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Jaakko Junikka

Evolution of Conflict and Cooperation in Human Groups

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ABSTRACT

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The scale of human cooperation and conflict is outstanding and evolutionarily challenging to explain. Cooperative and hostile behaviours have deep evolutionary roots and adaptive functions. However, theoretical models differ in how they explain these functions. Thus, my thesis aims to empirically test functional predictions about human cooperation and conflict. These experiments use a behavioural ecological framework, and pay also attention to the effects of social and developmental environments. In the first two chapters, I studied how group composition affects cooperation and individual success, and how people react to information of each other's cooperative behaviour. I found that cooperative contributions increased with greater group heterogeneity for those with high baseline cooperativeness, and decreased for those with lower baseline cooperativeness. However, people were insensitive to pre-information of group composition, even though group composition was essential for cooperation to be successful. In Chapter III, I compared evolutionary theories of human intergroup conflict by empirically testing whether intergroup aggression is motivated by public goods as predicted by models of group selection (i.e. Parochial Altruism models) or by private goods as predicted by models of individual selection (i.e. Male Warrior and Chimpanzee models). My results challenge group selection models by implying that private goods motivate intergroup hostilities even when they are socially inefficient. In chapter IV, I propose and test a hypothesis that harsh parental treatment intensifies group-beneficial prosocial and bellicose norms and thus contributes to group success in intergroup conflicts. I found, in accordance with my hypothesis, that harsh parental treatment increased both these traits in males and harsh parenting may thus bear cultural evolutionary consequences. Together, my results contribute further knowledge to our evolutionary understanding of the dynamics, backgrounds and patterns of human cooperation and conflict.

Keywords: Culture evolution; human cooperation; intergroup conflict; parental treatment.

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LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following original papers, which will be referred to in the text by their Roman numerals I–IV.

I van den Berg, P., Molleman, L., Junikka, J., Puurtinen, M., & Weissing, F. J. 2015. Human cooperation in groups: variation begets variation. *Scientific reports* 5: 16144.

II Junikka, J., Molleman, L., van den Berg, P., Weissing, F. J., & Puurtinen, M. 2017. Assortment, but not knowledge of assortment, affects cooperation and individual success in human groups. *PloS one* 12(10): e0185859.

III Junikka, J., Heap, S., Loehr, J., Rusch, H. 2018. Intergroup conflict: a battlefield of prosocial males in the chase for private goods. Manuscript.

IV Junikka, J., Loehr, J., Helle, S., Heap, S. 2018. Harsh parenting may increase performance in intergroup conflicts by intensifying male bellicosity and prosociality. Manuscript.

The contributions of authors to the original papers.

	I	II	III	IV
Original idea	PB, FW, LM, JJ, MP	JJ, MP	JJ	JJ
Study design	PB, FW, LM, JJ, MP	JJ, MP, LM, PB, FW	JJ, SH, HR	JJ, SH
Data collection	JJ, LM, PB	JJ, LM, PB	JJ, HR	JJ, HR
Data analysis	PB, LM	LM, JJ, MP	JJ, SH	SaH, JJ, SH
Writing	PB, LM, JJ, MP, FW	JJ, MP, LM, PB	JJ, SH, HR, JL	JJ, SH, SaH, JL

JJ: Jaakko Junikka, MP: Mikael Puurtinen, LM: Lucas Molleman, PB: Piet van den Berg, WJ: Franjo Weissing, SH: Stephen Heap, JL: John Loehr, HR: Hannes Rusch, SaH: Samuli Helle.
Chapter I has been included also in the thesis of van den Berg (2015).

1 INTRODUCTION

1.1 On the nature of human cooperation and conflict

We humans are a spectacular species in the scale of both cooperation and conflict. Many of us are prone to cooperate, to help each other from relatives to strangers, and our evolutionary and ecological success relies on this ability. But we also notoriously use this ability to cooperate against each other in intergroup conflicts. Cooperative intergroup conflicts and wars have been prevalent over cultures and known history (Boehm 2012, Gat 201, Glowacki *et al*. 2017).

Cooperation and conflict have deep evolutionary roots and adaptive functions but pose many evolutionary puzzles (Bourke 2011, Boehm 2012; Rusch 2014, Gómez *et al*. 2016). In the simplest case, the problem of costly cooperation lies with less cooperative individuals. If they can exploit the benefits of more cooperative individuals they should proliferate. Thus, it seems unlikely that evolution would produce tendencies to help strangers in situations when direct or indirect benefits of cooperation are not attainable, like in actions of donating blood or giving money to charity. And similarly, it remains an open issue of why evolution has not selected away our tendency to participate in violent intergroup conflicts where young men often voluntarily (Glowacki and Wrangham 2013) risk their lives and often are removed from the gene pool. How might evolution actually be responsible for these behaviours? What role does culture play and can cultural and genetic evolution co-evolve?

A number of different evolutionary and culture-evolutionary theories have been developed to solve these puzzles of human cooperation and between group conflicts (West *et al*. 2007b, Rusch 2014), but still active interdisciplinary research on this topic has many questions to solve (West *et al*. 2011, Burton-Chellew *et al*. 2017, Böhm *et al*. 2018). In my thesis, I tackle these questions by empirically testing functional predictions of reciprocal cooperation, positive assortment, intergroup conflict and cultural group selection models (Trivers

1971, Eshel and Cavalli-Sforza 1982, Bowles and Gintis 2011, Rusch 2014, Richerson *et al*. 2016).

1.2 On the evolutionary and cultural explanations for cooperation and intergroup conflict

1.2.1 Positive assortment

The assortment of individuals with similar cooperative tendencies (positive assortment) is a simple solution to the basic cooperation problem. Because human cooperativeness varies significantly, a hindrance to the evolution of cooperation can emerge from less cooperative individuals (Volk *et al*. 2012, Peysakhovich *et al*. 2014). If the non-cooperative individuals manage to enjoy the benefits of costly cooperation without paying the cost, the non-cooperative individuals benefit the most and get a selection advantage (West *et al*. 2011). Positive assortment solves this problem in a straight forward manner, as it prevents less cooperative people from exploiting more cooperative individuals (Eshel and Cavalli-Sforza 1982, Bowles and Gintis 2011).

Indeed, and not surprisingly, cooperative people tend to seek conditions of positive assortment in lab experiments and less cooperative people try to seek groups of cooperators (Ehrhart and Keser 1999, Pradel *et al*. 2009). Also, real world friend groups tend to show assemblages of positive assortment (Pradel *et al*. 2009, Apicella *et al*. 2012). If cooperators succeed in assorting together, their profits exceed those of less cooperative ones. If not, the opposite outcome is possible (Kurzban and Houser 2005, Burlando and Guala 2005, II).

1.2.2 Reciprocity

Theories of reciprocity (Trivers 1971, Nowak and Sigmund 2005) explain how cooperation can pay off even between unrelated individuals within large social groups that have variable cooperative behaviours (i.e. without positive assortment). The trick is to be sensitive to information of each other's previous cooperativeness and restrain cooperative efforts with those who are known to have been less cooperative, and cooperate only with those who are known to be cooperative. This information can be achieved through personal experience or reputation (Nowak and Sigmund 1998, Brandt and Sigmund 2004). Indeed, numerous experiments have proven that humans are sensitive to information of each other's cooperativeness and behave by and large in accordance within the framework of reciprocity (Gallo and Yan 2015, Swakman *et al*. 2015).

1.2.3 Parochial Altruism, Chimpanzee and Male Warrior models

Evolutionary theories of between-group conflicts are also theories of within-group cooperation. This is because between-group conflict can select for

cooperation within groups, as more cooperative groups can outperform the less cooperative ones (Bourke 2011, Bowles and Gintis 2011). Thus, within-group cooperation and between group conflicts seem to be two sides of the same coin. Evolutionary theories show that human intergroup conflicts can evolve based on public goods (indirect benefits), like territorial gains that enhance the reproduction of all in-group members. Alternatively, they can be based on private goods (direct benefits), like greater access to mates and loot, that enhance the reproduction of focal warriors.

Chimpanzee and Male Warrior models are built on private goods. They frame that intergroup conflicts have evolved as groups of males cooperatively pursue direct benefits and that bellicosity is likely to evolve whenever the prospects of private goods are larger than individual risks (van Vugt *et al*. 2007, Wrangham and Glowacki 2012). Thus they view bellicosity as an ultimately selfish, fitness maximizing behaviour where the development of cooperation due to intergroup conflicts is restricted to mutually beneficial cooperation by warriors.

Parochial altruism, or group selection models, frame intergroup conflicts as arising from public good benefits, like territorial gains, which benefit the entire in-group through the altruistic sacrifice of warriors (Bowles 2006, Choi and Bowles 2007, Smirnov *et al*. 2007, García and van den Bergh 2011, Rusch 2014). According to these models altruism restricted to in-group members combined with bellicosity toward out-group members can coevolve as a trait called parochial altruism. Thus, in the framework of these models, intergroup conflicts can push the development of within-group cooperation even further beyond the selfish needs to the side of true individually costly altruism. However, these models demand certain conditions to work, like a combination of discriminative altruism and out-group bellicosity together with large enough genetic difference between groups (Choi and Bowles 2007, Bowles and Gintis 2011). As these models demand a genetic difference between groups, they are argued to ultimately be based in kin-selection models under group contest conditions (West *et al*. 2007a, 2011).

1.2.4 Cultural group selection

The behaviours of cooperation and conflict are deep-rooted biological phenomenon (Bourke 2011, Rusch 2014). However, the expression of human cooperativeness and conflict depends considerably on the impact of many cultural factors (Ockenfels and Weimann 1999, Henrich *et al*. 2005, Gächter and Herrmann 2009). In particular relevance to this thesis, individual development depends considerably on early childhood conditions, especially parental treatment (Klebanov, Marianna and Travis, Adam 2014, Waltes *et al*. 2016, Vaiserman and Koliada 2017).

Since cultures vary considerably (Prescott 1975, Lansford *et al*. 2010, Saucier *et al*. 2015), cultural group selection models argue that intergroup conflicts select from this cultural variability all such norms, practices and institutions that enhance a group's success in intergroup conflicts and warfare

(Boyd and Richerson 2009, Bowles and Gintis 2011, Zefferman and Mathew 2015). As individual traits of cooperativeness and bellicosity contribute to war success, especially when occurring together (Choi and Bowles 2007, Lehmann and Feldman 2008), cultural group selection should have selected for such cultural practices that intensify the expression of these traits. Further, the cooperation-enhancing social systems within groups selected by intergroup competition are further argued to have selected for cooperative genes that account for contemporary extensive cooperativeness (Boyd and Richerson 2009, Richerson *et al*. 2016).

1.3 Objectives of the research

1.3.1 Test how people respond to heterogeneous cooperation of their group members (I)

Humans vary substantially and consistently in their cooperation tendencies (Volk *et al*. 2012, Peysakhovich *et al*. 2014). The outcome of cooperative interactions at the individual and group level depends on the variability of cooperation tendencies within a group (Eshel and Cavalli-Sforza 1982, II) and on how people adjust their cooperation in response to this variability (Trivers 1971, Nowak and Sigmund 2005). However, little is known about how the degree of variation in cooperation within a group affects the cooperative decisions of the individual and whether these responses vary along with cooperative tendency. Thus, we compared the cooperative decisions of individuals with different cooperative tendencies in situations where the mean cooperation of group members is held constant but variation differs.

1.3.2 Test how group composition and information on it interact to affect individual cooperation and success (II)

The positive assortment of individuals with different cooperative tendencies is important for the success of cooperation (Eshel and Cavalli-Sforza 1982, de Oliveira *et al*. 2014), likewise is a person's sensitivity to information on the cooperation of others (Trivers 1971, Nowak and Sigmund 2005). However, how these two factors interact and affect the cooperation and success of individuals with different cooperative tendencies is poorly known. I thus measured individuals' cooperative tendencies and grouped them accordingly in a cooperative task. I then compared a situation when information of the positive assortment grouping procedure was provided and when it was not. Further, to assess the effect of positive assortment alone I compared positive assortment to random grouping.

1.3.3 Test evolutionary theories of intergroup conflicts (III)

Evolutionary theories about human between group conflicts are opposed on how to frame the benefits of fighting: as either i) public goods shared among the whole in-group or ii) as private goods accrued by individual warriors (Rusch 2014). Even though anthropological evidence has shown the importance of private goods in motivating bellicosity (Glowacki and Wrangham 2013), and theoretical studies point out their straightforward salience for the evolution of intergroup conflicts (van Vugt *et al*. 2007, Wrangham and Glowacki 2012), empirical research has been done solely on the premise of public goods. Thus, I tested different evolutionary theories of human intergroup conflicts by assessing how much public and private goods motivate bellicosity and whether the premises of parochial altruism model by Choi and Bowles (2007) hold with regard to the associations of prosociality and bellicosity.

1.3.4 Test a cultural-evolutionary hypothesis that harsh parenting is associated with prosociality and bellicosity (IV)

Parental harshness (e.g. domestic fighting, negative physical or emotional contact) has become common around the world after the cultural change to agrarian societies (Klebanov, Marianna and Travis, Adam 2014, Hewlett 2017, Khaleque and Ali 2017). This poses a cultural evolutionary puzzle as harsh parenting often is individually toxic (Narvaez *et al*. 2016, Afifi *et al*. 2017) and should thus be selected against if it does not provide some benefits. I propose a hypothesis that harsh parental treatment might have brought group-level benefits in inter-group conflicts by intensifying a set of traits that enhance a group's competitive ability. I test this hypothesis by measuring whether harsh parenting is associated with the traits of bellicosity and prosociality, as these traits should contribute to group success in intergroup conflicts, especially when occurring in combination (Choi and Bowles 2007). I consider the effects of parental treatment on bellicosity and prosociality by taking into account also the effects of religiosity, endorsement of an honour code, and feelings of belongingness as these traits are associated with both parental care and the traits under inspection (Prescott 1975, McCullough *et al*. 2013, Lucas and Livingston 2014, Corrales *et al*. 2016, Purzycki *et al*. 2016).

2 METHODS

2.1 Experiment 1 (I, II)

To test how group composition and information on it affects cooperation I used the well-established Public Goods Game (PGG, Ledyard 1995). PGG poses individuals with the basic problems of cooperation: the temptation to free-ride and the difficulties of sustaining cooperation that is individually costly across separate interactions. In PGG, subjects make decisions to cooperate i.e. contribute money to a cooperative project. The money contributed to a project is multiplied and shared with group members equally, irrespective of their contributions. Thus, group and average individual payoffs are maximized if everyone fully cooperates. However, each cooperative decision decreases personal profits, and thus everyone's monetary interest is not to cooperate and just to free-ride on others' cooperation.

The experiment consisted of three parts, which I used to study the effects of positive assortment and information on this assortment across individuals with different cooperative tendencies. In the first part, I assessed subjects' cooperative tendencies in a 'stranger' design, in which subjects played ten rounds of PGG in randomly changing anonymous groups. Thus, contributions in each round represented their baseline cooperative tendency, as there were no reputation concerns or possibilities for strategic cooperation. The second part assessed the effect of information on positive assortment. I put subjects into fixed groups for 15 rounds based on their cooperative tendencies measured in part one, and posited them with information of the grouping process. I could then compare patterns of cooperation in this treatment with a control in which no information was provided. To assess the effect of positive assortment on its own, I also compared the control (positive assortment, no information) to randomly formed fixed groups. In the third part, I assessed how heterogeneity in cooperation within a group affects cooperative decisions for individuals with different baseline cooperative tendencies. For that, I ran a strategy set, where I

compared cooperative decisions in situations where mean contributions for the group were the same, but their variation differed.

This experiment was run in a computer laboratory at the University of Groningen (The Netherlands). Participants (n=240, aged 19-33, 71 % females) were mostly university students from various disciplines. For statistical analyses I used a linear mixed model, Brown-Forsythe test and Tukey Honest Significant Differences test to assess how heterogeneity in cooperation within groups affects cooperation of individuals with different cooperation tendencies (I). To test if positive assortment and information of it affect cooperation and success of individuals belonging to different cooperative tendencies I used Linear Mixed Models and ANOVA (II).

