Human cooperation in social dilemmas: comparing the Snowdrift game with the Prisoner's Dilemma

Rolf Kümmerli[1,2,*], Caroline Colliard[1], Nicolas Fiechter[1], Blaise Petitpierre[1], Flavien Russier[1] and Laurent Keller[1]

[1]*Department of Ecology and Evolution, Biophore, University of Lausanne, 1015 Lausanne, Switzerland*
[2]*Institute of Evolutionary Biology, University of Edinburgh, West Mains Road, Edinburgh EH9 3JT, UK*

Explaining the evolution of cooperation among non-relatives is one of the major challenges for evolutionary biology. In this study, we experimentally examined human cooperation in the iterated Snowdrift game (ISD), which has received little attention so far, and compared it with human cooperation in the iterated Prisoner's Dilemma (IPD), which has become the paradigm for the evolution of cooperation. We show that iteration in the ISD leads to consistently higher levels of cooperation than in the IPD. We further demonstrate that the most successful strategies known for the IPD (generous Tit-for-Tat and Pavlov) were also successfully used in the ISD. Interestingly, we found that female players cooperated significantly more often than male players in the IPD but not in the ISD. Moreover, female players in the IPD applied Tit-for-Tat-like or Pavlovian strategies significantly more often than male players, thereby achieving significantly higher pay-offs than male players did. These data demonstrate that the willingness to cooperate does not only depend on the type of the social dilemma, but also on the class of individuals involved. Altogether, our study shows that the ISD can potentially explain high levels of cooperation among non-relatives in humans. In addition, the ISD seems to reflect the social dilemma more realistically than the IPD because individuals obtain immediate direct benefits from the cooperative acts they perform and costs of cooperation are shared between cooperators.

Keywords: human cooperation; evolution of cooperation; social dilemma; Tit-for-Tat; Pavlov

1. INTRODUCTION

The occurrence of cooperation is one of the greatest challenges for evolutionary biology (Hamilton 1964; Maynard-Smith & Szathmary 1995; Frank 1998). The problem is how can a behaviour that is costly to the actor but benefits other individuals be maintained by natural selection? Hamilton's inclusive fitness theory (Hamilton 1964) provides a solution to this problem when cooperative acts preferentially occur between relatives (Foster *et al*. 2006; Lehmann & Keller 2006). However, cooperation remains a problem in species such as humans, where cooperation often occurs between non-relatives (Fehr & Fischbacher 2003).

The problem of cooperation is easily illustrated in the famous Prisoner's Dilemma (PD) where two players have the opportunity to either cooperate or defect, with cooperation resulting in a benefit to the opposing player but entailing a cost to the cooperator. In this situation, an individual player in a one-shot interaction is always better off when defecting, independent of what the other player does (table 1*a*). The PD reflects a social dilemma because if everybody defects, the mean group pay-off is lower than if everybody had cooperated (Axelrod & Hamilton 1981). However, the PD does not represent the frequent situation where individuals obtain immediate direct benefits from the cooperative acts they perform and costs of cooperation are shared between cooperators. Such a situation is

encapsulated in the Snowdrift (SD) game, which derives its name from the following situation: two drivers are trapped on either side of a snowdrift and have the options of staying in the car or removing the snowdrift. Letting the opponent do all the work is the best option but if the other player stays in the car it is better to shovel (Sugden 1986). Hence, in this game, cooperation yields a benefit (b) that is accessible to both players (i.e. free passage to go home), whereas the cost (c; i.e. removing the snowdrift) is shared between cooperators (Doebeli & Hauert 2005; table 1*b*). Importantly, the SD is still a social dilemma (Dawes 1980) because defection is favoured when the other player cooperates, which occurs at the cost of the overall group pay-off. Situations similar to the SD are ubiquitous in human working life. For example, two scientists accomplishing a research project would each benefit if the other invests more time than oneself in the writing of the paper reporting the collaborative work. But if one of the collaborators does not contribute at all, the best option probably remains to do all the work on one's own.

