out-to-Switch	Intercept	−0.68	0.28	(−1.23, −0.12)	
	Partner cooperated	−0.95	0.28	(0.39, 1.51)	1
	Partner withdrew	−0.37	0.37	(−1.11, 0.37)	0.28
	Partner punished	−0.32	0.40	(−1.11, 0.47)	0.24
No-switching	Intercept	−0.68	0.21	(−1.08, −0.28)	
	Partner cooperated	1.14	0.19	(0.75, 1.52)	1
	Partner withdrew	0.79	0.42	(−0.04, 1.62)	0.66
	Partner punished	0.43	0.34	(−0.25, 1.10)	0.44

beneficial in the real world or even in less impoverished laboratory conditions (e.g. Barclay, 2006; dos Santos et al., 2011, 2013; Raihani & Bshary, 2015). Thus, this explanation requires that subjects made decisions under cognitive constraints.

Our experiment had two types of cost for switching partners: a direct cost of L$1 (Pay-to-Switch) and an opportunity cost of sitting out one round, missing the presumed L$1 one would obtain from mutual defection (Sit-Out-to-Switch). The type of cost had no significant effect on participants' cooperation or their willingness to leave uncooperative partners. This suggests that participants viewed the two types of cost equally, though this requires further investigation. Future studies should explore individual reactions to abandonment depending on whether being dumped involves no cost to the dumpee (as in Pay-to-Switch) or an opportunity cost to the dumpee to find a new partner (as in Sit-Out-to-Switch). No previous experiments involved direct costs for leaving partners — the only experiment we know of with any cost for switching partners used a cost for getting new partners after leaving (Bednarik et al., 2014). As such, it remains to be fully tested whether opportunity costs and direct costs have the same psychological effects and produce similar effects on cooperation.

It is somewhat surprising that punishment had no positive effect on individual cooperation in this study. In our experiment, the only thing that made defectors more likely to cooperate was if their partner cooperated the previous round (as in Bone et al., 2015). The ineffectiveness of punishment is unlikely to be something specific to our local population: this population has previously shown positive effects of punishment in public goods games (Sparks, Burleigh, & Barclay, in preparation), and its high levels of cooperation (Sparks & Barclay, 2013) would normally make punishment effective (Herrmann et al., 2008. The ineffectiveness of punishment is also unlikely to be because of the binary cooperate–defect decisions in our experiment, given that other work has found no effect of punishment on non-binary cooperation decisions in a Prisoner's Dilemma (Bone et al., unpublished data).

We tentatively suggest that receiving punishment was ineffective at motivating defectors in this experiment because receiving punishment has different effects in two-player games (e.g., Prisoner's Dilemma) than in multi-player games (e.g. public goods game). Most studies on punishment test the effects of punishment *opportunities* on group cooperation, not the effects of *receiving* punishment on a defector's cooperation (Balliet, Mulder, & Van Lange, 2011). When they do test the latter, experiments with public goods games tend to find that low contributors are usually more cooperative after receiving punishment (e.g. Fehr & Gächter, 2002; Denant-Boemont, et. al., 2007; Herrmann et al., 2008; but see Nikiforakis & Engelmann, 2011). By contrast, the few studies examining Prisoner's Dilemmas have found that receiving punishment does not motivate cooperation (Bone et al., 2015; Dreber et al., 2008; Wu et al., 2009). Punishment's failure in Prisoner's Dilemmas is not simply due to questionable experimental constraints that prevent punishers from also being cooperators (for criticisms of Dreber et al., 2008 and Wu et al., 2009, see Rankin, dos Santos, & Wedekind, 2009), because such failures have also been found when those experimental constraints are absent (Bone et al., 2015).

We offer three speculations as to why costly punishment may be less effective at motivating cooperation in two-player games than in multi-player games. First, the identity of the punisher is obvious in two-player games, which facilitates retaliation. Second, in two-player games, the cheapest way to control a specific partner is by conditional cooperation (defecting on a defector); this was the most common response to defectors in all conditions of our experiment. Third, paying extra to reduce someone's earnings may appear malicious in a Prisoner's Dilemma, thus reducing the moral legitimacy which is crucial for punishment's effectiveness (Fehr & Rockenbach, 2003). By contrast, in larger groups, targeted punishment may be seen as more legitimate because conditional cooperation cannot target defectors alone (Boyd & Richerson, 1988), and because all cooperators in the group benefit from the punisher's actions.

In contrast to punishment, it is less surprising that being abandoned had no positive effect on a person's cooperation. The theoretical work has focused on the evolutionary consequences of partner choice rather than the effects within the individual's lifetime (e.g. Aktipis, 2004; Enquist & Leimar, 1993; McNamara et al., 2008), and partner choice has positive effects on cooperation rates because it allows the cooperators to assort with each other rather than having to defect against the defectors they are stuck with (e.g. Page et al., 2005). The empirical work has largely focused on people increasing their cooperation to be chosen (Barclay & Willer, 2007; Sylwester & Roberts, 2010), rather than the reactions of people who were not chosen. As such, it is unclear whether the experience of being abandoned should motivate individuals to cooperate. Previous studies of ostracism have produced mixed effects: some studies show that being ostracized motivates better behavior in the future (Feinberg, Willer, & Schultz, 2014), but other studies show that it triggers negative feelings that suppress cooperation (reviewed by Balliet & Ferris, 2013). Abandonment – or the threat thereof – may be more effective when new partners are harder to find (unlike the present experiment), such that individuals are motivated to avoid the high search costs from abandonment in subsequent interactions. It is these high search costs that prevent the appearance of "roving defector" strategies who exploit partners and quickly move on to new victims to exploit (Dugatkin & Wilson, 1991).

6.1. Summary and conclusions

Our results show that cooperation is higher when people can leave uncooperative partners. When they cannot escape a bad partner, people are more likely to punish than to withdraw, but when escape is possible they withdraw as often as they punish. The possibility of escaping bad partners did not affect people's willingness to use Tit-for-Tat-like cooperation by simply defecting on defectors. Unexpectedly, the presence of partner switching tended to increase punishment, most likely because people punish and then leave before experiencing retaliation. Defectors

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were not more cooperative after receiving punishment, possibly because punishment is less effective in two-player games where it is easier to retaliate by defecting in the next round. Future work should try to generalize the other results to larger groups as well.

Together, these results suggest that partner choice may be more of a factor in human cooperation than punishment is (at least in dyadic contexts). Partner choice allows people to escape bad partners, and thus receive higher cooperation in the future from other partners. By contrast, costly punishment seems less effective — it may reduce the fitness differential between cooperators and defectors (Price et. al., 2002), but does not seem to increase the cooperation that one receives. Thus, punishment may be used more when one competes directly with partners (scale of competition: Barclay & Stoller, 2014; Gardner & West, 2004) and partner choice used more when competition is more global.

Supplementary materials

Supplementary data to this article and supplementary analyses can be found online at http://dx.doi.org/10.1016/j.evolhumbehav.2015.12.004.

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