2.2 Experiment 2 (III, IV)

To test evolutionary theories of warfare against each other I used an intergroup prisoner's dilemma game (IPD, Bornstein 1992, as described in Thielmann & Böhm 2016) that is well established in the study of intergroup aggressions. In the IPD game, subjects make monetary contributions in order to benefit the in-group at the expense of another group.

To test between evolutionary theories of warfare we modified the IPD game on how the profits of contributions were divided between the in-group and individual aggressors. In particular, I tested how subjects value the benefits from intergroup conflicts as either i) public goods, in line with parochial altruism models (Rusch 2014), or ii) as private goods, in line with the Male Warrior Hypothesis and Chimpanzee Model (Van Vugt *et al*. 2007, Wrangham and Glowacki 2012).

To specifically test the premises of the parochial altruism model regarding expected associations between bellicosity and prosociality toward in- and out-groups (Choi and Bowles 2007), I used the Social Value Orientation measure (SVO, Murphy, Ackermann, & Handgraaf, 2011). In SVO subjects make six monetary decisions with themselves and a random partner in a situation of interdependence. Based on these decisions, a prosociality measure is calculated that classifies individuals on a continuous scale from competitive to individualistic, prosocial and altruistic based on how much one valued their partner's payoff in relation to their own. To test the premises of the parochial altruism model, I replaced the random other with three in-group members to assess prosociality toward in-groups and with three out-group members for prosociality toward out-groups.

This experiment was an online experiment conducted with Amazon Mechanical Turk (Buhrmester *et al*. 2011) by USA residents (n=192, mean age 36, 49% females). Subjects made a series of monetary decision that affected their own and their interaction partners' payoffs. To test whether mean attack contributions differed depending on the share of benefits as public and private goods I used Repeated Measures ANOVA (III).

2.3 Questionnaire (IV)

With a questionnaire included at the end of experiment 2, I studied whether harsh parenting intensifies prosociality and bellicosity, which serves group level benefits in intergroup conflicts along the lines of my hypothesis. This was tested within a wider context of variables that could influence bellicosity and prosociality: religiosity, code of honour and belongingness. The questionnaire consisted of statements that were answered using a seven-point Likert scale. For the parental treatment scale, I used ten questions adopted from Pedersen *et al*. (2014), which assesses early life exposure to family neglect, conflict and violence. To assess individuals' endorsement of a Code of Honour, I used a ten-item scale from Pedersen *et al* (2014). Code of Honor predicts, among other things, individual aggressiveness and proneness to the exploitation of strangers (Vandello *et al*. 2008, McCullough *et al*. 2013). To assess individuals religiosity I used three questions on religiosity adopted from the Arizona Life History battery (Figueredo 2007). And lastly, to assess participants sense of belonging, I used a scale from Lee and Robbins (1995). I used structural equation modelling to test the associations between parental harshness and both prosociality and bellicosity, including also indirect effects via religiousness, belongingness and Code of Honour.

3 RESULTS AND DISCUSSION

3.1 Variation in human cooperative tendencies matters (I, II)

In chapters I and II, I explored how group composition (in terms of baseline cooperation) and information of group members past cooperation affects cooperative decisions in groups and the success of individuals with different cooperative tendencies. In chapter II, I found that the ability for a group to maintain cooperation depends considerably on the composition of the group, which is in line with previous studies (Burlando and Guala 2005, Gunnthorsdottir *et al*. 2007). Not surprisingly, those groups that consisted of individuals whose premeasured cooperative tendency belonged to the highest quartile started cooperating at a higher level and maintained cooperation considerably better than groups consisting of less cooperative individuals.

The results of chapter I bring further insight on how this observed difference in group cooperation can arise in positively assorted groups. I found that those in the highest and lowest quartile of cooperative tendency react in opposite manners to observed heterogeneity in group cooperation. Those in the highest quartile tended to increase their cooperation, whereas those in the lowest quartile tended to decrease their cooperation, in response to heterogeneity. This type of reaction difference might intensify the differences in group cooperation levels (Chapter II), as individuals in groups of highest quartile cooperators tend to follow the highest example of their group members and ignore occasional low cooperation decisions. Whereas those from lowest quartile tend to follow the example of the lowest contributor in their group, which likely explains the fast collapse of cooperation in their groups.

As depicted by evolutionary models (Eshel and Cavalli-Sforza 1982, Bowles and Gintis 2011), positive assortment created group level differences in cooperation, which can lead to a positive association between cooperative tendency and individual success. In line with the empirical study by Kurzban & Houser (2005), this association was absent when groups were formed randomly. Thus positive assortment may serve a simple explanation for

cooperation to evolve. However in our evolutionary history, it was not always possible for small groups of hunter-gatherers to select their group members, and thus positive assortment alone is likely not a sufficient explanation for the evolution of human cooperation.

3.2 Information on the cooperative tendencies of group members is ignored at the beginning of new interactions (I, II)

Numerous studies have shown that information of others past cooperativeness affects cooperation, along the lines of reciprocity theories (Swakman *et al*. 2015). That is, we direct cooperative efforts to those who we believe to have been previously cooperative and restrict cooperation with those who are known to be less cooperative. Taking the convergent significant findings of other studies that test for information effects, our result that information did not affect cooperation in chapter II is interesting and implies that some special reason for ignoring information in that particular setting apply.

Together with a similar study (de Oliveira *et al*. 2014), it looks like the information of others' past cooperativeness is ignored at the beginning of a new interaction round. A possible reason might lie in the benefits of signalling one's cooperativeness at the beginning of a new interactions in order to form new cooperative relationships, in line with the Handicap principle (Zahavi 1995), rather than responding to behaviour from previous interactions.

However, in my setup of positive assortment, information might also have been ineffective if the False Consensus Effect (FCE, Mullen *et al*., 1985) has taken place. According to FCE people think others behave in a similar manner to themselves. Thus, providing individuals with information that they have been grouped with others who have a similar level of cooperation might have just enforced the beliefs they already held and would not have inflicted a change in behaviour.

3.3 Direct benefits seem to stand as the root cause for the evolution of intergroup conflicts (III)

My results challenge the multilevel-selection-based Parochial Altruism model (PA) of Choi and Bowles (2007) and speak in favour of the individual-selection-based Chimpanzee Model and Male Warrior Hypothesis (CM/MWH (van Vugt *et al*. 2007, Wrangham and Glowacki 2012) as a more plausible evolutionary root of human intergroup conflicts. I found, against the predictions of PA, that subjects in both genders were considerably motivated to attack via the production of private goods even if this carried a social efficiency cost. I also found substantial contributions to the public good attack, but my data also

suggest that these may be explained by expectations of larger individual benefits taken that others attacked as well. In line West *et al*. (2007a, 2011) have argued that even single shot public good contributions may not reflect altruistic motivation but tendency for mutually beneficial cooperation. This kind of mutually beneficial cooperative attack is in line with CM/MWH as they frame attacking as a particularly cooperative action.

Previous studies have found contradicting evidence on whether prosociality is associated with a tendency to attack (in accordance with PA) or cooperate with out-groups (Cashdan 2001, Thielmann and Böhm 2016, Yamagishi and Mifune 2016). My results set further light to this by showing that both sides are right when males are considered. I found that in-group prosociality was positively associated with out-group prosociality in both genders. Furthermore, prosociality to both the in- and out-group were positively associated with attacking, but only in males. Thus, against the premises of PA, parochialism is not a necessity for attacking other groups and male prosociality seems to be a double-edged sword. That is, prosocial males can either cooperate with out groups or attack them, depending on circumstances. Thus my results together imply that the evolutionary roots of human intergroup conflict might lie more in direct benefits from private goods pursued by mutually beneficial cooperation than with indirect benefits of public goods pursued by self-sacrifice.

This study is the first empirical experiment to consider private goods as motivating intergroup aggressions. This is surprising given the parsimonious theoretical and biological basis and the supporting anthropological findings speaking in favor for CM/MWH (Manson and Wrangham 1991, Glowacki and Wrangham 2013, Rusch 2014). Further, as I theorize, already the sheer existence of private goods makes the option of producing public goods via sacrificing oneself less viable. Thus, more empirical and modeling studies in line with CM/MWH are needed to get further knowledge on the nature of human intergroup aggression and its evolutionary roots.

3.4 Behavioral strategies differ at ends of cooperation tendencies (I, III)

My results from Chapters I and III suggest that individuals vary in their behavioral strategies according to their cooperative tendencies. In particular, less cooperative individuals were prone to respond by decreasing their cooperation in response to heterogeneity in group cooperation, and were unwilling to participate in intergroup attacks. Whereas more cooperative individuals had the opposite behavioral responses, they increased their cooperation in response to group heterogeneity in cooperation, and males were willing to participate in intergroup conflicts.

This suggests that less cooperative individuals are more risk-averse to the problems of cooperation. In particular, less cooperative individuals might be avoiding the risk of being exploited by others within groups, and thus follow the behaviour of the least cooperative individuals. Similarly intergroup conflict contains personal risks, which they apparently were unwilling to take. Whereas cooperative individuals were more ready to bear the risks of being exploited by group members and were more prone to engage in risky between-group conflicts.

3.5 Harsh parenting increases group beneficial prosociality and bellicosity in males and likely bears cultural evolutionary implications (IV)

I found that harsh parenting significantly increased male prosociality and bellicosity toward out-groups. Whereas religiosity, code of honour and feeling of belongingness had no effects on either of these traits. Prosociality and bellicosity, especially when occurring simultaneously, should aid group success in intergroup conflicts (Choi and Bowles 2007). Thus my result supports my hypothesis that harsh parenting is associated with a set of traits that should aid group success in intergroup conflicts. The support for this hypothesis opens interesting cultural-evolutionary possibilities.

First, our result might partly explain why individually costly harsh parenting has spread across the world. In hunter-gatherers harsh parenting is rare, but it is common in more developed societies (Turchin *et al*. 2013, Morris 2014). This might be explained by the larger cultural-evolutionary selection pressure of between-group conflicts that came with the change in subsistence foraging to agriculture (Turchin *et al*. 2013, Morris 2014). In other words the benefits of harsh parenting via between-group selection might have exceeded the individual level costs.

Second, religions, especially those with beliefs centred on moralizing punishing gods, have been argued to increase prosociality and serve for the emergence of large complex societies across the world (Norenzayan *et al*. 2016, Purzycki *et al*. 2016, Shariff *et al*. 2016, Bennett and Einolf 2017). However, conservative religions with beliefs in punishing gods are associated with high levels of harsh parenting (Prescott 1975, Hoffmann *et al*. 2017, Martinez *et al*. 2017). Thi together with my results, which show no impact of religiosity, suggests that the prosociality increasing effects and following culture evolutionary consequences of religions might stem from parenting practices instead of belief per se.

Together these results bring to the fore the substantial effect of childhood conditions on the development of human behavioral tendencies, which has been vastly understudied in economic experiments and cultural-evolutionary studies.

3.6 Societal implications (III, IV)

"We don't yet know, above all, what the world might be like if children were to grow up without being subjected to humiliation, if parents would respect them and take them seriously as people."

- Alice Miller (2002), p. 177.

3.6.1 Parenting might be associated with peace even at between-group levels (III, IV)

My result of the positive association of harsh parental treatment and bellicosity toward out-group aligns with cross-cultural studies (Prescott 1975, Lansford and Dodge 2008). Also, individual level studies have found an association of harsh parenting and increased right-wing authoritarianism, discrimination and prejudice against other groups (Gabriel 2009, Kandler *et al*. 2016). Thus, these results together imply that the manner we treat our children seems to have significant consequences on peacefulness between ethnic groups and nationalities. Still, the consequences of child maltreatment has had little attention in social sciences and in interdisciplinary research (Bottoms *et al*. 2004, Dentan 2008, Klebanov, Marianna and Travis, Adam 2014) even though it clearly deserves much more.

Further, along the lines of my hypothesis, harsh parenting might spread through warfare. This kind of culture evolutionary process might be taking place currently in the spread of fundamental religious groups like ISIS. Thus, more research needs to be done on the role of child maltreatment on the emergence of radical bellicose phenomena like ISIS, terrorism and racism. Also, more emphasis on national and international policy should be placed to improve the living conditions of children and parental treatment especially in their first years of life when largest developmental impacts take place.

3.6.2 Harsh parental treatment decreases feeling of belongingness in adults (IV)

Humans are highly social animals for which the need to belong, to feel an emotional connection to others and to truly be a part of some social group is one of our fundamental needs (Baumeister *et al*. 2007). Lack of belongingness has been found to be associated with, among other things, depression, feeling a lack in meaning, decreased physical and mental health and premature death (Pittman and Richmond 2007, Lambert *et al*. 2013, Holt-Lunstad 2018). In line with Corrales *et al*. (2016), I found that a lack of belongingness was significantly associated with harsh parenting. Thus, improving the early years of children may not only decrease violence on all levels of societies, but may also help individuals to establish social connections and live healthy meaningful lives.

4 CONCLUSION

Together my results contribute further knowledge on the dynamics, backgrounds and patterns of human cooperation and conflict and suggest that many evolutionary mechanisms have operated simultaneously.

In particular, in lines with positive assortment models (Eshel and Cavalli-Sforza 1982, Bowles and Gintis 2011) I found that grouping people according to their cooperation tendencies creates a difference in groups' cooperation levels, which further leads to a positive association between cooperation tendency and success (II). Also, I found that people react sensitively to information of each other's cooperation in line with reciprocity theories (Trivers 1971, Nowak and Sigmund 2005), but in a nuanced manner. The most cooperative individuals increased their cooperation when perceiving heterogeneity in group members' level of cooperation, whereas the least cooperative ones decreased their efforts (I). Additionally, contrary to reciprocity theories but in line with the Handicap Principle (Zahavi 1995), when new interaction rounds began people ignored information about each other's level of cooperation, likely to advertise their cooperativeness in order to build new cooperative interactions (II).

Within-group cooperation and between group conflicts have likely evolved hand in hand, pushing each other's evolution further (van Vugt *et al*. 2007, Choi and Bowles 2007, Wrangham and Glowacki 2012, Rusch 2014). Thus, a mechanism that evolved cooperation within-groups might have made exploiting other groups possible for cooperative males. Whether the tendency to embark on intergroup conflicts evolved via in-group beneficial public goods or individual beneficial private goods has not been experimentally tested until now. My results imply that the evolutionary roots of human intergroup conflicts might lie more in the direct benefits that warriors achieved by mutually beneficial cooperation rather than in altruistically accrued indirect benefits (III). Somewhat paradoxically the tendency for men to embark on intergroup conflicts is associated with their tendency to cooperate with out-groups. Thus, human behaviour in respect to other groups is flexible, containing possibilities for both cooperation and conflict.

Cooperation and conflict behaviours are impacted considerably by cultural factors (Boyd and Richerson 2009, Richerson *et al*. 2016). I presented a hypothesis that harsh parenting might intensify a set of psychological traits that enhance group-beneficial prosocial and bellicose tendencies that together serve a group's competitive ability in intergroup conflicts. I found support for the hypothesis, as harsh parental treatment was associated with increased prosociality and bellicosity in males (IV). These traits should bring success in warfare especially when they occur in combination (Choi and Bowles 2007, Bowles and Gintis 2011). Thus, my results suggest that groups adopting harsh parenting practices might have received selective benefits in intergroup conflicts. Further, this suggests an explanation why harsh parenting might have spread only after a change in subsistence use from foraging to farming, as the cultural selection pressure from warfare grew greater in post forager societies (Turchin *et al*. 2013, Morris 2014). Additionally, my results, with supporting evidence, suggest that some effects of religiosity on prosociality may stem from the developmental effects caused by harsh parenting practices.