In one-shot interactions, the predicted proportion of cooperative acts is zero for the PD, while the SD results in a mixed evolutionary stable state with the proportion of cooperative acts being $1 - c/(2b - c)$ (Doebeli & Hauert 2005). The assumption of one-shot interactions is, however, not always realistic because repeated interactions among the same individuals often occur with iteration having been shown to favour cooperation in the iterated Prisoner's Dilemma (IPD; Axelrod & Hamilton 1981; Axelrod 1984; Nowak & Sigmund 1992, 1993). When players react on the opponent's last

Table 1. Pay-off matrices of (*a*) the Prisoner's Dilemma (PD) and (*b*) the Snowdrift game (SD). (In both the games, the benefit (*b*) to the opposing player is greater than the cost (*c*) to the cooperator. The characteristic pay-off (*P*) ranking for the PD is $P_{DC} > P_{CC} > P_{DD} > P_{CD}$ and $P_{DC} > P_{CC} > P_{CD} > P_{DD}$ for the SD. The values in brackets indicate the pay-off matrices that were used for the experiment.)

	cooperation (C)		defection (D)	
(*a*) *Prisoner's Dilemma*				
pay-off to C	$b-c$	(300)	$-c$	(-100)
pay-off to D	b	(400)	0	(0)
(*b*) *Snowdrift game*				
pay-off to C	$b-c/2$	(200)	$b-c$	(100)
pay-off to D	b	(300)	0	(0)

move, a strategy called Tit-for-Tat (TFT) is most successful (Axelrod & Hamilton 1981). TFT players cooperate in the first interaction and then play whatever the opponent played in the previous round. However, TFT performs poorly if players can make mistakes, as players may be caught in long series of mutual retaliation. This problem can be addressed by considering probabilistic strategies, which reveals a strategy called generous TFT (which retaliates only with a probability of 2/3) as the most successful outcome (Nowak & Sigmund 1992). Thus, generous TFT players cooperate when both players cooperated with probability $p_1 = 1$, when the focal individual cooperated and the opponent defected with $p_2 = 1/3$, when the focal individual defected and the opponent cooperated with $p_3 = 1$, and when both defected with $p_4 = 1/3$. When players react not only on the opponent's but also on their own previous move, a new most successful strategy called Pavlov emerged (Nowak & Sigmund 1993), whereby players apply the simple rule of win-stay, lose-shift. This strategy consists of repeating a successful previous move (i.e. a high pay-off obtained when both players cooperated or when the focal individual defected and the opponent cooperated) and of switching to the opposite behaviour if the previous move was unsuccessful (i.e. a low pay-off obtained when both players defected or when the focal individual cooperated and the opponent defected). The Pavlov (win-stay, lose-shift) strategy is therefore described by $p_1 = 1$, $p_2 = 0$, $p_3 = 0$ and $p_4 = 1$. While empirical work indeed showed that human players successfully apply both TFT-like and Pavlovian strategies in the IPD (Wedekind & Milinski 1996), it is unknown whether the same strategies are also used in the iterated Snowdrift game (ISD). Moreover, it is also unclear whether iteration generally favours cooperation in the ISD when compared with one-shot interactions (Doebeli & Hauert 2005).

Despite its potential importance for explaining cooperation among non-relatives, the SD or the ISD has received little attention. This is surprising because similar social dilemmas such as the Hawk–Dove game (Maynard-Smith 1982) or the Chicken game (Sugden 1986), which have the same pay-off ranking but a different matrix structure, have been successfully used in behavioural ecology to study cooperation and conflicts in animals (reviewed by Kun *et al.* 2006) and in politics, economy and sociology to study the effects of various

factors on human cooperation (Wit & Wilke 1992; Kollock 1998; Hertel *et al.* 2000; Mosterd & Rutte 2000; Bornstein & Gilula 2003).

The aim of this study is to compare human cooperative behaviour in the IPD and the ISD in anonymous repeated interactions between two players. First, we aimed to test whether iteration in both the games leads to higher proportion of cooperative acts when compared with predicted values in one-shot interactions. Second, we tested whether cooperation is higher in the ISD than in the IPD, as it is predicted for one-shot interactions. Third, we examine whether and in what frequency players apply TFT-like and Pavlovian strategies in both the IPD and the ISD. Finally, we tested whether women and men differ in their cooperative behaviour and whether they apply different strategies. This is interesting because social science gender theory predicts sex differences in cooperative behaviour in social situations similar to the SD but not in situations similar to the PD (Simpson 2003).

2. MATERIAL AND METHODS
(a) *Experimental design*
We let 96 students (38 female and 58 male students) of the University of Lausanne, Switzerland, either play the IPD or the ISD. The games took place on 3 days within one week in 2006, with the experiments carried out in three different faculty buildings to ensure that students playing the game on different days did not know each other. The students were assigned to groups consisting of six individuals, and, within groups, students were randomly arranged in pairs, without knowing the identity and sex of their opponent. This resulted in 48 pairs of players in 16 groups, with the first group playing the IPD, the second group playing the ISD and then alternating.

The pay-off matrices used for the IPD and the ISD are given in table 1. The pay-offs for P_{DC}, P_{CC}, P_{DD} and P_{CD} (the four possible outcomes when two players have the choice to either cooperate (C) or cheat (D)) were chosen such that the average pay-off across outcomes is the same in both the games. This is important to allow direct comparison of pay-offs between the games. Consequently, the values for the benefit (*b*) of being the recipient of a cooperative act and the cost (*c*) to the cooperator differed between the games (IPD: $b = 400$ and $c = 100$; ISD: $b = 300$ and $c = 200$). Importantly, these differences should not bias the proportion of cooperative acts in the two games because the increased benefit to the recipient ($b_{IPD} - b_{ISD} = 100$) in the IPD when compared with the ISD is directly offset by the reduced cost of cooperation ($c_{IPD} - c_{ISD} = -100$).

The players were separated from one another and had visual contact only with the game instructors but not with the other players. There were three game instructors: two who coordinated the game (coordinators) and one who immediately recorded all players' moves and the resulting pay-offs after each interaction (administrator). The coordinators distributed the written game instructions containing the pay-off matrix (table 1*a*,*b*) to the players and 800 units of Monopoly (Parker Brothers) money. For each interaction, the players indicated whether they cooperated (C) or defected (D) by holding up a card with the letter 'C' or 'D' (Wedekind & Milinski 1996; Milinski & Wedekind 1998). The administrator entered the data immediately into a previously programmed computer file, where the pay-off of

each interaction was calculated automatically. After each interaction, the coordinators distributed the pay-off to the players in the following standardized procedure: the coordinators went to each player (whether or not an individual gained or lost money) and put the maximal pay-off in Monopoly money on the table, and then took back the amount of money to equal the exact pay-off of each player. At the end of the game, the players had to fill in a questionnaire stating their sex and whether they had previously heard about game theory (which was the case for 29.2% of the students).

Each game between two players lasted 12 interactions, although the players were told that the end of the game is randomly determined and might occur after any interaction. The students were further instructed that players with the four highest pay-offs among all players of the same game would receive 40 Swiss francs (CHF), 30 CHF, 20 CHF or 10 CHF, respectively. These latter incentives created competition at a global scale (i.e. among all individuals playing the same game; West *et al.* 2006), such that players were enforced to pursue a strategy that is best among all players and not just to beat the opponent (Wedekind & Milinski 1996; Milinski & Wedekind 1998).

(b) *Data analyses*
Our unit of analysis was the pair of players ($n=48$) playing either the IPD ($n=24$) or the ISD ($n=24$), with the proportion of cooperative acts among player pairs across all 12 interactions being the dependent variable. We first tested whether previous knowledge about game theory and the date of experiments had an effect on cooperation and found that they did not (see §3). We then tested whether the proportion of cooperative acts among player pairs differed between the two games (IPD or ISD) and between different sex combinations within player pairs (two females, two males or a male and a female). We also compared whether the mean proportion of cooperative acts in the IPD and the ISD differs from the expected values for one-shot interactions, which are 0 for the PD and 0.5 for the SD. Finally, we calculated the proportion of cooperative acts for each interaction separately and tested whether there is a significant correlation in the proportion of cooperative acts with increasing number of interactions.

To discriminate between TFT-like and Pavlovian strategies, we calculated for each player the p_3 value (the probability of cooperation after oneself defected and the opponent cooperated). As $p_3=1$ for any type of TFT and $p_3=0$ for Pavlov, the p_3 value can be used to discriminate between the two strategies (Wedekind & Milinski 1996). We assigned strategies only to players with at least two data points available to calculate p_3, and considered individuals with $p_3 \geq 2/3$ as TFT-like players, individuals with $p_3 \leq 1/3$ as Pavlovian players, whereas all other individuals were classified as players using an undefined strategy.

We first tested whether the number of players using TFT-like, Pavlovian or undefined strategies differed within and between the games. We then examined whether TFT-like and Pavlovian strategies yielded higher pay-offs than undefined strategies. Finally, we tested whether female and male players differ in their use of strategy and in their pay-offs achieved.