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YHTEENVETO (RÉSUMÉ IN FINNISH)

Ihmisen yhteistyö- ja konfliktikäyttäytymisen evoluutio

Yhteistyö- ja konfliktikäyttäytyminen ovat pohjimmiltaan biologisia ilmiöitä. Näitä käyttäytymispiirteitä tavataan yleisesti bakteereista sosiaalisiin hyönteisiin, lintuihin ja ihmisapinoihin. Yhteistyön ja konfliktien evoluutio on osoittautunut haasteelliseksi tutkia. Kuinka lisääntymismenestykseen nojaava evoluutio on voinut suosia yksilöitä, jotka ovat valmiita omalla kustannuksellaan hyödyttämään muita esimerkiksi ruuan hankinnassa tai uusia elinalueita lajitovereiltaan vallatessaan?

Ihmisen yhteistyökäyttäytymiseen johtaneen evoluution tutkiminen on ollut erityisen haasteellista sen poikkeuksellisesta laajuudesta johtuen. Me emme rajoita yhteistyötämme useimpien eläinlajien tavoin ainoastaan sukulaisiin tai pienen ryhmän sisälle. Me teemme yhteistyötä isoissa ryhmissä ohi sukulaisrajojen ja jopa kertaluontoisissa kohtaamisissa vieraiden ihmisten kanssa, lahjoitamme hyväntekeväisyyteen ja luovutamme verta.

Monimutkaiseksi on osoittautunut myös yhteistyön vastakohdan, ryhmien välisten konfliktien eli sotimisen evoluutio. Miksi toisaalta ystävälliset ja yhteistyöhalukkaat ihmiset ovat olleet läpi tunnetun historian ja kulttuurien kirjon toistuvasti valmiita riskeeraamaan henkensä ja siten lisääntymismahdollisuutensa sodissa toisia ryhmiä vastaan? Vai selittääkö kulttuuri nämä evolutiivisesti vaikeasti selitettävät taipumuksemme, vai voiko kulttuuri edes olla evoluutiosta irrallinen osa?

Väitöskirjani koostuu neljästä empiirisestä osatyöstä, joissa tutkin ihmisen yhteistyö- ja konfliktikäyttäytymistä ja niiden evoluutiota sekä kulttuuristen tekijöiden, erityisesti lapsuusajan kasvuolosuhteiden vaikutusta. Yhteistyön ja konfliktien evoluutiosta on esitetty useita evolutiivisia teorioita, joiden ennusteita vertailin havaittuun käyttäytymiseen.

Kahdessa ensimmäisessä osatyössäni tutkin miten ryhmän koostuminen yhteistyötaipumuksiltaan erilaisista yksilöistä ja yksilön tieto muiden ryhmän jäsenten yhteistyötaipumuksista vaikuttaa yksilöiden ja ryhmän yhteistyökäyttäytymiseen ja yksilöiden välisiin menestymiseroihin ja siten yhteistyön evoluutioon. Havaitsin ihmisten yhteistyötaipuvuuden vaihtelevan merkitsevästi yksilöiden välillä. Ryhmien kyky ylläpitää yksilölle kustannuksellista, mutta ryhmää kokonaisuudessaan hyödyttävää yhteistyötä vaihteli merkitsevästi ryhmän yksilöiden yhteistyötaipumusten mukaan. Syntyneestä ryhmien yhteistyömäärän eroista seurasi yksilöiden yhteistyötaipuvuuden ja menestymisen välinen positiivinen korrelaatio. Ryhmien rakenteen ollessa sattumanvarainen kyseistä korrelaatio ei syntynyt. Lisäksi havaitsin yhteistyötaipumuksiltaan vähäisten ja yhteistyötaipuvaisten reagoivan päinvastaisesti tilanteeseen, jossa ryhmän sisäinen yhteistyö oli vaihtelevaa. Yhteistyötaipuvaiset seurasivat ryhmän eniten yhteistyötä tekevän esimerkkiä, kun taas vähiten yhteistyötaipuvaiset seurasivat ryhmänsä vähiten yhteistyötä tekevän esimerkkiä. Nämä ominaisuuserot suurentavat havaitsemaani ryhmien yhteistyötason eroa sekä yksilöiden menes-

tymisen eroa silloin kun ryhmät ovat muodostettu yhteistyötaipumuksiltaan samankaltaisista yksilöistä.

Kolmannessa osatyössä tutkin ryhmien välistä konfliktikäyttäytymistä ja sotien evolutiivisten teorioiden oikeellisuutta vertailemalla teorioiden erilaisia näkemyksiä ihmisen yhteistyö- ja konfliktitaipumuksien luonteesta. Teoriat eroavat etenkin siinä kuinka sodasta seuraavat hyödyt jakautuvat koko sisäryhmän ja hyökkäävien taistelijoiden kesken. Parochial Altrusim teorian mukaan sotiminen on ryhmän puolesta uhrautuvaa altruistista käyttäytymistä, kun taas Male Warrior ja Chimpanzee Model teorian mukaan, sotiminen on kehittynyt hyökkääjien parantuneiden yksityisten lisääntymishyötyjen seurauksena. Vaikka antropologien havainnot, biologiset lajien väliset vertailututkimukset sekä biologiset teoriat tukevat näkemystä yksilöllisten hyötyjen oleellisuudesta konfliktikäyttäytymiselle ja sotien evoluutiolle, niiden roolia ei ennen tutkimustani ollut kokeellisesti testattu. Havaitsin ulkoryhmään kohdistuvan konfliktikäyttäytymisen motivoituvan huomattavan paljon yksilölle koituvista itsekkäistä eduista, jopa oman sisäryhmän etujen kustannuksella. Lisäksi tulokset tuovat uutta tietoa osoittaessaan sekä miesten että naisten yleisen prososiaalisuuden (yhteistyötaipuvaisuuden) korreloivan ryhmärajat ylittävän prososiaalisuuden kanssa, mutta vain miehillä sama prososiaalisuus korreloi myös alttiuteen eskaloida ryhmien välistä konfliktia. Miesten prososiaalisuus osoittautui siis kaksiteräiseksi miekaksi, olosuhteista riippuen prososiaaliset miehet olivat valmiita yhteistyöhön tai konfliktiin muiden ryhmien kanssa. Yhdessä nämä tulokset viittaavat vallalla olevaa Parochial Altrusim teoriaa vastaan ja tukevat vähemmälle huomiolle jääneitä Male Warrior ja Chimpanzee Model teorioita, joiden mukaan ryhmien välisen konfliktin evolutiiviset juuret ovat ennen kaikkea prososiaalisille, yhteistyötaipuvaisille miehille voitokkaasta sodasta seuranneissa yksityisissä eduissa.

Neljännessä osatyössä esitin hypoteesin ankarien lastenkasvatusmenetelmien kulttuurievoluutiosta. Ankaralla lastenkasvatusmenetelmillä tarkoitan fyysistä ja henkistä kurinpitoa ja kaltoinkohtelua vanhempien toimesta. Ankarilla lastenkasvatusmenetelmillä on haitallisia psykososiaalisia ja -emotionaalisia vaikutuksia ja siksi ne pitäisi karsiutua kulttuureista. Kuitenkin kyseisenlaiset kasvatusmenetelmät ovat yhä erittäin yleisiä ympärimaailman lukuun ottamatta metsästäjä-keräilijäyhteisöjä. Hypoteesissani esitän ankaran lastenkasvatuksen vahvistavan useita psykologisia piirteitä, joiden on osoitettu edistävän ryhmän menestystä ryhmien välisissä konflikteissa. Ryhmien välisistä konflikteista seurannut kulttuurinen valintapaine kasvoi huomattavasti sen jälkeen kun yhteisöt siirtyivät metsästäjä-keräilijä yhteisöistä maatalouden myötä suurempiin ja kompleksisempiin yhteisöihin. Täten ankara lastenkohtelu on saattanut kasvattaa ryhmän valintaetua monille yksilölle koituvista kustannuksista huolimatta. Testasin hypoteesiani tutkimalla ankarien lasten kasvatusmenetelmien vaikutusta prososiaalisuuteen ja ryhmienväliseen hyökkäävyyteen, sillä näiden taipumusten esiintyminen etenkin yhtäaikaisesti pitäisi kasvattaa ryhmän menestymistä ryhmien välisessä konfliktissa. Havaitsin hypoteesiani tukevasti että ankara lastenkohtelu kasvatti sekä ryhmää auttavaa prososiaali-

suutta että hyökkäävyyttä, mutta ainoastaan miehillä. Täten tulokseni ja lukuisat hypoteesiani tukevat tutkimukset viittaavat siihen että ankarat lastenkasvatusmenetelmät ovat saattaneet levitä parantuneen sotamenestyksen seurauksena.

Kaiken kaikkiaan tulosteni perusteella ihmisen yhteistyö- ja konfliktikäyttäytymisen kehittymiseen on todennäköisesti vaikuttanut useat evolutiiviset mekanismit. Lisäksi kulttuuriset vaikutukset, etenkin lastenkasvatusmenelmät ovat merkittävät näiden käyttäytymispiirteiden psykologiselle kehittymiselle sekä ryhmien välisille suhteille ja menestymiselle konfliktitilanteissa.

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ORIGINAL PAPERS

I

HUMAN COOPERATION IN GROUPS: VARIATION BEGETS VARIATION

by

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Human cooperation in groups: variation begets variation

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Many experiments on human cooperation have revealed that individuals differ systematically in their tendency to cooperate with others. It has also been shown that individuals condition their behaviour on the overall cooperation level of their peers. Yet, little is known about how individuals respond to heterogeneity in cooperativeness in their neighbourhood. Here, we present an experimental study investigating whether and how people respond to heterogeneous behaviour in a public goods game. We find that a large majority of subjects does respond to heterogeneity in their group, but they respond in quite different ways. Most subjects contribute less to the public good when the contributions of their peers are more heterogeneous, but a substantial fraction of individuals consistently contributes more in this case. In addition, we find that individuals that respond positively to heterogeneity have a higher general cooperation tendency. The finding that social responsiveness occurs in different forms and is correlated with cooperativeness may have important implications for the outcome of cooperative interactions.

Scientists of various disciplines have since long been interested in cooperation[1–4]. For biologists, it is a major challenge to explain why natural selection sometimes favours behaviour that benefits other individuals (cooperation), especially when it is costly to perform[5–8]. The biological world is rife with examples of such behaviour (from birds and social insects to bacteria), and humans are no exception. In fact, human cooperation is in many ways more extreme than cooperation in most other animal species: we cooperate with non-related strangers and on enormous scales[9–11]. Not surprisingly, scholars from the social sciences also have a long tradition in studying cooperation[12–16].

Studies using a range of methods have consistently shown that there is considerable individual variation in human cooperative behaviour. This is true for the general propensity to cooperate (cooperation tendency)[14–17], but also for the ways people condition their cooperation on the cooperation of others (cooperation strategy)[18–21]. Importantly, the presence of those individual differences can significantly impact the outcomes of cooperative interactions in groups[19,22]. Recent theoretical studies have shown that the presence of even small amounts of variation in cooperative behaviour can be decisive for the evolution of cooperation[23–26]. Interestingly, also environmental variation in cooperation has been found to favour cooperative and forgiving strategies[27–30]. The success of cooperative and forgiving strategies in the presence of environmental variation stems from their ability to uphold profitable interactions even when partners mistakenly fail to cooperate, or when a cooperative act is mistakenly perceived as defection.

Given the prevalence of individual differences in cooperative behaviour, and the importance of variation for determining outcomes of cooperative interactions, it is surprising that little is known about how people condition their own cooperation on variation in cooperative behaviour in their social group. In studies designed to assess individuals' cooperation strategies, response to heterogeneity is often disregarded. Many of these studies are based on the public goods game (PGG), where individuals are grouped

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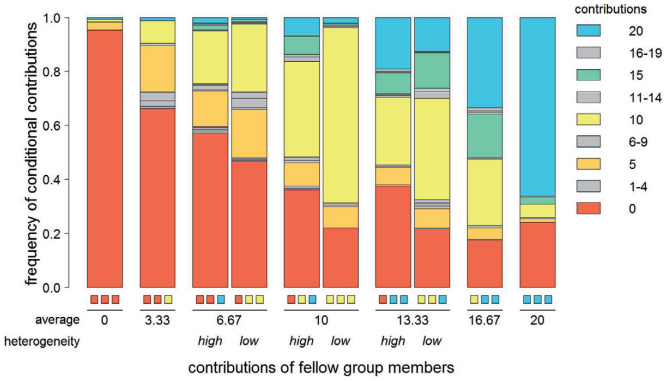

Figure 1. Contributions to the group project in response to various combinations of peer contributions. Each bar shows a breakdown of how subjects responded to a specific combination of contributions of the three other group members (indicated by the three coloured blocks under each bar). Bars are grouped together for cases that have the same average contribution of fellow group members, but where heterogeneity in peer contributions differs. Completely unresponsive individuals (contributing the same regardless of peer contributions) were omitted from the analysis (see Methods).

and endowed with a sum of money, and then have to decide how much of the money to contribute to an account that benefits all members of their group. In this set-up, the total earnings of the group increase with increasing group member contributions, but individuals maximize their earnings by contributing nothing. To get an idea of the cooperation strategies employed by different individuals, subjects are asked how much they would contribute given various hypothetical average contribution levels of their fellow group members[18,31]. Such studies generally find that a large proportion of individuals is willing to contribute about equally much (or slightly less) as the average contribution of their fellow group members (they are often classified as 'conditional cooperators'); others contribute nothing, regardless of the average peer contribution ('free-riders'); still others contribute most when the average cooperation level of their interaction partners is intermediate.

One might expect that people take this variation in cooperation strategies into account when making decisions on their own degree of cooperation. In fact, some studies[32–34] have reported that, on average, individuals tend to reduce their contribution to a public good if the contributions of their peers are more heterogeneous. However, it is not clear how this effect arises. Does the response to heterogeneity reflect a specific conditional strategy or a more general cautiousness in a variable environment? Do all individuals respond to heterogeneity in the same way, or are there consistent differences between individuals? If there are differences, how are they related to general cooperation tendency?

To answer these questions, we conducted an experiment that consisted of two parts. In the first part, subjects played ten rounds of a PGG in groups of four, where group composition changed in every round. In each round, subjects decided how to distribute an endowment of 20 points between their personal account and an account that benefitted all group members (see Methods for details). We interpret the average contribution of a subject to the group project in these ten rounds as a measure of the subject's general 'cooperation tendency'. In the second part, the same individuals decided how much they would contribute in a PGG, for ten hypothetical scenarios concerning the contributions of their fellow group members. In these scenarios, the hypothetical group member contributions were always either 0, 10 or 20 points, yielding a total of ten possible combinations of peer contributions. Six of these ten combinations were pairs of cases within which the average peer contribution was the same, but their heterogeneity was different. Comparing subjects' conditional contributions between these scenarios allowed us to investigate how subjects respond to heterogeneity in peer contributions.

Results

Figure 1 shows a detailed breakdown of the conditional contributions made in the second part of the experiment, for each combination of peer contributions. Overall, response contributions increased with peer contributions. If all fellow group members contributed nothing (leftmost bar), 95% of individuals also contributed nothing in response. Conversely, if all fellow group members contributed the maximum (rightmost bar), 72% of subjects also contributed the maximum in response. The grouped bars show pairs of scenarios where the average contribution of fellow group members is the same, but the heterogeneity in contributions differs. For example, the two middle bars (the 5th and 6th bar) show two cases where the average contribution is 10, but where the contributions are either heterogeneous (0, 10 and 20;

Peer contributions		Response contributions			
Mean	Heterogeneity	Mean	s.d.	% min	% max
6.67	*low*	4.32	4.61	41.7	0.5
	high	3.74	5.07	53.2	1.8
10.00	*low*	7.65	4.58	14.7	1.8
	high	6.90	6.20	30.3	6.9
13.33	*low*	9.42	6.32	14.2	13.3
	high	8.30	7.66	31.6	20.6

Table 1. Contribution to the group project in response to peer contributions differing in their mean and heterogeneity. The table shows averages, standard deviations, and percentage of minimum and maximum contributions (respectively 0 and 20). In each row, two situations are compared where the peer contributions were equal on average, but differed in heterogeneity (see Fig. 1).