Whenever possible, we used appropriate parametric statistical procedures for data analyses and applied the false discovery rate control method to adjust the nominal α of 5% in *post hoc* multiple comparisons (Benjamini & Hochberg 1995). Some variables (the proportion of cooperative acts in a single interaction and p_3 values), however, deviated

significantly from normal distributions (Shapiro–Wilk test: $p \leq 0.05$). In analyses using these variables, we used non-parametric randomization tests (Manly 1997) based on 1000 iterations.

3. RESULTS
Previous knowledge about game theory did not influence the proportion of cooperative acts per pair (ANOVA for IPD: $F_{1,22}=0.30$, $p=0.59$; for ISD: $F_{2,21}=0.48$, $p=0.62$). The proportion of cooperative acts was also not significantly different between the 3 days on which the experiment was conducted (ANOVA for IPD: $F_{2,21}=0.03$, $p=0.97$; for ISD: $F_{2,21}=1.52$, $p=0.24$).

The proportion of cooperative acts was higher in the ISD (0.48 ± 0.02, mean $\pm$ s.e.) than in the IPD (0.29 ± 0.03), with this difference being highly significant (ANOVA: $F_{1,44}=27.80$, $p<0.00001$). The mean level of cooperation during the 12 interactions was close to the expected equilibrium value (0.5) for one-shot interactions in the SD (one-sample t-test: $t_{23}=-1.04$, $p=0.31$). By contrast, the level of cooperation was significantly higher than the expected value for one-shot interactions in the PD (one-sample t-test: $t_{23}=8.37$, $p<0.00001$).

There was a significant difference in the proportion of cooperative acts depending on whether two male, two female or a male and a female student played against each other (figure 1; ANOVA: $F_{2,44}=3.40$, $p=0.042$). Separate analyses revealed that the proportion of cooperative acts was only different in the IPD (figure 1; ANOVA: $F_{2,21}=4.64$, $p=0.021$) but not in the ISD (ANOVA: $F_{2,21}=0.63$, $p=0.54$), with the proportion of cooperative acts being significantly higher in female–female and female–male pairs than in male–male pairs (*post hoc* pairwise comparisons: both $p=0.012$).

There was a significant decrease in the proportion of cooperative acts across interactions (figure 2) for the IPD (randomization correlation analysis: $p=0.036$) and the ISD ($p=0.002$). These relationships were, however, no longer significant when excluding the first interaction (IPD: $p=0.41$; ISD: $p=0.19$).

Out of the 96 players, 19 (19.8%) used a TFT-like strategy, 32 (33.3%) used a Pavlovian strategy, while 45 (46.9%) players had an undefined strategy. Players with previous knowledge about game theory were not more likely to apply a TFT-like or a Pavlovian strategy than completely naive players (for IPD: $\chi_1^2=0.12$, $p=0.73$; for ISD: $\chi_1^2=0.52$, $p=0.47$). A comparison of the probability values p_1, p_2, p_3 and p_4 for TFT-like and Pavlovian strategies (see figure 3 for pooled data across games) shows that TFT-like and Pavlovian players differ significantly only in their p_3 values (randomization ANOVA: $n=51$, $p=0.001$) but not in p_1, p_2 and p_4 values (randomization ANOVA tests, p_1: $n=24$, $p=0.78$; p_2: $n=31$, $p=0.61$; p_4: $n=46$, $p=0.43$). There was no significant difference in the frequency at which players used either a TFT-like or a Pavlovian strategy ($\chi_1^2=2.82$, $p=0.09$). There was also no significant difference between the IPD and the ISD in the frequency of players using TFT-like (7 versus 12), Pavlovian (15 versus 17) and undefined (26 versus 19) strategies ($\chi_2^2=2.53$, $p=0.28$).

In both the games, there were significant differences in the pay-offs achieved between the different strategies (ANOVA for IPD: $F_{2,45}=11.42$, $p=0.0001$; for ISD:
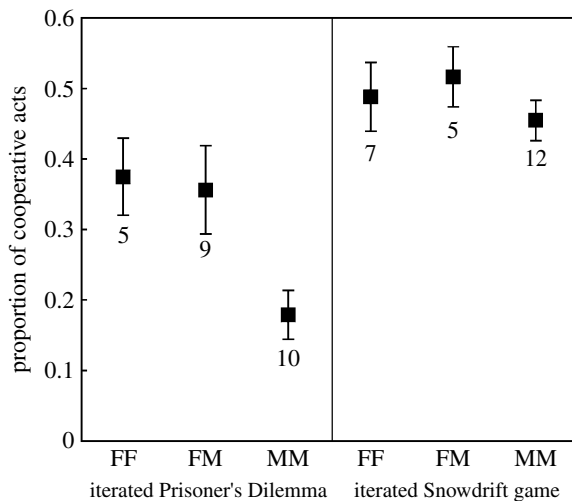
Figure 1. The mean ±s.e. proportion of cooperative acts in 12 interactions between two females (FF), a female and a male (FM) or two males (MM) in the IPD and the ISD. Numbers below the data points represent the sample size (i.e. the number of player pairs).
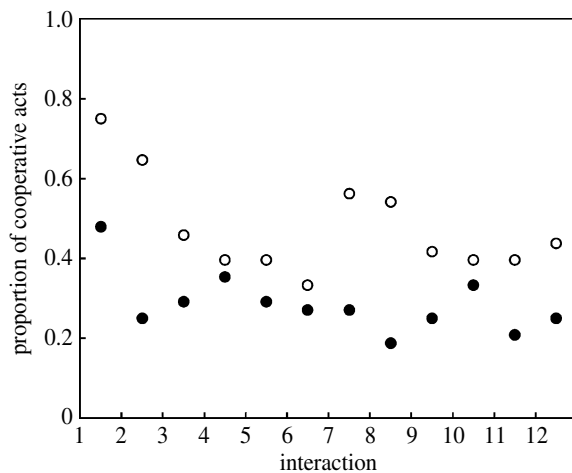

Figure 2. Fluctuation in the proportion of cooperative acts across 12 interactions in the IPD (filled circles) and the ISD (open circles; $n=24$ pairs of players in both games).

$F_{2,45}=6.99$, $p=0.002$; figure 4). *Post hoc* comparisons revealed that pay-offs were significantly higher for TFT-like and Pavlovian than for undefined strategies (TFT-like versus undefined strategies, IPD: $p=0.007$, ISD: $p=0.006$; Pavlovian versus undefined strategies, IPD: $p=0.002$, ISD: $p=0.006$), while there was no significant difference in the pay-offs between TFT-like and Pavlovian strategies (IPD: $p=0.73$, ISD: $p=0.95$).

In the IPD, 12 out of 19 (63.2%) female players and 10 out of 29 (34.5%) male players applied either a TFT-like or a Pavlovian strategy, with female players using these strategies marginally significantly more often than male players ($\chi_1^2=3.80$, $p=0.051$). As a consequence, female players in the IPD obtained significantly higher pay-offs (1441 ± 275, mean±s.e.) than male players (783 ± 122; ANOVA: $F_{1,46}=5.46$, $p=0.024$). There were no such significant differences in the ISD, where similar propor-tions of females (10 out of 19; 52.6%) and males (19 out of 29; 65.5%) used either a TFT-like or a Pavlovian strategy ($\chi_1^2=0.80$, $p=0.37$) obtaining almost identical pay-offs (female players: 1737 ± 116; male players: 1745 ± 65; ANOVA: $F_{1,46}=0.004$, $p=0.95$).

4. DISCUSSION

Our experiment on human cooperation showed that the proportion of cooperative acts is significantly higher in the ISD than in the IPD. As the two social dilemmas represent two different social situations, our result shows that humans adjust their cooperative behaviour according to the social context. Hence, in a social context with a high risk of being exploited by a defector (IPD), humans have a low willingness to cooperate, while in a social context with reduced costs of being defected (ISD) human willingness to cooperate increases.

While theoretical work consistently showed that iteration favours cooperation in the IPD, models based on the ISD game are scarce and revealed mixed results (reviewed by Doebeli & Hauert 2005). Here, we show that iteration led to higher mean levels of cooperation, when compared with one-shot interactions, in the IPD but not in the ISD. This suggests that iteration in the ISD maintains cooperation but does not favour it.

Our comparison of the proportion of cooperative acts over time indicates that iteration leads to reasonably stable levels of cooperation (figure 2). An exception is only the first interaction where the proportion of cooperative acts was considerably higher than in all other interactions. Because players in our experiment obtained no training, the overall decrease in cooperation across interactions might be due to learning and/or strategy effects (Ledyard 1995).