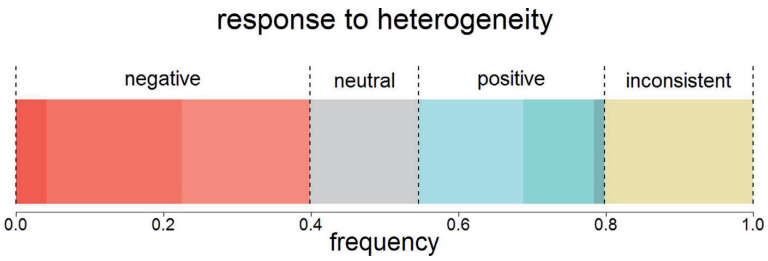

Figure 2. Response to heterogeneity in peer contributions. The bar shows a breakdown of subjects in how they responded to increased heterogeneity in peer contributions. We considered the three cases where the average of peer contributions was the same, but heterogeneity in peer contributions was different (grouped bars in Fig. 1). Subjects that contributed less when there was more heterogeneity in peer contributions in at least one of those cases, and never contributed more, were categorised as 'negative' responders to heterogeneity. Whether they contributed less in response to increasing heterogeneity in one, two, or all three cases is indicated with increasingly darker shading. 'Positive' responders to heterogeneity were classified similarly. If individuals contributed exactly the same for high and low heterogeneity in all three cases, they were classified as 'neutral' responders to heterogeneity. If individuals contributed less in some of the cases and more in others, they were classified as 'inconsistent'.

bar 5) or homogeneous (three times 10; bar 6). From now on, we will focus on these pairs of scenarios. For all three pairs, Table 1 systematically compares the low- and the high-heterogeneity case concerning the average contribution of the subjects, the standard deviation of these contributions, and the frequency of extreme contributions (both minimum and maximum).

On average, individuals tended to contribute less when there was more heterogeneity in peer contributions (linear mixed model with subject as random factor, $P < 0.001$; see Supplementary Information, section 3 for a detailed overview of statistical methods). This is in accordance with earlier studies[32–34]. In addition, we observe that in two of the three comparisons the variation in response contributions was higher in case of more heterogeneity in peer contributions (for averages 10 and 13.33, Brown-Forsythe test: $P < 0.001$; for average 6.67, Brown-Forsythe test: $P = 0.733$). Finally, subjects were more likely to make extreme contributions when there was more heterogeneity in peer contributions – this was the case for both contributing the minimal amount 0 (logistic generalized mixed model with subject as a random factor, $P = 0.001$) and the maximal amount 20 ($P < 0.001$). Generally speaking, more heterogeneity in peer contributions caused subjects to make more extreme contributions themselves.

Figure 2 reveals that individuals responded to heterogeneity in peer contributions in different ways. We classified subjects by comparing their contributions within each of the three pairs of scenarios that had the same average peer contribution, but different heterogeneity in peer contributions. If they contributed more in the cases with more heterogeneity, they were classified as 'positive' responders to heterogeneity, and if they contributed less, they were classified as 'negative' responders. If they contributed equally within all three comparisons, they were classified as 'neutral', and if they contributed more in case of high heterogeneity in some of the three comparisons, and less in others, they were classified as 'inconsistent'. In line with the finding that, on average, contributions were lower in case of more heterogeneity

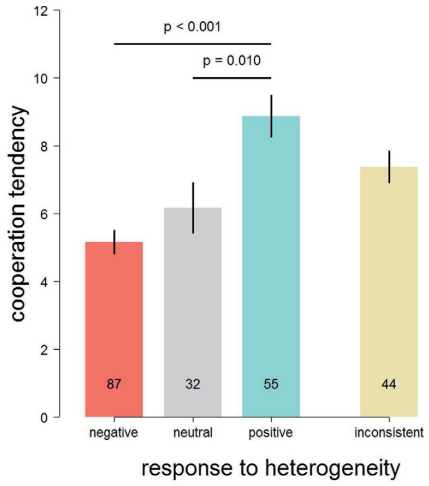

Figure 3. Response to heterogeneity in peer contributions is associated with cooperation tendency. Bars show the average and SEM of contributions over ten rounds of a public goods game, where group composition was randomised before every round, for negative, neutral, positive, and inconsistent responders to heterogeneity. Statistically significant differences between types are indicated (Tukey Honest Significant Differences), except for differences between inconsistent responders and any of the other groups. Numbers at the bottom of each bar indicate the number of subjects falling in this category.

(see Table 1), more subjects were classified as negative (39.9%) than positive (25.2%), but the fraction of positive individuals is substantial. Smaller fractions of individuals were neutral (14.7%) or inconsistent (20.2%) in their response to heterogeneity.

Figure 3 shows that there is a clear relation between the response to heterogeneity as measured in the second part of the experiment, and the general tendency to cooperate as determined in the first part. Specifically, average contributions in the first part were 72% higher for individuals that responded positively to heterogeneity when compared to individuals that responded negatively; individuals that had a neutral or inconsistent response to heterogeneity were in between. This association cannot be explained by 'spill-over' effects[18] between the two parts of the experiment; it is still observed when controlling for peer cooperation in the first part of the experiment (see Supplementary Information, section 3). Moreover, we still observe this clear difference when only considering the first interaction round of the first part, or the 'unconditional contribution' of the second part (see Methods) to determine general cooperation tendency. In these cases, contributions of individuals that positively responded to heterogeneity were respectively 50% and 40% higher than those of individuals that responded negatively; those differences were highly significant in both cases (See Supplementary Information, section 2 for graphic representations and details).

Discussion

The results of our experiment can be summarised in three points. First, we confirm earlier observations that when the contributions of fellow group members to a public good are more heterogeneous, people on average respond by contributing less. However, this is not the whole story; more heterogeneity in peer contributions also leads to more variable (and more extreme) contributions in response ('variation begets variation'). Second, we observe substantial individual differences in how people respond to the degree of heterogeneity in peer cooperation. Some individuals consistently contribute more when there is more heterogeneity, whereas others consistently contribute less. Smaller fractions were either neutral or inconsistent in their response to increased heterogeneity in peer cooperation. Third, we find a clear relation between general cooperation tendency and conditional responses to heterogeneity in peer contributions. Individuals that respond positively to heterogeneity in peer contributions tend to be more cooperative in a public goods game than individuals that respond negatively. Individuals that respond neutrally or inconsistently are intermediate in their cooperation tendency.

At first sight, it may seem that the classification of the individual variation that we made in our experiment (between positive, neutral, negative, and inconsistent individuals) does not reflect very clear differences between individuals. For example, an individual that was classified as 'positive' may in fact only have responded positively to heterogeneity in one of three comparisons, and neutrally in both others. Sure enough, our experiment should be considered as a first step in charting the individual

differences in how people respond to heterogeneity in the cooperative behaviour of their peers; further studies will be needed to come to a more comprehensive account. Having said this, we observed that even individuals that responded marginally positively (the lightest blue shade in Fig. 2) to heterogeneity have a significantly higher cooperation tendency than individuals that responded marginally negatively (the lightest red shade in Fig. 2; see Supplementary Information, section 1 for details). The fact that even small differences in response to heterogeneity are associated with large differences in general cooperation tendency suggests that these differences cannot simply be regarded as random noise. In this study, we found an association between self-assessed competitiveness and response to variation; this link could be more thoroughly investigated (for instance, by measuring competitiveness experimentally rather than through self-assessment). Associations with other factors, such as aspects of personality, may also be interesting to explore.

Individual variation is currently attracting much attention in all the behavioural sciences, including biology[25,35–37] (including cultural evolution research[21,38,39]), psychology and neuroscience[40–42], and economics[18,31,43]. Biologists have shown that consistent individual differences in behavioural tendencies often have an adaptive explanation, and are likely to emerge in the course of evolution under a broad range of circumstances[37,44]. Moreover, various theoretical models[24,45,46] show that the presence of consistent individual variation in social behaviour will induce the evolution of sensitivity and responsiveness to this variation. In line with the results reported here, these models predict that individuals differ consistently not only in their behaviour, but also in their response to the behaviour of others, and that both are correlated.

Our empirical results demonstrate that individuals vary not only in the degree of responsiveness, but also in the type of response to the social environment (i.e., there are positive and negative responders). This suggests that there exists a previously unrecognised dimension to social responsiveness. The observed link between the type of response and cooperation tendency can have important implications for the performance of cooperation strategies. For example, if cooperators typically assort together[47–49], a positive response to heterogeneity may help in maintaining cooperation by 'forgiving' occasional non-cooperation by a member of the group due to mistakes or temporary inability[27–30,50–52]. The types of responsiveness we observe might be related to personality characteristics, such as differences in 'lifestyle'. Theory predicts that evolution will often result in 'pace of life' syndromes, with individuals with a 'fast' and a 'slow' lifestyle coexisting in a population[44,53]. 'Fast' individuals are focused on short-term benefits, while 'slow' individuals are willing to take short-term losses if this is likely to result in longer-term benefits. One might speculate that cooperativeness and a positive response to variation are both facets of a slow lifestyle; 'slow' individuals are more cooperative, since they hope to elicit long-term cooperation, and they respond more positively to variation, since they interpret heterogeneity as an opportunity for longer-term cooperation rather than as a threat. Similar arguments may be used to interpret non-cooperativeness in a social dilemma and a negative response to variation as facets of a fast lifestyle. Formal evolutionary models have to be developed to check if these verbal arguments can be substantiated. Quite obviously, the implications of individual differences in type of responsiveness for the dynamics of social interactions and performance of cooperation strategies merit further empirical and theoretical scrutiny.

Methods

A total of 240 subjects (71% female, mostly students) participated in experimental sessions consisting of 16 subjects each, at the University of Groningen (the Netherlands). Participation was by informed consent, and the experimental setup was approved by the Sociological Laboratory of the University of Groningen. The experimental sessions were carried out in accordance with the approved guidelines. During the sessions (lasting approximately one hour), subjects made a number of simultaneous and anonymous decisions on computers. Subjects earned points (50 points = €1) with the decisions they made, and were paid accordingly in cash at the end of the session (mean payoff: €14.87±1.90; ranging from €10.60 to €19.30; subjects were unaware of the earnings of others). Subjects received written instructions, which were also read out loud by the experimenters at the start of each session (see Supplementary Information, section 5 for instructions). Each session consisted of two parts that were separately explained on the computer screen before they started, after which subjects filled out a short quiz to check their comprehension. This experiment was conducted in conjunction with another experiment; see Supplementary Information, section 4 for details. The experiment was run with the experimental software z-Tree[54] (code available upon request).

In the first part of the experiment, individuals played ten rounds of a PGG, in groups of four. Individuals were grouped randomly at the start of every round, and were made explicitly aware of this in the instructions before this part, as well as at the start of every new round. At the beginning of each round, subjects were allocated 20 points to distribute between a group project and their personal account. After all subjects had made their decision, the total contributions to the group project were doubled and divided equally among the group members (irrespective of their contributions), and subjects were shown their earnings (as well as the contributions and earnings of their fellow group members).

In the second part of the experiment, subjects were asked how much they would contribute (0–20 points) depending on the contributions of their fellow group members. We confronted them with ten hypothetical scenarios (on a single screen, in fixed order), where the contributions of their fellow group members were always 0, 10 or 20 points (see Fig. 1). Out of these ten scenarios, we pay particular attention to those pairs of cases that have the same average peer contribution, but differ in heterogeneity in

peer contributions. Comparing subjects' conditional contributions within these paired cases allowed us to determine how individuals respond to heterogeneity in peer contributions. In addition to the ten conditional contributions, each subject also entered one 'unconditional contribution' (where the choice was limited to 0, 10 or 20 points). This unconditional contribution was simply the contribution that individuals would make to the group project in case they did not know the contributions of their fellow group members. After this, one round of a PGG was played in randomly formed groups of four. From each group, three randomly chosen subjects automatically made their unconditional contribution, and the remaining subject made their corresponding conditional contribution. A total of 22 subjects (8.8%) contributed the same amount regardless of the peer contributions; all except one of these individuals were unconditional free-riders, contributing 0 for every scenario (the remaining individual was an unconditional cooperator, always contributing 20). Under our classification, these individuals would have been labelled as neutral responders to variation, but they are in fact completely unresponsive to peer contributions altogether. Therefore, these individuals were excluded from the analysis. Their exclusion did not affect the main results presented in this paper (see Supplementary Information, section 3).

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Author Contributions

P.V.D.B., L.M., J.J., M.P. and F.J.W. designed the experiment; P.v.d.B., L.M. and J.J. carried out the experiment; P.v.d.B., L.M., J.J., M.P. and F.J.W. wrote the paper.

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by

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Assortment, but not knowledge of assortment, affects cooperation and individual success in human groups

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Abstract

The success or failure of human collective action often depends on the cooperation tendencies of individuals in groups, and on the information that individuals have about each other's cooperativeness. However, it is unclear whether these two factors have an interactive effect on cooperation dynamics. Using a decision-making experiment, we confirm that groups comprising individuals with higher cooperation tendencies cooperate at a higher level than groups comprising individuals with low cooperation tendencies. Moreover, assorting individuals with similar cooperation tendency together affected behaviour so that the most cooperative individuals tended to cooperate more and the least cooperative individuals cooperated less, compared to their behaviour in randomly formed groups. In line with predictions of evolutionary models of cooperation, there was a strong positive association between individuals' cooperation tendency and success when groups were formed assortatively, whereas such association did not exist when groups were formed randomly. Surprisingly, information about group members' cooperativeness in assorted groups had no effect on cooperation levels. We discuss potential explanations for why information about cooperativeness of others may be disregarded in certain circumstances.

Introduction

The evolution of cooperation has been challenging to explain because free-riding individuals, who reap the benefits of cooperation without contributing to its costs, will often achieve higher payoffs than cooperators [1,2]. Explanations of human cooperation have largely been based on reciprocity, in which cooperation is directed to those who are expected to cooperate in kind. Reciprocity relies on information about the previous behaviour of interaction partners [3–6].

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An individual can gather information about the cooperativeness of others through personal interaction [7,8], or through third parties [9,10]. Many experiments have shown that humans mainly cooperate with those who have cooperated with them in the past [11,12], or with those who have been cooperative in interactions with third parties [12–15].

Gathering information on others' cooperativeness is critical for social decision making: studies from a range of disciplines have shown that there are individual differences in human cooperation tendencies [12,16–22], and these tendencies are consistent across time and context [19,21,23–25]. Evolutionary theories predict that this variation in human cooperativeness plays an important role in the performance of groups [26,27]. Empirical evidence, by and large, confirms these predictions: when individuals with similar cooperation tendencies group together through positive assortment, cooperators may thrive as they can enjoy the benefits of cooperation without being exploited by less cooperative individuals [17,21,28,29].

Despite the importance of assortment and information about partner cooperativeness for the evolution of human cooperation, it remains poorly understood how these two factors interact. De Oliveira et al. [30] found that in assorted groups, cooperative decisions of both the most and the least cooperative individuals were insensitive to information about the cooperation tendencies of their group members. In addition, work by Gächter and Thöni [31,32] suggests that information on the similarity of group members' past cooperative decisions has no effect on overall cooperation level. As these findings contrast with numerous studies showing the substantial effect of information on others past cooperativeness (e.g. 11–14), additional experiments are needed to unravel the interplay of information and assortment.

Here we study how assorting individuals with similar cooperation tendencies to groups, and information about group members' cooperativeness in assorted groups, affect cooperation and the success of individuals in a public goods game. Specifically, we conducted a decision-making experiment to test three main hypotheses: i) assortment leads to differences in the level of cooperation across groups comprising different types of individuals; ii) assortment leads to a positive association between individual cooperation tendency and earnings in the game, whereas such an association should not exist in the absence of assortment; iii) providing information on the nature of assortment amplifies the differences in cooperation levels between assorted groups.

These hypotheses are based on previous findings that individual differences in cooperativeness are consistent [19,23] and that individuals tend to adjust their cooperation to the anticipated cooperation of their group members as suggested by models of direct and indirect reciprocity (e.g. 5,14,16). Thus, as cooperation depends on the anticipated cooperation of others, informing the most cooperative individuals that they will interact only with other highly cooperative individuals should fuel trust and cooperation through anticipated reciprocity. Similarly, informing the least cooperative individuals that they will interact with other non-cooperators should create anticipation of defection, leading to lower levels of cooperation.

We show that assorting individuals into groups based on individual cooperativeness had substantial effects on the level of cooperation within groups, partly because assortment seemed to make more cooperative individuals cooperate more and the least cooperative individuals cooperate less, compared to a random grouping setting. Further, we found a consistent positive association between individuals' cooperation tendency and success when groups were formed assortatively, but not when groups were formed randomly. Surprisingly, however, we found that individuals were insensitive to the provided information on the composition of their group.

Methods

To study the effects of assortment and information about assortment on cooperation in groups, we conducted an experiment based on the public goods game (PGG). The PGG reflects a situation in which temptation to free-ride makes it difficult to maintain individually costly cooperation. In a linear PGG, the average payoff per group member is maximized if all group members cooperate, that is if everybody contributes maximally to the public good. Yet, any personal contribution decreases the net payoff to the individual group member. Therefore, in each single round of the PGG, individual payoff is maximised by contributing nothing and profiting from the contributions of others.

In each of our experimental sessions, sixteen subjects were arranged in groups of four, in which they repeatedly played a PGG. At the beginning of each round, each subject was allocated 20 points to distribute between a group project and their personal account. After all four subjects had made their decisions, the total contributions to the group project were doubled and divided equally among the group members, irrespective of their contributions. After each round, subjects were presented with the anonymized contributions and earnings of each of their fellow group members.

The experimental setup consisted of two stages. In Stage 1, subjects interacted over ten rounds of a PGG, with group composition randomly changing after every round. This means that subjects essentially played a series of one-shot PGGs. In this setup, there are no possibilities for strategic cooperation or build-up of reputation, and contributing nothing is the dominant strategy. Accordingly, we interpret the average contribution level (on the range 0–20) over all rounds of Stage 1 as a measure of a subject's cooperation tendency. Subjects in each session were classified to four 'cooperative tiers' based on their behaviour in Stage 1, with four subjects with the highest cooperation tendency belonging to tier 1, the four second most cooperative to tier 2, the four third most to tier 3, and the four least cooperative to tier 4. The subjects did not know that Stage 1 was designed to measure their cooperation tendency, nor were they aware of the nature of Stage 2 before it began. In the beginning of the experiment, the subjects were only informed that the study would continue after Stage 1 and that they would receive new instructions on their computer screen after completing Stage 1.

Stage 2 was designed to study if assorting individuals with similar cooperation tendencies affects cooperation and if information about previous cooperativeness of group members affects cooperation in assorted groups. In Stage 2, subjects interacted additional 15 rounds of the PGG, this time with group composition remaining fixed over all rounds. We implemented three treatments (Fig 1): Informed Assortment (IA), Uninformed Assortment (UA) and Uninformed Random grouping (UR). To test if assortment affects cooperation of individuals from different cooperative tiers we compared treatments UA and UR, and to test if information about assortment affects cooperation in assorted groups we compared treatments IA and UA.

In treatments IA and UA, subjects were assorted into groups based on their cooperativeness in Stage 1 so that individuals from the same cooperative tier in Stage 1 were grouped together. In treatment IA, subjects were informed at the beginning of Stage 2 about the assortment procedure and to which cooperative tier they belonged (e.g. "Now all players are ranked and grouped according to their contributions in the first ten rounds. The player that contributed most is ranked #1 and the player contributed the least is ranked #16. You are in the group of players ranked 13–16"). In treatment UA, the subjects were informed that the groups were now fixed, but they were not informed about the assortment procedure. In treatment UR, groups were formed randomly with respect to the cooperative tier in Stage 1, and the subjects were only informed that the groups were now fixed.

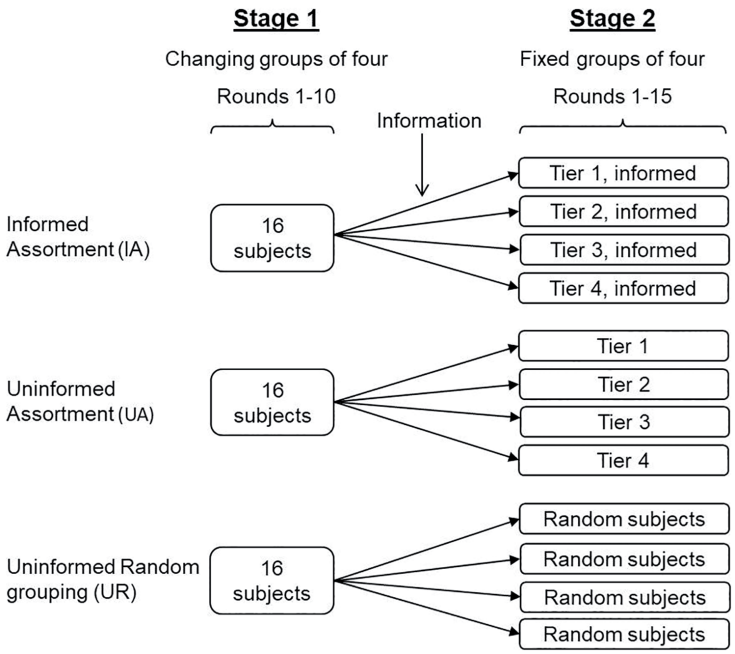

Fig 1. Experimental procedure. Subjects played a total of 25 rounds of the PGG in three experimental treatments: Informed Assortment (IA), Uninformed Assortment (UA) and Uninformed Random grouping (UR). Each treatment was replicated 5 times. Each of the 15 replicates was run in a session involving 16 subjects. In Stage 1, the subjects played 10 rounds of the PGG in groups of four where group composition changed randomly after each round. After Stage 1, all subjects were informed that the groups were fixed for the next 15 rounds of PGG of Stage 2. In the IA and UA treatments the four fixed groups were formed by assorting the 16 subjects according to their mean contributions in the 10 rounds of Stage 1. Only in the IA treatment, subjects received the additional information that the groups were assorted according to cooperativeness, and to which cooperative tier they were allocated. In the UR treatment, the four fixed groups were formed at random.

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The experiment consisted of fifteen sessions, with five sessions for each of the three treatments (sixteen subjects in each session, total N = 240; 71% females (50–94% per session), aged 19–33 years, mostly university students across variety of disciplines, 68% had earlier experience with economic experiments. The level of cooperation in the first round did not differ between male and female subjects (ANOVA: $F_{1,190} = 0.123$, $p = 0.726$) and was not impacted by earlier experience with participation in economic experiments ($F_{1,190} = 2.367$, $p = 0.126$). Subjects gave written informed consent before participating. The experimental setup was approved by the Sociological Laboratory of the University of Groningen. We followed the guidelines established by the VSNU Code of Conduct for Scientific Practice when running experimental sessions.

Instructions for the experiment were read out loud by the experimenter at the start of each session. Instructions for the two separate stages, including the number of rounds, were explained to subjects on their computer screens at the beginning of each stage. Before the start of each stage, subjects filled out a short quiz to check their comprehension. Sessions lasted about one hour and subjects earned on average €14.87 (ranging from €10.56 to €18.35).

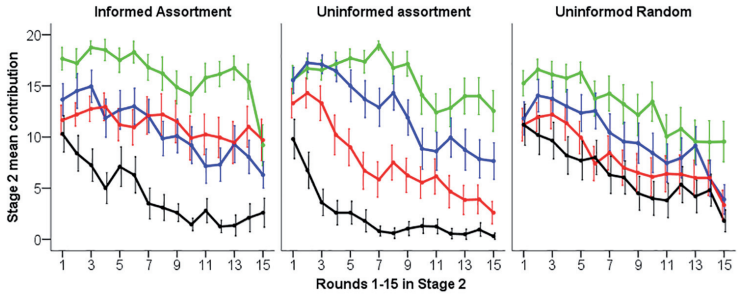

Fig 2. Cooperation by subjects from different cooperative tiers in assorted and random groups in Stage 2. In treatments Informed Assortment and Uninformed Assortment, groups were formed by assorting subjects according to their cooperation tendencies measured in Stage 1. In the Uninformed Random grouping treatment, groups were formed randomly. Note that while in treatments Informed Assortment and Uninformed Assortment subjects in a group belong to the same cooperative tier, in the Uninformed Random treatment groups comprised individuals from different cooperative tiers. Lines indicate mean contribution of individuals belonging to the same cooperative tier across five replicate sessions (green: tier 1, blue: tier 2, red: tier 3, black: tier 4). Error bars indicate ±1 s.e of individual contributions. See Table 1 for statistical analysis of effects of information and assortment on contribution levels.

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Subjects were paid in cash at the end of the experiment and were unaware of the earnings of others. The experiment was programmed and conducted with the experiment software z-Tree [33] (code available upon request from the first author). All statistical analyses were conducted with SPSS (v. 20.0.0.2) and R (v. 3.1.3).

Results

As expected, when individuals with similar cooperation tendencies were grouped together, there were strong differences in the level of cooperation between groups, depending on the cooperative tier of the subjects (Fig 2 treatments IA and UA, Table 1). In Stage 2, cooperation

Table 1. Anova based on Linear Mixed Models (LMMs) fitted to contributions in Stage 2, using 'subject nested in group' as a random effect. The model estimates are given in the Supporting Information (S1 Table). The analysis includes a comparison of (i) Uninformed Assortment and Uninformed Random grouping to study the effect of assortment and (ii) a comparison of Informed Assortment and Uninformed Assortment to study the effect of information. The factors "Assortment" and "Information" compare treatments. 'Round' is the round number (1–15) to account for time trends in cooperation levels in Stage 2 (Fig 2) and 'Cooperative tier' is a factor reflecting individuals' tier rank (1, 2, 3 or 4) based on cooperation in Stage 1. The significant interaction between 'Assortment' and 'Cooperative tier' results from larger differences between individuals with the highest and lowest cooperation tendencies in assortment compared to the random grouping treatment (i.e., assortment amplifies existing cooperation tendencies). Surprisingly, the effect of 'Information' is not significant. In each treatment, there were 80 subjects (five sessions with 16 subjects in each session).

Uninformed Assortment vs Uninformed Random grouping	**SS**	**MS**	**df**	**F**	**p**
Assortment	0.10	0.10	1	0.00	0.96
Round	14876.50	14876.50	1	572.74	< 0.01
Cooperative tier	755.80	251.90	3	9.70	< 0.01
Assortment * Cooperative tier	261.40	87.10	3	3.36	0.03
Informed Assortment vs Uninformed Random grouping	**SS**	**MS**	**df**	**F**	**p**
Information	20.50	20.50	1	0.68	0.42
Round	11400.90	11400.90	1	377.34	< 0.01
Cooperative tier	1283.60	427.90	3	14.16	< 0.01
Information * Cooperative tier	60.80	20.30	3	0.67	0.58

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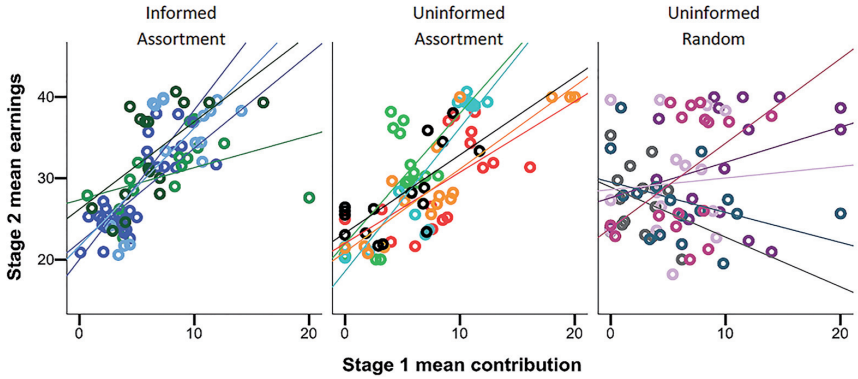

Fig 3. Association between cooperativeness and earnings. The relationship between individual mean contribution in Stage 1 (measuring cooperation tendency) and mean earnings in Stage 2 (measuring success) for each of the three treatments. Coloured dots indicate individuals from each session (each session comprising 16 individuals) and lines indicate linear regressions for each session.

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levels in assorted groups corresponded to the 'cooperative tiers' assigned to individuals in Stage 1 (with tier 1 having the highest cooperation level, followed by 2, 3 and then 4).

As a consequence of the between-tier differences in cooperation levels in assorted groups (treatments UA and IA), there was a positive association between individual cooperation tendency measured in Stage 1 and earnings in Stage 2 (Fig 3). However, such an association was not observed when groups were formed randomly (treatment UR). The association between cooperation tendency and earnings was quantified by linear regression coefficient of earnings in Stage 2 on mean contributions in Stage 1 for each experimental session ($\beta_{\text{Treatment}}$ = mean regression coefficient, lower and upper 95% confidence limits in parentheses: $\beta_{\text{IA}} = 1.78$ (0.78, 2.78); $\beta_{\text{UA}} = 1.88$ (1.22, 2.64); $\beta_{\text{UR}} = 0.19$ (-1.03, 1.41)). The regression coefficients differed significantly between the treatments (ANOVA: $F_{2,\ 14} = 6.70$, $p = 0.01$), and a Tukey test revealed that the coefficients in the random grouping treatment differed significantly from those in both assortment treatments (UR vs IA: $p = 0.024$, UR vs UA: $p = 0.018$).

Moreover, assortment modulated the cooperative behaviour of individuals. As can be seen in Figs 2 and 4, the differences in the level of cooperation of individuals belonging to different cooperative tiers were larger when groups were formed by assortment than when they were formed at random. This result is corroborated by a statistically significant interaction between the effects of assortment and cooperative tier on mean contributions in Stage 2 (Table 1; $p = 0.03$). The strongest effect of assortment on cooperation was observed among the least cooperative individuals (tier 4; see Fig 4).

However, contrary to our expectations, informing individuals about the assortment procedure and the cooperativeness of fellow group members did not affect overall or per-tier levels of cooperation in assorted groups (Table 1: comparison between treatments UA and IA; 'Information' and interaction between 'Information' and 'Cooperative tier' are not significantly different from zero). In all tiers, cooperation decreased over time (Fig 2).

In order to explicitly test if information on the assortment procedure affected cooperation immediately after this information was received, we compared mean contributions in the first round of Stage 2 in each cooperative tier in treatment UA with those in treatment IA

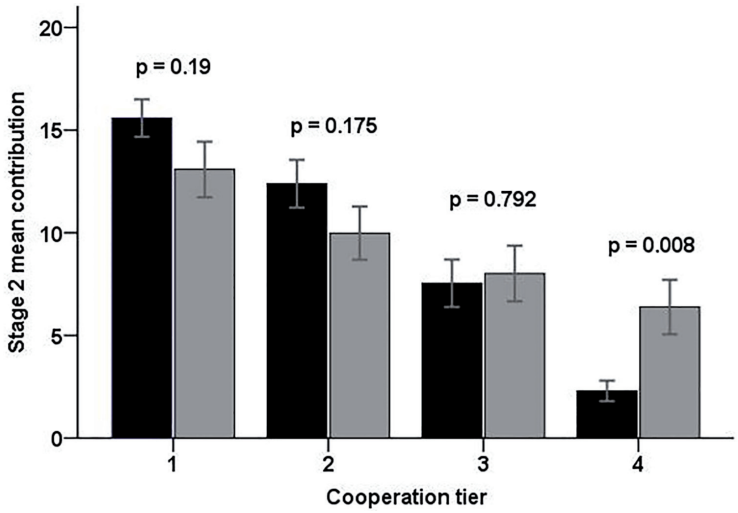

Fig 4. Effect of assortment on cooperation for the four cooperative tiers. Black bars represent the individuals in the Uninformed Assortment treatment and grey bars represent the individuals in the Uninformed Random treatment. Significance values refer to independent sample t-tests (not assuming equal variances) comparing contributions within each cooperative tier. Error bars indicate ±1 s.e.