The rewarding scheme and the pay-off matrix compo-sition are known to have an important effect on the proportion of cooperative acts (Ledyard 1995). In our experiment, only players who were best among all players were rewarded, which creates competition at a global scale (i.e. among all individuals playing the same game). Such a rewarding scheme is known to lead to higher proportions of cooperative acts when compared with situations where players just need to beat the opponent to get rewarded (i.e. competition at a local scale; see West *et al.* 2006). Another widely used rewarding scheme is when each player gets monetary rewards according to his/her final pay-off at the end of the game (Ledyard 1995). It is possible that such a rewarding scheme would lead to different proportions of cooperative acts than in our rewarding scheme. Similarly, other matrix compositions (e.g. higher or lower b and c values) might also influence the proportion of cooperative acts. However, if this is the case, the proportion of cooperative acts should be similarly affected in the IPD and the ISD such that the observed differences between the two games should hold under various rewarding schemes and matrix compositions.

Another interesting result of our study is that female and male players behaved differentially in the IPD (but not in the ISD), with cooperative acts between two female players occurring more than twice as often as between two male players (figure 1). Women also applied TFT-like or Pavlovian strategies significantly more often than men and achieved significantly higher pay-offs than men did. These data indicate that in a social context with a high risk of being exploited by a defector (IPD), women choose more successful and more cooperative strategies than men. However, males were not unconditional poor cooperators as they apparently altered their strategy in response to the more cooperative female strategy by being less cooperative when playing against males than against females. All these sex differences in cooperative behaviour were absent in the
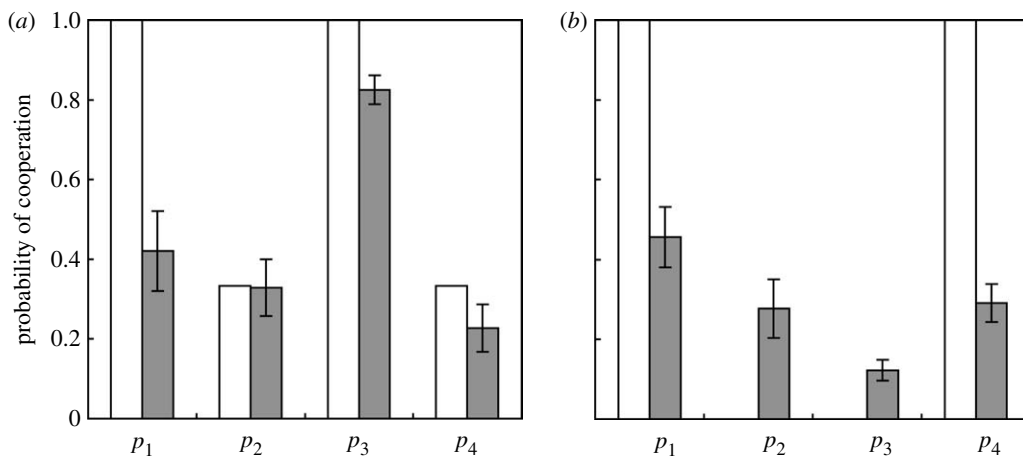
Figure 3. The players' strategies classified as (*a*) a TFT-like strategy (grey bars, $n = 19$; white bars represent expected values for generous TFT) or (*b*) a Pavlovian strategy (grey bars, $n = 32$; white bars represent expected values for Pavlov). The *p*-values (mean±s.e.) indicate the probability of cooperation after both players cooperated (p_1), after the focal individual cooperated and opponent defected (p_2), after the focal individual defected and the opponent cooperated (p_3) and after both players defected (p_4). As there were no significant differences in the p_{1-4} values between the IPD and the ISD, we present the pooled results across both the games.

ISD, hence, in a social context with reduced costs of being exploited. Whether the different responses of females and males to different social contexts are the result of selection remains, however, speculative and needs to be explored in more detail.

Our results on sex differences in cooperation occurring in the IPD but not in the ISD contrast with theory of social sciences, which predicts the opposite pattern. These predictions are based on the idea that males defect out of greed (i.e. they defect in the hope that the opponent cooperates), whereas females defect out of fear (i.e. they defect because they fear that the opponent defects; Eagly & Wood 1999; Simpson 2003). Because the PD allows defection out of greed and fear, no sex differences in cooperation are expected. In the SD, however, defection can only occur out of greed, thus predicting females to be more cooperative than males (Simpson 2003). However, empirical tests of these hypotheses, which are mostly based on different variants of the PD (with and without greed and/or fear), revealed no clear support (reviewed by Sell *et al.* 1993; Ledyard 1995; Simpson 2003). These results combined with our findings suggest that there is no simple rule on how males and females behave in different social dilemmas but that, under certain conditions, sex differences in cooperation do occur.