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(Table 2). However, even in this restricted case, information on cooperativeness had no effect on the cooperation of any tier.

Discussion

In line with earlier studies [28,29,34], we found that when individuals are assorted to groups based on their cooperativeness, groups comprising more cooperative individuals are able to maintain higher levels of cooperation than groups comprising less cooperative individuals. However, as the level of cooperation slightly declined even in the most cooperative assorted groups, experiments with even more interaction rounds are needed to determine if differences in cooperation are maintained in the long run. We also demonstrate that in assorted groups, differences in the level of cooperation resulted in a consistent positive association between individual cooperation tendency and success. In contrast, when groups were formed

Table 2. Comparison of individual contributions in the first round of Stage 2 between Informed Assortment (IA) and Uninformed Assortment (UA). For each cooperative tier, we show the mean and standard error of individual contributions pooled over the five replicates. The group identity is not included in the analysis because the decisions of subjects in a group can be considered independent in the first round of Stage 2. The average contribution does not differ significantly between treatments in any of the four tiers (independent-samples t-test).

	Informed Assortment (IA)		Uninformed Assortment (UA)			
Cooperative tier	**mean**	**s.e.**	**mean**	**s.e.**	**t_{38}**	**p**
1st	17.65	1.10	15.60	1.38	1.16	0.25
2nd	13.65	1.57	15.55	1.26	-0.94	0.35
3rd	11.65	1.44	13.30	1.43	-0.81	0.42
4th	10.30	1.77	9.80	1.92	0.19	0.85

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randomly, there was no consistent association between individual cooperation tendency and success, as in the study by Kurzban and Houser [19]. These results support evolutionary theories holding that positive assortment is important for the success of cooperation [26,27].

Interestingly, we find that assortment influenced cooperation so that the individuals with the highest cooperation tendencies were inclined to cooperate even more when assorted with other cooperators, and the individuals with the lowest cooperation tendencies cooperated at an even lower level when grouped with other non-cooperators, in comparison to the situation where groups were formed randomly with respect to subjects' cooperation tendencies. This finding is in line with results of Van den Berg et al. [22], who found that individuals with lowest cooperation tendencies are likely to follow the example of the least cooperative behaviour in a group, whereas the most cooperative individuals tended to follow the example of more cooperative behaviour. These different responses to the behaviour of others may partly explain the strong differences in levels of cooperation among different cooperative tiers in the assorted groups.

Contrary to our expectations, information about assortment and cooperativeness of fellow group members did not affect the level of cooperation or the success of individuals with different cooperation tendencies. The provided information did not influence individual cooperative decisions of individuals from any cooperative tier even in the first round of Stage 2, immediately after the information was received (Table 2). Our result is in line with Gächter and Thöni (2011), who found no effect of knowledge of being grouped with "like-minded" cooperators on mean cooperation. Our result is also in line with De Oliveira et al. (30), who found that providing information about the heterogeneity of cooperative types (conditional cooperators and selfish types) within groups did not affect cooperation in either homogenous or heterogeneous groups. Our study differed from De Oliveira et al.'s (30) in three main respects: i) the information given (previous cooperativeness and assortment vs. variation in cooperative type), ii) in composition of groups (whole population with homogenous groups of cooperative tiers vs. population subset of selfish and conditional cooperator types in heterogeneous and homogeneous groups) and in iii) group size (4 instead of 3). Even so, both studies arrive at similar conclusions, suggesting that our findings do not reflect specifics of the experimental implementation.

Our finding that information concerning the previous behaviour of group members has no effect on cooperation seems surprising in view of numerous other studies stressing the importance of such information for cooperative decision making (e.g. 6,8,9,11). One possible reason why information about past cooperation did not have an effect in our study may be connected to the timing of information provision. As in the study of de Oliveira et al. [30], also we provided information about group composition at the beginning of a new interaction stage. At the beginning of a new interaction stage, people tend to return to their original levels of cooperation, even after experiencing the collapse of cooperation in previous interactions, a phenomenon known as 'restart effect' [35,36]. These previous findings, together with our results, suggest that people neglect information about the cooperativeness of others from previous stages, or at least they are not sensitive to this information when a new stage begins.

Attempts to signal one's cooperativeness at the start of new series of interactions may give rise to such restart effects [37]. Evolutionary models based on the handicap principle [38] suggest that such costly signaling can function as the basis for partner choice, enabling cooperators to assort and form new successful cooperative interactions [37,39–41]. Less cooperative individuals could also benefit from such signaling, as it is in their interest to be part of a cooperative group. Another mechanism that may have contributed similar cooperation levels in informed and uninformed assorted groups is the so-called False Consensus Effect [42,43], which states that people tend to deem their own behaviour common and appropriate, and

accordingly believe that others will behave in a similar way. If this were the case in our experiment, then subjects in our Uninformed Assortment treatment already believed that others were similar to themselves and information provided in our Informed Assortment treatment would only have confirmed pre-existing beliefs.

To conclude, our experiment showed that assorting individuals into groups based on varying individual cooperation tendencies have a substantial effect on groups' ability to achieve cooperation. This was partially caused by assortment amplifying individual differences in cooperation, particularly due to the collapse of cooperation in groups comprising only individuals with lowest cooperation tendencies. Further, assortment had significant effects on the earnings of individuals: cooperators outperformed non-cooperators in the presence of assortment, but not when grouping was random. Surprisingly, however, individuals by all cooperation tiers were insensitive to the provided information on group composition, suggesting that humans are facultative users of potentially critical information.

Supporting information

S1 Table. Determinants of cooperation in fixed groups. Both models present estimates of a Linear Mixed Model fit to individual contributions in stage 2, with 'subject nested in group' as a random effect. Model 1 focuses on the effects of assortment by comparing the Uniformed Assortment and the Uniformed Random treatments. 'Uninformed Random' and 'tier 4' are the baseline categories. Model 2 focuses on the effects of information about assortment by comparing the Informed Assortment and Uninformed Assortment treatments. 'Uninformed Assortment' lsquo;and 'tier 4' are the baseline categories. Significance codes: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.
(DOCX)

S1 Raw Data.
(TXT)

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III

INTERGROUP CONFLICT: A BATTLEFIELD OF PROSOCIAL MALES IN THE CHASE FOR PRIVATE GOODS

by

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Abstract

Scientists across disciplines have explored the roots of violent intergroup conflict for centuries. Evolutionary models that explain intergroup conflict in humans differ substantially in their assumptions about how the benefits of successful attacks are divided within the group. Parochial Altruism (PA) models treat these benefits as public goods (e.g. territorial gains) whereas the Male Warrior Hypothesis (MWH) and the Chimpanzee Model (CM) treat benefits as private goods (e.g. increased access to mates and boosted status for warriors). Here, we report the results of an experiment designed to test the core assumptions of these models. Firstly, we tested whether attacking out-groups were motivated by accruing public or private goods. We found that subjects attacked other groups via both public and private good options, but against the predictions of PA they were considerably ready to disregard the production of socially beneficial public goods in order to seek personal benefits. Second, we tested the premise of PA that parochial prosociality toward the in-group is associated with a greater tendency to attack out-groups. We found that contributions to attack out-groups were positively associated with prosociality toward the in-group for males, along the lines of PA. However, against the premises of PA, we found that attacking out-groups was also positively associated with prosociality toward them and that attack contributions decreased with increasing parochialism. These results indicate that parochialism is not necessary for male aggression. Further, even though in-group prosociality was positively associated with attacking out-groups for males, it was also associated with out-group prosociality in both genders. Our results thereby indicate that male prosociality is a double-edged sword in the sense that it can promote social valuation across group boundaries, but also allows in-group males to cooperate at the expense of out-groups. Overall, our results partly contrast with the premises and predictions of the Parochial Altruism Model but fit closer with the Chimpanzee Model and Male Warrior Hypothesis. Thus, motivations for private goods may have played a greater role in the evolution of human intergroup conflict than often considered, and warfare might have been evolutionarily beneficial for cooperative males in the pursuit of private goods.

Keywords: Public goods, Private goods, Intergroup conflict, Parochial Altruism, Social Value orientation, Prosociality.

Introduction

The roots of human intergroup conflict have been explored by scientists and philosophers for centuries' (Darwin 1873; Allen *et al.* 2016; Richerson *et al.* 2016). Despite controversy among anthropologists (Fry and Söderberg 2013; Glowacki *et al.* 2017), accumulating evidence across disciplines implies that intergroup conflicts are part of our biological heritage and have likely caused considerable evolutionary selection pressure (Wrangham and Glowacki 2012; McDonald *et al.* 2012; Rusch 2014; Gat 2015; Gómez *et al.* 2016). However, intergroup conflict still holds an evolutionary mystery: why do individuals voluntarily (as is often the case in forager societies) participate in risky endeavors that aim to kill members of neighboring groups (Wrangham 1999; Bowles 2009; Glowacki and Wrangham 2013; Gat 2015)?

Several evolutionary models have shown that motivations to engage in intergroup conflict can evolve despite individual costs (Rusch 2014). This can occur when the benefits from victory are public goods, like territorial gains and resources that enhance the reproduction of all in-group members. But it can also occur when the benefits are private goods, like loot, status and increased reproductive access for individual warriors. Group selection models like Parochial Altruism (PA; Choi and Bowles 2007; Smirnov et al. 2007; García and van den Bergh 2011; Bowles 2006) focus on public goods. They frame attacks on out-groups as self-sacrificial, altruistic actions, in which warriors are ready to bear substantial costs while the benefits accrue to all in-group members. When successful warriors can gain additional private goods in these models, the tendency for embarking upon intergroup conflicts evolves even more readily (Choi and Bowles 2007; Lehmann and Feldman 2008; Rusch 2014). In contrast, the Chimpanzee Model (CM; Wrangham and Glowacki 2012; Wrangham 1999) and the Male Warrior Hypothesis (MWH; Van Vugt et al. 2007; McDonald et al. 2012) focus on private goods. They view the cooperative killing of out-group members as adaptive and likely to evolve whenever it can be done safely enough such that private benefits exceed individual risks (see also "risk contract" theory by Tooby and Cosmides 1988). As opposed to PA models, the CM and the MWH suggest that cooperative intergroup fighting is mutually beneficial for warriors in the longer run. That is, it is maximizes individual fitness and this is sufficient to explain intergroup conflict, rendering the public goods created through warring mere by-products (Rusch 2014).

In line with CM and MWH, anthropological evidence indicates that intergroup conflicts are motivated by the prospect of gaining private goods like loot (Manson and Wrangham 1991; Glowacki and Wrangham 2013), reproductive access to out-group females (Manson and Wrangham 1991; Gat 2000; Kohler and Turner 2006; Glowacki and Wrangham 2013; Walker and Bailey 2013) and status as a distinguished warrior (Chagnon 1988; Lee 2007; Rusch *et al.* 2014). On the other hand, the production of public goods has not been found to motivate intergroup conflicts in small-scale societies and thus do not support PA models (for an overview see Glowacki and Wrangham, 2013).

Similarly, evidence from nonhuman animals indicates that contributions to intergroup conflict are often sensitive to direct fitness benefits (Rusch 2014). Yet despite anthropological evidence highlighting the motivational role of private goods alongside their biological relevancy (Van Vugt *et al.* 2007; McDonald *et al.* 2012; Rusch and Gavrilets 2017), their effects in the context of intergroup conflict have not been experimentally addressed.

In order to test the validity of evolutionary models on human intergroup conflict, we conducted a decision-making experiment to assess whether behavior follows the predictions and premises of PA using CM/MWH as a more parsimonious alternative explanation. In particular, we tested if attacking (taking money from) an out-group is motivated by the production of public goods in spite of the possibility for private goods, as predicted by PA. In addition, we tested the controversial premise of PA (Cashdan 2001; Thielmann and Böhm 2016; Yamagishi and Mifune 2016), in that contributions to intergroup conflict are associated with i) prosociality toward an in-group, ii) spite toward out-groups and iii) elevated in-group bias.

Methods

Experimental Procedure

Our experiment consisted of three parts, in which subjects made decisions with monetary outcomes for themselves and other participants. Parts One and Two were played in fixed groups of four that were randomly paired with each other. Part One assessed individual Social Value Orientations using the slider method (SVO, Murphy et al. 2011). SVO has been defined as "the weights people assign to their own and others' outcomes in situations of interdependence" (Balliet et al. 2009, p. 533). It has been linked to behavior in intergroup conflict (Thielmann and Böhm 2016) and cooperation (Balliet *et al.* 2009; Melamed *et al.* 2017). This method asks individuals to allocate resources between themselves and a social partner in six different allocation situations. Participants' choices in these six tasks are then mapped onto an angle measure of prosociality, i.e. a continuous scale ranging across competitive (maximizing payoff difference), individualistic (maximizing own payoff), prosocial (maximizing mutual payoffs) and altruistic (maximizing other's payoff) orientations. Our approach differed from the standard method by replacing the single random social partner first with three in-group members (ISVO) and then with three out-group members (OSVO), while keeping the monetary shares identical. Part Three assessed subjects' Standard Social Value Orientation (SSVO, Murphy, Ackermann, and Handgraaf, 2011). This was done in order to connect the new prosociality measures of ISVO and OSVO with the literature.

Part Two assessed whether decisions to attack out-groups were motivated by public or private goods. For this, we allocated $5 USD to each individual and allowed them to freely distribute these funds between 'Account A' (the Attack Account) and a 'Private Account'. The subject would keep any money in their Private Account, but could receive returns from investments to the Attack

Account at a cost to the out-group (hereafter 'attacking'). To successfully attack the out-group, the sum of all individual contributions to the Attack Account had to exceed the 'defense level' of the out-group. Each dollar that exceeded the defense level reduced $2 from the out-group ($0.50 per member). If the value of the Attack Account did not exceed the defense level, then these contributions were lost. Subjects made a series of five attack decisions across different defense levels of the partner group ($0, $1-5, $6-10, $11-15, $15-20).

We conducted Part Two with three independent treatments (see Table 1 for illustrations of the pay-offs). In the Public Good treatment, the benefits from attacking were divided equally among all in-group members irrespective of how much they contributed to the attack. Specifically, each dollar contributed to attacking that exceeded defense yielded $0.50 to each of the four in-group members ($2 to the group). This payoff structure is identical to that used in the well-established intergroup prisoner's dilemma game (IPD; Bornstein 1992, as described in Thielmann and Böhm 2016) and faces subjects with a typical cooperative dilemma in which contributing is individually costly (minus $0.50) but group beneficial. In the Private Good treatment, each dollar contributed to a successful attack yielded $1.50 to the contributor and nothing to others. Thus it was individually beneficial, yielding a $0.50 gain. The remaining $0.50 from the $2 deducted from the out-group was lost as an 'efficiency cost'. In the Trade-off treatment, subjects had options for both Public and Private Attack Accounts. As the Public attack option is more efficient than the Private attack (net $1 for group vs. $0.50 for self), but individually costly if others do not equally attack, subjects faced a social dilemma between their own interests and those of their group.

Subjects were then instructed that group roles were now reversed and they may be at risk of losing money to the out-group. Here we allocated each individual $10 to their Private Account (the maximum they can lose to an attack), from which they could invest a maximum of $5 (full investment of $5 from all group members will match a full attack) to 'Account G' (the Defense Account). Each dollar contributed to the Defense Account protected the whole group at a total value of $2 ($0.50 for each individual) and thus were public goods. Any investments over the summed value of the other group's Attack Account were lost.

Through use of the different treatments, we tested the predictions of PA by Choi and Bowles (2007), which assumes that the motivation to attack is the altruistic production of public goods for the in-group. Thus, (i) attack contributions to the Public Good Account should be significantly larger than contributions to the Private Good Account in the Trade-off treatment; and (ii) there should be no significant difference in contributions to the Public Good Accounts between singular and trade-off treatments, as the possibility to gain less efficient private goods in the trade-off should not diminish motivations to acquire more efficient public goods.

We conducted the experiment using Amazon Mechanical Turk (Buhrmester *et al.* 2011) with 192 USA residents (98 males and 94 females, average age 36). For each individual, we randomly selected one decision from

the 24 involved in the experiment to calculate their monetary payoff. Participation was by informed consent. We gave individuals full information of the rules at the beginning of each part. Then, comprehension questions had to be answered correctly to be able to proceed. In order to strengthen group identification, we emphasized the nature of fixed groupings for Parts One and Two in the instructions. Full instructions for the experiment can be found in the supplementary materials.

Statistical analysis

We analyzed genders separately because males and females have likely experienced different adaptive challenges regarding intergroup conflicts (Van Vugt *et al.* 2007; McDonald *et al.* 2012; Rusch 2014). Indeed, gender differences related to behavior in intergroup conflict have been repeatedly observed (e.g. McDonald *et al.* 2012; Van Vugt *et al.* 2007; Rusch and Gavrilets 2017; Van Vugt 2009).

In order to ensure the reliability of our data, we had to remove those participants (93 individuals) who did not read the instructions of Stage Two. These individuals were likely unable to understand the conditions of the game and their consequent decisions were more-or-less random. These participants, who managed to read the long instructions and pass the comprehension questions in less than 25 seconds, form a clear and distinctive spike in a histogram of instruction reading times (see supplementary material Figure S1 and S2). The rest of the participants, analyzed here, formed a normal distribution around 317 seconds (see supplementary material Figure S1). We present the results of the whole dataset in the supplementary material. All of the main results presented here are qualitatively similar to the results of the whole data set. The only partial difference between the full data and the filtered data was found in the associations of female SVO with attack and defense (brought up in the Discussion section).

To test how the share of attack profits (public vs. private) and the strength of defense affect the motivations to attack across the treatments, we used two Repeated Measures ANOVAs. In the first, we used a polynomial contrast on the within-subject repeated measure of the five attack contributions (against varying defense levels). Contributions to Public and Private Good Accounts in the three treatments (four accounts together) were the between-subject factors. We contrasted all Public and Private Attack Account contributions against each other, except contributions within the Trade-off treatment as contributions there were not independent of each other. Thus to test whether contributions within Trade-off treatment differed from each other we run second Repeated Measures ANOVA by using two within-subject factors. The first within-subject factor were the five attack decisions against varying defense levels and the second were the contributions to Public and Private Good Accounts. As our data in both Repeated Measure ANOVAs violated the assumption of sphericity we used a Huynh-Feldt correction.

Results

Private goods motivate attack contributions as much as public goods, even at the expense of group efficiency

The mean contributions to Public and Private Attack Accounts differed between treatments for both genders, but in different manners (Figure 1, Males: $F_{3,58}$ = 4.07, p = 0.011; Females: $F_{3,66}$ = 6.01, p = 0.001). For males, there was no significant difference in contributions to the Attack Account between Public and Private Good treatments (Figure 1, Table 2), nor within the Trade-off treatment ($F_{1, 16}$ = 0.40, p = 0.536, Figure 1). However, contributions to both Public and Private Attack Accounts were significantly lower in the Trade-off treatment compared to contributions when public and private attacks were the only option (Table 2). For females, contributions to the Attack Accounts in the Public Good and Trade-off treatments did not differ from each other (Table 2, Figure 2, Within Trade-off treatment: $F_{1, 15}$ = 0.29, p = 0.600). However, contributions in the Private Goods treatment were significantly greater than contributions in the Public Goods or Trade-off treatment (Table 2, Figure 2). In both genders, the attack contributions were insensitive to the strength of defense (Main effects -Males: $F_{3.11,180.35}$ = 0.27, p = 0.856; Females: $F_{2.77, 182.65}$ = 0.68, p = 0.555; Interaction effects - Males: $F_{9.33, 180.35}$ = 1.07, p = 0.39; Females: $F_{8,30, 182.65}$ = 0.80, p = 0.605).

Prosociality extends across group boundaries, although there is a bias toward in-groups

In-group Social Value Orientation (ISVO) was positively associated with Out-group Social Value Orientation (OSVO, Figure 2, Table 3). Yet, subjects of both genders allocated less to out-groups than in-groups on average (Figure 2; one-sample t-test of ISVO-OSVO = 0 - Males: t_{44}=4.7, p < 0.001, Females: t_{53}=5.40, p < 0,001). We also find that the Standard Social Value Orientation (SSVO) was strongly correlated with both ISVO and OSVO for both genders (Table 3).

Prosociality is associated with a tendency to attack and defend in males, and a tendency to defend in females

Both mean attack and mean defense contributions were positively associated with all SVO measures for males (Figures 3, 4; Table 3). Further, this positive relationship was insensitive to whether profits from attacks were Public or Private, as the associations between SVOs and Attack contributions were positive for all SVO measures across Public and Private goods treatments (2-tailed significant correlations are marked by * for p < 0.05 and ** for p < 0.001. Public Good treatment ISVO: r = 0.567*, OSVO: r = 0.693**, SSVO: r = 0.643*. Private Good treatment ISVO: r = 0.902**; OSVO: r = 0.739**; SSVO: r = 0.697**). For females, we found no association between SVO measures and Attack contributions in any treatment. However, there was a significant correlation between both SSVO and ISVO for Defense contributions (Figures 3, 4; Table 3).

Prosocial males who do not discriminate against the out-group are the ones that attack

We tested how in-group preference (ISVO minus OSVO, see Figure 2) influenced attack contributions with a Hierarchical Multiple Regression. We used ISVO and in-group preference as predictors. The results confirmed that attack contributions for males increase with ISVO ($\beta = 0.60$, $t = 4.81$, $p < 0.000$). However, males with greater in-group preferences contributed less to attacks for a given ISVO ($\beta = -0.31$, $t = 2.46$, $p = 0.018$). For females, neither ISVO ($\beta = 0.02$, $t = 0.63$, $p = 0.530$) nor in-group preference ($\beta = 0.15$, $t = 0.99$, $p = 0.343$) predicted attack contributions.

Discussion

Our results imply that attacking subjects were considerably ready to disregard the production of socially beneficial public goods in order to seek personal benefits, which challenges the underlying assumptions of Parochial Altruism models (Choi and Bowles 2007). Whereas they are in line with the Chimpanzee Model (Wrangham and Glowacki 2012; Wrangham 1999) and Male Warrior Hypothesis (Van Vugt et al. 2007; McDonald et al. 2012) and are supported by anthropological findings (Glowacki and Wrangham 2013; Glowacki *et al.* 2017).

According to the framings of PA, adding the option for less efficient private goods should not affect contributions to more efficient public goods, since individuals are motivated to support their group at their own expense. Instead, we found that half of the contributions went to private goods for both genders under trade-off conditions. Moreover, in males the level of attacking for public goods was 62% lower in the Trade-off treatment, where private goods were available, compared to the singular Public Good treatment. Thus, subjects were ready to considerably forego the group interest in order to improve individual payoff.

Moreover, the considerable difference in public good contributions between treatments indicate that public good contributions may not be pure indications of altruistic motivations, but rather an expectation for direct benefits (as expected from CM/MWH). This view is in line with arguments that one-shot public good contributions do not reflect altruistic tendencies but rather proximate mechanisms of reciprocal altruism (West *et al.* 2007, 2011). This interpretation also holds for the public goods contributions in the Trade-off treatment.

Previous studies have come to conflicting results whether prosociality exceeds group boundaries or whether prosociality is associated with hostility toward out-groups (Cashdan 2001; Thielmann and Böhm 2016; Yamagishi and Mifune 2016). Our data support both sides when males are considered. Prosociality measures toward in-group and out-group were strongly positively correlated in both genders, but in males all prosociality measures were also associated with a tendency to attack. The positive association between male out-

group prosociality and proneness to attack sharply contrasts with the premises of PA. This surprising association was reinforced by the finding that those men who were less discriminative of out-groups in terms of SVO (i.e. were strongly prosocial with both in-group and out-group) were also the most prone to attack. Thus, male prosociality appears to be a double-edged sword. That is, the expression of prosociality toward out-groups does not exclude the potential for hostility toward them, and parochialism is not a necessary prerequisite for male aggression against out-groups.

On the other hand, the associations between prosociality and attack comply with CM and MWH, which frame that attacking occurs only when the prospects for individual benefits outweigh the risks, and that the benefits of attacking are greatest for males. When it comes to attacking other human groups, the benefits can only outweigh the risks with cooperation - a feature closely associated with prosociality (Balliet *et al.* 2009). Thus, our finding that the most prosocial males were the most prone to attack comes as no surprise. For individualistic males, selection should have favored avoiding intergroup conflict, as prospects for the success of un-cooperative attacks are small and the risks large. Indeed, our data indicate that individualistic males were unwilling to participate in attacks in both Public and Private Good treatments. Furthermore, we found no such relationships for females. The association between prosociality and attack is not expected in females to the same degree as males, as female mortality rates from intergroup conflict have been much smaller and the benefits gained from intergroup attacks do not apply as strongly (Bowles 2009). Whereas if the benefits of attack were public goods that apply to all, in lines of the PA model, the positive association between prosociality and attacking should be found to a similar degree in both genders.

Contrary to anthropological findings (Van Vugt *et al.* 2007; Wrangham and Glowacki 2012) and the expectations of all models, we did not find any response from attack contributions to the strength of the defense. However, some theoretical proposals speculate that individuals may be relatively insensitive to risk during intergroup conflict. To a certain extent, the mortality of risk-takers in intergroup conflicts does not impact the average fitness of the risk-taker type, providing that surviving risk-takers replace the reproduction of fallen comrades (Tooby and Cosmides 1988). Reinforcing this, high relatedness within groups –as is the case in hunter-gatherer groups (Hill *et al.* 2011) –can substantially dampen the cost of a few fatalities among warring comrades (Lehmann and Feldman 2008). Thus our experimental risk of losing a little bit of money is probably less than the threshold risk that would have prevented attacking.

Human intergroup conflict has been argued to lead to the development of altruism since Darwin (Darwin 1871; Choi and Bowles 2007). This view was later supported by Parochial Altruism models (see review by Rusch 2014). However, private goods from intergroup conflict might work against the evolution of altruism and instead evolve cooperation through mutual benefit. To simplify, this is because the possibility to acquire private goods from an attack allows individuals to directly benefit from mutually beneficial

cooperation. The larger the direct benefits from private goods are, the more likely they can outweigh the indirect benefits of altruistic sacrifice for public goods. Therefore, the considerable private goods accessible through intergroup conflict (e.g. Wrangham and Glowacki 2012; Walker and Bailey 2013; Chagnon 1988) might per se turn selection to favor those that cooperate for private goods from those that sacrifice for public goods. Naturally, exploring further how the ratio of public and private goods affects the evolution of altruism and mutually beneficial cooperation calls for modeling studies.

Overall, our results on the motivations for intergroup attack and its associations with prosociality were more parsimonious with the Male Warrior Hypothesis and Chimpanzee Model as the basis of human intergroup conflict compared to the Parochial Altruism Model. In sum, our results together with supporting anthropological (e.g. Glowacki and Wrangham 2013; Kohler and Turner 2006) and experimental evidence (Yamagishi and Mifune, 2009) suggest that the drive for the evolution of human intergroup conflict has been more from warriors acquiring private goods than from warriors acquiring public goods through self-sacrifice.

Acknowledgements

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Table 1. Outcomes for self, three in-group members and four out-group members for each contributed dollar to attack under each treatment. These payoffs hold for conditions where attacks exceed the strength of defense. Options in bold indicate the selfish/rational decisions and options in italics indicate the most socially efficient decisions for the in-group.

Treatment	Account	Payoff for each $1.00 contributed		
		Self	In-Group	Out-Group
Public Attack Treatment	**Personal**	1.00	0.00	0.00
	Public Attack	0.50	1.50	-2.00
Private Attack Treatment	Personal	1.00	0.00	0.00
	Private Attack	1.50	0.00	-2.00
Trade-off Treatment	Personal	1.00	0.00	0.00
	Public Attack	0.50	1.50	-2.00
	Private Attack	1.50	0.00	-2.00

Table 2. Repeated Measure ANOVA contrasts for the effect of treatment on contributions to Public and Private Good Attack Accounts

Contrast		Females			Males		
		Estimate	**SE**	**Sig.**	**Estimate**	**SE**	**Sig.**
Public Goods	Private	1.02	0.39	0.010	0.17	0.48	0.730
	Trade-off Public	-0.47	0.40	0.245	-1.13	0.46	0.018
	Trade-off Private	-0.33	0.41	0.431	-0.97	0.46	0.039
Private Goods	Trade-off Public	-1.49	0.40	0.000	-1.29	0.45	0.005
	Trade-off Private	-1.36	0.41	0.002	-1.13	0.44	0.012

Table 3. Pearson Correlations (2-tailed) of mean attack contributions, mean defense contributions and SVO measures (ISVO: In-group Social Value Orientation, OSVO: Out-group Social Value Orientation, SSVO: Standard Social Value Orientation). Results for males (n = 45) are above the diagonal and females (n = 54) below. Significant correlations are marked by * for $p < 0.05$ and ** for $p < 0.001$.

	Attack	Defense	ISVO	OSVO	SSVO
Attack		0.517**	0.534**	0.589**	0.477**
Defense	0.408**		0.506**	0.440**	0.557**
ISVO	0.122	0.306*		0.668**	0.786**
OSVO	-0.035	0.069	0.543**		0.723**
SSVO	0.261	0.326*	0.676**	0.589**	

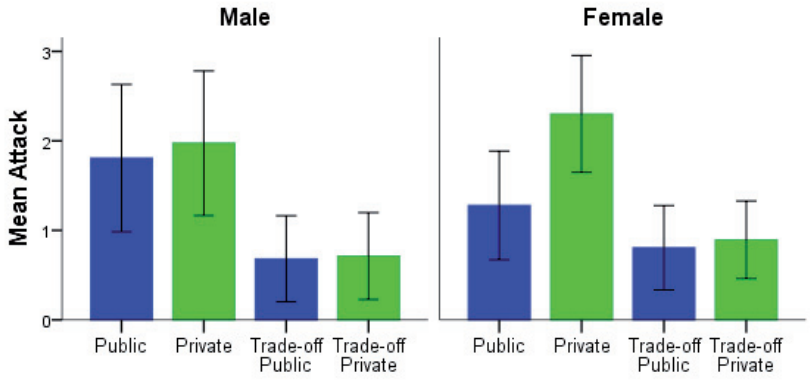

Figure 1. Mean attack contributions across treatments, separated by gender. Blue bars represent contributions to the Public Good Attack Account and green bars represent contributions to the Private Good Attack Account. Error bars indicate +/- 2 s.e..

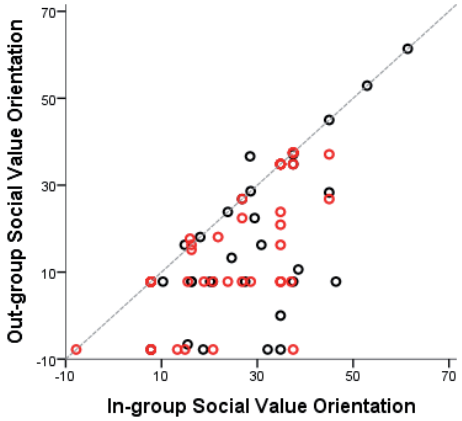

Figure 2. The relationship between Social Value Orientation toward in-group members

(ISVO) and out-group members (OSVO). The diagonal dashed line represents the span of equal SVOs. Black circles represent males, red females.