Our analyses reveal that TFT-like and Pavlovian strategies are successfully used not only in the IPD but also in the ISD. The pattern of strategy use was remarkably similar between the two games with similar number of players applying TFT-like and Pavlovian strategies and with both strategies leading to higher pay-offs than the pay-off of all other strategies (figure 4). This comparison shows that TFT-like and Pavlovian strategies, which have been shown to be the most successful strategies in the IPD (Nowak & Sigmund 1992, 1993), are equally successful in the ISD.

Although many players played TFT-like and Pavlovian strategies, there were subtle but consistent differences from the expected behaviour under the generous TFT and Pavlov strategies (figure 3). While p_2, p_3 and p_4 values of TFT-like players were quite well matched with the expected values of generous TFT, the p_1 value (the probability of cooperation
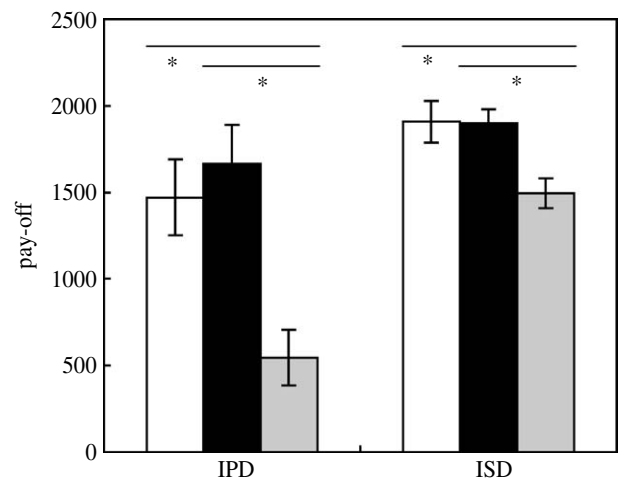

Figure 4. Comparison of the total pay-off (mean±s.e.) after 12 interactions achieved by players using a TFT-like (white bars), a Pavlovian (black bars) or an undefined (grey bars) strategy in the IPD and the ISD. Asterisks indicate significant differences in the pay-off between two strategies.

after both players cooperated) was much lower. A similar pattern could be observed for Pavlovian players where not only the observed p_1 but also the p_4 value was much lower than the expected values. The strategies found here can be better than classical generous TFT and Pavlov strategies because it pays off not to cooperate after both players cooperated (low p_1), when playing against an unconditional cooperator. Likewise, one gets less exploited when not automatically switching to cooperation after mutual defection (low p_4), when playing against an unconditional defector. Our results of lower than expected p_1 and p_4 values are in line with the findings of Wedekind & Milinski (1996) and indicate that both in the IPD and the ISD players use more sophisticated strategies than the ones expected from computer simulations (Nowak & Sigmund 1992, 1993).

In conclusion, our study demonstrates that the ISD is an important model for studying human cooperation, which can be used complementary to the IPD that has often been applied in empirical studies (Ledyard 1995; Wedekind & Milinski 1996; Milinski & Wedekind 1998; West *et al.* 2006). Our data show that the ISD can

potentially explain high levels of cooperation among non-relatives in humans. Moreover, the ISD might even reflect the social dilemma more realistically because it corresponds to frequently observed natural situations where cooperators contribute to a public good that is exploitable by cheaters but also provides immediate direct benefit to the cooperator.

REFERENCES

Axelrod, R. 1984 *The evolution of cooperation*. New York, NY: Basic Books.

Axelrod, R. & Hamilton, W. D. 1981 The evolution of cooperation. *Science* **211**, 1390–1396. (doi:10.1126/science.7466396)

Benjamini, Y. & Hochberg, Y. 1995 Controlling the false discovery rate: a pratical and powerful approach to multiple testing. *J. R. Stat. Soc. A* **57**, 289–300.

Bornstein, G. & Gilula, Z. 2003 Between-group communication and conflict resolution in assurance and chicken games. *J. Conflict Resolut.* **47**, 326–339.

Dawes, R. M. 1980 Social dilemmas. *Annu. Rev. Psychol.* **31**, 169–193. (doi:10.1146/annurev.ps.31.020180.001125)

Doebeli, M. & Hauert, C. 2005 Models of cooperation based on the Prisoner's Dilemma and the Snowdrift game. *Ecol. Lett.* **8**, 748–766. (doi:10.1111/j.1461-0248.2005.00773.x)

Eagly, A. H. & Wood, W. 1999 The origins of sex differences in human behavior—evolved dispositions versus social roles. *Am. Psychol.* **54**, 408–423. (doi:10.1037/0003-066X.54.6.408)

Fehr, E. & Fischbacher, U. 2003 The nature of human altruism. *Nature* **425**, 785–791. (doi:10.1038/nature02043)

Foster, K. R., Wenseleers, T. & Ratnieks, F. L. W. 2006 Kin selection is the key to altruism. *Trends Ecol. Evol.* **21**, 57–60. (doi:10.1016/j.tree.2005.11.020)

Frank, S. A. 1998 *Foundations of social evolution*. Princeton, NJ: Princeton University Press.

Hamilton, W. D. 1964 The genetical evolution of social behaviour. *J. Theor. Biol.* **7**, 1–52. (doi:10.1016/0022-5193(64)90038-4)

Hertel, G., Neuhof, J., Theuer, T. & Kerr, N. L. 2000 Mood effects on cooperation in small groups: does positive mood simply lead to more cooperation? *Cogn. Emot.* **14**, 441–472. (doi:10.1080/026999300402754)

Kollock, P. 1998 Social dilemmas: the anatomy of cooperation. *Annu. Rev. Sociol.* **24**, 183–214. (doi:10.1146/annurev.soc.24.1.183)

Kun, A., Boza, G. & Scheuring, I. 2006 Asynchronous snowdrift game with synergistic effect as a model of cooperation. *Behav. Ecol.* **17**, 633–641. (doi:10.1093/beheco/ark009)

Ledyard, J. O. 1995 Public good: a survey of experimental research. In *The handbook of experimental economics* (eds J. Kagel & A. E. Roth), pp. 111–194. Princeton, NJ: Princeton University Press.

Lehmann, L. & Keller, L. 2006 The evolution of cooperation and altruism—a general framework and a classification of models. *J. Evol. Biol.* **19**, 1365–1376. (doi:10.1111/j.1420-9101.2006.01119.x)

Manly, B. F. J. 1997 *Randomization, bootstrap and monte carlo methods in biology*. London, UK: Chapman and Hall.

Maynard-Smith, J. 1982 *Evolution and the theory of games*. Cambridge, UK: Cambridge University Press.

Maynard-Smith, J. & Szathmary, E. 1995 *The major transitions in evolution*. Oxford, UK: Freeman.

Milinski, M. & Wedekind, C. 1998 Working memory constrains human cooperation in the Prisoner's Dilemma. *Proc. Natl Acad. Sci. USA* **95**, 13 755–13 758. (doi:10.1073/pnas.95.23.13755)

Mosterd, I. & Rutte, C. G. 2000 Effects of time pressure and accountability to constituents on negotiation. *Int. J. Conflict Manage.* **11**, 227–247.

Nowak, M. A. & Sigmund, K. 1992 Tit for tat in heterogeneous populations. *Nature* **355**, 250–253. (doi:10.1038/355250a0)

Nowak, M. & Sigmund, K. 1993 A strategy of win-stay, lose-shift that outperforms tit-for-tat in the Prisoner's Dilemma game. *Nature* **364**, 56–58. (doi:10.1038/364056a0)

Sell, J., Griffith, W. I. & Wilson, R. K. 1993 Are women more cooperative than men in social dilemmas. *Soc. Psychol. Q.* **56**, 211–222. (doi:10.2307/2786779)

Simpson, B. 2003 Sex, fear, and greed: a social dilemma analysis of gender and cooperation. *Soc. Forces* **82**, 35–52. (doi:10.1353/sof.2003.0081)

Sugden, R. 1986 *The economics of rights, cooperation and welfare*. Oxford, UK; New York, NY: Blackwell.

Wedekind, C. & Milinski, M. 1996 Human cooperation in the simultaneous and the alternating Prisoner's Dilemma: Pavlov versus generous tit-for-tat. *Proc. Natl Acad. Sci. USA* **93**, 2686–2689. (doi:10.1073/pnas.93.7.2686)

West, S. A., Gardner, A., Shuker, D. M., Reynolds, T., Burton-Chellow, M., Sykes, E. M., Guinnee, M. A. & Griffin, A. 2006 Cooperation and the scale of competition in humans. *Curr. Biol.* **16**, 1103–1106. (doi:10.1016/j.cub.2006.03.069)

Wit, A. P. & Wilke, H. A. M. 1992 The effect of social categorization on cooperation in 3 types of social dilemmas. *J. Econ. Psychol.* **13**, 135–151. (doi:10.1016/0167-4870(92)90056-D)