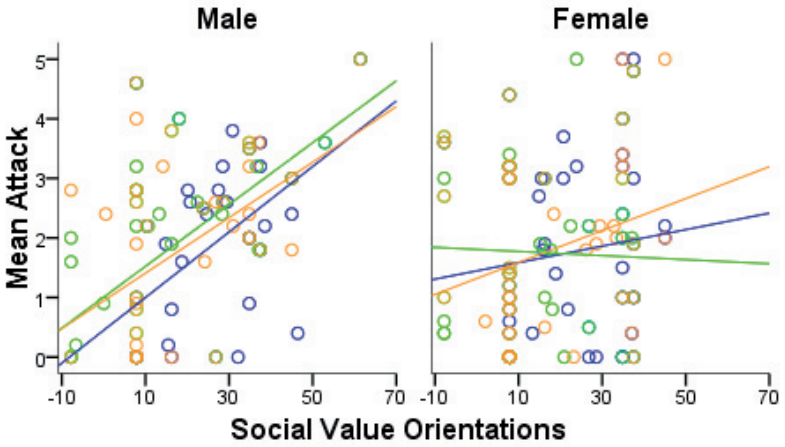

Figure 3. Associations between Social Value Orientation angles (prosociality) and mean attack contribution (blue: ISVO, green: OSVO, orange: SSVO).

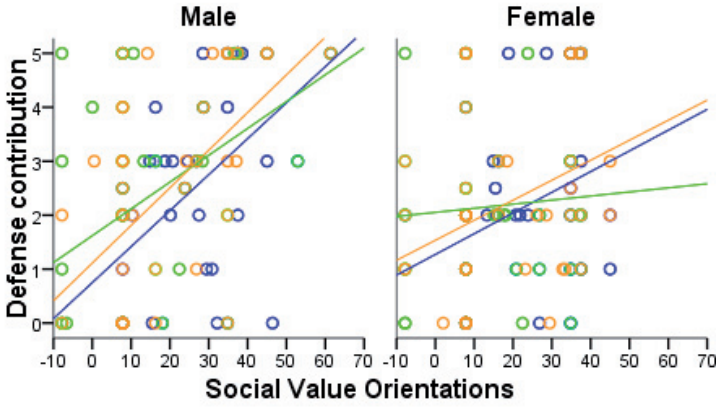

Figure 4. Association between Social Value Orientation angle and mean defense contributions (blue: ISVO, green: OSVO, orange: SSVO).

IV

HARSH PARENTING MAY INCREASE PERFORMANCE IN INTERGROUP CONFLICTS BY INTENSIFYING MALE BELLICOSITY AND PROSOCIALITY

by

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Abstract

Harsh parental treatment is common worldwide and we propose that it may have spread by intensifying a set of individual traits that contribute to success in intergroup conflicts. We test our hypothesis with an economic decision making experiment by measuring individual traits of prosociality and bellicosity toward out-groups (parochial altruism). These traits are argued to determine group success, especially when occurring simultaneously. We considered the structural associations between these traits and harsh parental treatment in a wider context including religiosity, perceptions of a code of honor, and feelings of belonging. In support of our hypothesis we show for the first time that, of the traits considered, only harsh parenting was positively associated with both bellicosity and prosociality and only in men. These results together with supporting evidence suggest that harsh parenting may have spread via the benefits it promotes for intergroup conflict, especially in post-forager societies after cultural selection pressures from warfare increased.

Keywords: prosociality, bellicosity, parochial altruism, parental treatment, intergroup conflict, religiousness, culture evolution

Introduction

Human intergroup conflict and warfare are prevalent over known history and across cultures, and are argued to play a large role in genetic and cultural evolutionary processes (Bowles 2009; Bowles and Gintis 2011; Richerson *et al.* 2016). These processes are suggested to select for genes, cultural norms, institutions and practices that increase and broaden prosocial tendencies, which enhances group-level competitive ability (Darwin 1873; Boyd and Richerson 2009; Norenzayan *et al.* 2016). If this prosociality is combined with bellicosity toward other groups -often termed parochial altruism- it can bring even stronger cultural advantages (Choi and Bowles 2007; Bowles and Gintis 2011). To understand this process requires that we link the adoption of traits that enhance group-level competitive ability (like broad-spectrum prosociality and bellicosity) with the mechanistic social interactions responsible for their phenotypic development. We suggest that parental caretaking practices and habits (i.e. parental treatment) are a critical but yet under-studied mechanism developing social behaviours that have culturally adaptive consequences.

Parental treatment generally involves the responsiveness of the parent to the innate needs of a child alongside the placement of behavioural and psychological demands (Baumrind 2012). We argue that patterns of parental treatment play an important role in cultural evolution because it fulfils the three required principles of adaptive change (Mesoudi *et al.* 2004). First, there is substantial variation in parental treatment styles within and across societies

(Prescott 1975; Lansford *et al.* 2010; Saucier *et al.* 2015). Second, patterns of parental treatment in the first years of development can have epigenetic effects on brain development that promote variation in behavioural tendencies with fitness consequences (Anreiter *et al.* 2017; Perry *et al.* 2017; Vaiserman and Koliada 2017). Specifically related to this article, parental treatment affects the development of prosociality and bellicosity (Anda *et al.* 2006; Tuvblad and Baker 2011; Waltes *et al.* 2016; Zhang *et al.* 2018) which likely bear large culture evolutionary consequences (e.g. Bowles and Gintis 2011). Parental treatment can also affect mental and physical health (Narvaez *et al.* 2013; Klebanov and Travis 2014). Third, parental treatment styles are heritable, with practices and their consequences passing to following generations through affected psychological compulsions (Kretchmar, Molly and Deborah 2002; Klebanov and Travis 2014; Lomanowska *et al.* 2017). Thus, we expect that cultural traits of parental treatment can undergo cultural selection and adapt to persist and spread.

We specifically consider the trait of harsh parental treatment, which refers to the relationship's level of physical and emotional violence or neglect. Harsh parental treatment is commonly practiced across the globe (Runyan *et al.* 2010; Khaleque and Ali 2017; Klebanov and Travis 2014), yet this seems to not have always been the case as it is argued to have become common only after the cultural change from foraging to pastoral and agricultural subsistence (Pollock, Linda 1983; Hewlett and Lamb 2017; Narvaez 2017). This suggests that some aspects of post-forager life have promoted the spread of harsh parenting, and we propose that one aspect could have been intergroup conflict.

This is because harsh parenting may contribute to the development of prosocial and bellicose individuals (Anda *et al.* 2006; Tuvblad and Baker 2011; Waltes *et al.* 2016; Zhang *et al.* 2018) and these traits can together contribute toward success in conflicts (Choi and Bowles 2007; Bowles and Gintis 2011). Harsh parenting practices may then spread as a cultural trait through intergroup conflict even despite the potential for toxic psycho-social effects on the child or in-group (Narvaez *et al.* 2013; Afifi and Romano 2017; Khaleque and Ali 2017; Klebanov and Travis 2014). Further, this proposes one explanation for why harsh parenting has become common only after the change from foraging as cultural selection pressure from intergroup conflicts increased (Turchin *et al.* 2013; Morris 2014).

In support with this hypothesis, cross cultural studies have found an association between harsh parenting and greater aggression towards out-groups (Eckhardt 1973; Prescott 1975; Ember and Ember 1994; Lansford and Dodge 2008). Also, studies at the individual level have found an association between harsh parenting and right-wing authoritarianism and social dominance orientations, which are both associated with aggressive attitudes toward subordinate groups (Gabriel 2009; Kandler *et al.* 2016). Further, studies suggest that parental harshness can promote obedience to norms (Baumrind 1978; Kandler *et al.* 2016), a willingness to punish transgressions (Narby *et al.* 1993), the valuation of hierarchical institutions (Duckitt 2001; Cross and Fletcher 2011; Kandler *et al.* 2016), and the intensification of social emotions like shame

and guilt (Capps 1995). Such traits can contribute to a form of prosociality and cooperation that is effective at out-competing other groups through labour or military effectiveness (Bowles and Gintis 2011; Turchin *et al.* 2013).

We hypothesize that harsh parenting intensifies a set of individual traits, like prosociality and bellicosity, that promote success in warfare. We use data from an empirical experiment to test this hypothesis, and are the first to test whether harsh parental treatment is simultaneously associated with both prosociality and hostility toward out-groups. We analyse the structural relationships between harsh parenting practices (e.g. domestic fighting, negative physical or emotional contact) and prosocial and bellicose behaviours within a wider context that includes indirect relationships via religiosity, a sense of belonging, and perceptions of an honor code. We place parental treatment at the beginning of the assumed causal structure because its effects are present in the earliest years of development and occur before socialization. Furthermore, parental treatment is known to epigenetically affect the development of brain structure and function, with subsequent behavioural consequences (Anreiter *et al.* 2017; Perry *et al.* 2017; Vaiserman and Koliada 2017). Foster-parent studies with rhesus macaques (*Macaca mulatta*) also speak to the foundational effects of parental treatment (Maestripieri 2018), as do twin studies in humans (Kandler *et al.* 2016). The additional factors are considered because they each have been found to be associated with parental treatment, prosociality and bellicosity. Specifically, harsh parenting has been found to be associated with religious activity and religions may contribute toward prosociality (Prescott 1975; Purzycki *et al.* 2016). A sense of belonging has been found to associate with both parental treatment and less prosocial decisions in social dilemmas and enables dehumanization of out-groups (Waytz and Epley 2012; Lucas and Livingston 2014; Corrales *et al.* 2016). Finally, agreement with a Code of Honor may associate with violent behaviour and be promoted by harsh parental treatment (McCullough *et al.* 2013; Pedersen *et al.* 2014). We consider gender as a factor because evolutionary theories of intergroup competition and life history indicate sex-dependent selection (Wilson and Daly 1985; Belsky *et al.* 1991; McDonald *et al.* 2012), and parental effects are known to interact with gender (Schore, Allan 2017).

Methods

Participants

We conducted our experiment with informed consent on 192 USA residents (average age = 36, SD = 10.2, 49% female) using Amazon Mechanical Turk (Buhrmester et al. 2011). The experiment consisted of three parts. For each part participants first had to read a set of instructions for the experiment and answer a series of comprehension questions in order to proceed. Regarding the part that measured bellicosity, we had 93 cases of missing data because participants did not read the instructions. We could identify those that did not participate

reliably because it took them less than 25 seconds to proceed through the instructions of approximately 3000 words and pass the comprehension questions (see supplementary material). Regarding the bellicosity measure we thus included only the 99 participants that passed attention checks (54 female; average age = 37).

Experimental Procedure

After accepting the task on Mechanical Turk, participants were divided into groups of four and partnered with another group. They were directed to a Qualtrics (Qualtrics, Provo, UT) survey and given full information for the rules of the decision making game, which they played with monetary consequences (Chapter III, Supplementary Information). Part One was not involved in this experiment (Chapter III). In Part Two, we measured individual bellicosity toward out-groups using a game modelled after the Intergroup Prisoner's Dilemma (IPD; Bornstein, 1992 as described in Thielmann and Böhm, 2016). In Part Three, we measured prosociality by using the slider method to calculate individual Social Value Orientations (SVO; (Murphy *et al.* 2011a)). There were three treatments not involved in this experiment that manipulated the conditions of Part Two. However, these manipulations had no effect on the measures of Bellicosity or SVO and were thus pooled (Supplementary Table S3). We paid participants according to the outcome of one randomly selected decision of the 24 that they made during the game.

For Part Two, regarding the measurement of bellicosity, participants were each allocated $5 USD and asked to distribute funds between a Private Account and 'Account A'. Subjects would keep any money in their Private Account but could benefit from funds invested in Account A at the expense of the partnered group (hereafter, 'attacking' and 'the Attack Account'; our measure of bellicosity). A successful attack requires that the sum of all individual contributions to the Attack Account exceeds the funds invested by the partner group in 'Account D' (hereafter 'defense level' and 'the Defense Account'). Each dollar that exceeded the defense level deducted $2 from the partner group ($0.5/member). The entire contribution to the Attack Account was lost if it did not exceed the partner group's defense level. Subjects made a series of five attack decisions across different defense levels ($0, $1-5, $6-10, $11-15, $15-20). There were no significant differences between levels (see chapter III), so individual responses were pooled to generate each player's Attack Score.

With regards to Part Three, and our measure of prosociality, participants did a monetary allocation decision between themselves and a random partner across six conditions of interdependence (Murphy *et al.* 2011a). The six responses are combined to calculate the subject's Social Value Orientation (SVO). This nominally measures the relative value people attach to themselves and others in trade-off situations; it thus serves as a measure of prosocial or other-regarding preferences. From low-to-high, SVO scores correspond with competitive (maximizing payoff differences), individualistic (maximzing own payoff), prosocial (maximizing mutual payoffs) and altruistic (maximizing other payoffs) orientations.

Survey

Following the main experiment, we had subjects provide answers to questions on a 7-point Likert Scale. The survey assessed the level of Parental Harshness with a 10-item scale that measures an individual's exposure to family neglect, conflict and violence. Questions were adopted from Pedersen et al. (Pedersen *et al.* 2014). Example questions include: 'How often did a parent or other adult in the household… swear at you, insult you, put you down, or act in a way that made you feel threatened?', '… push, grab, shove, or slap you?'. The 3-item Religiosity Scale was adapted from the religiosity component of the Arizona Life History Battery (Figueredo 2007). Example questions include: 'I am closely connected to and involved in my religion', 'I am a religious person'. Our 10-item Honor Code scale was the 'Street Code' component from Pedersen et al. (2014). Example questions include: 'When someone insults you or harms you, it's up to you to handle it yourself', 'Sometimes you have to fight to uphold your honor, or put someone in his or her place'. The 8-item Belongingness scale was adapted from the Social Connectedness and Social Assurance (Lee and Robbins 1995) scales. Questions included: 'Even around people I know, I don't feel that I really belong', 'I feel disconnected from the world around me'.

Statistical Procedure

We used structural equation modeling (SEM, Kline 2016) on each sex to contrast the direct associations of Parental Harshness on SVO and Attack, alongside its indirect effects through Religiosity, Honor Code and Belongingness. We began the analysis by evaluating potential measurement invariance between the sexes, i.e. we tested that factors represent similar constructs for both sexes. Specifically, we wanted to establish invariance with respect to factor loadings (i.e. metric invariance), since this is needed for the reliable comparison of structural path coefficients (i.e. those direct and indirect effects of main interest here) between men and women (Guenole and Brown 2014). This was achieved by conducting likelihood ratio tests, one factor a time, between a model that assumes equal factor loadings among the sexes with a model that assumes free loadings among the sexes. We found evidence for initial non-invariance with respect to the factors of Belongingness ($\chi^2_7 = 15.6$, $p = 0.029$) and Honor Code ($\chi^2_9 = 23.7$, $p = 0.005$). We achieved metric invariance for all factors (Table 1) after identifying and one-by-one removing the items showing the largest absolute non-invariance between the sexes (item 5 in Belongingness and items 2, 5 and 10 in Honor Code).

Because fitting a full-scale SEM into these data would have resulted in the estimation of 94 parameters and hence likely produced an over-fitted model, we chose to use single-indicator latent variables, i.e. factor scores that were corrected for measurement error using the reliability estimates specific for each factor (Hayduk and Littvay 2012). We used congeneric reliabilities (Raykov 2004) calculated by sex as scale reliability estimates (Table 2), which indicated very high reliability for factor scales. Moreover, factor determinacy values

(which report the correlation between true factor scores and the factors scores obtained from the model) suggest high convergence (Table 2).

The structural equation model was used to examine whether the direct effects from Parental Harshness on SVO and Attack differed among sexes by comparing models with constrained and freed direct effects using likelihood ratio tests. Next, the same procedure was applied to indirect effects examining whether the associations from Parental Harshness on SVO and Attack were mediated by Religiosity, Honor Code and Belongingness. If these tests indicated statistically significant sex-differences, we continued by examining those direct and indirect effects individually. In addition to direct and indirect effects we also report total effects (a sum of direct and indirect effects) of Parental Harshness on SVO and Attack, and the direct effects of Religiosity, Honor Code and Belongingness on SVO and Attack. The model also assumed a residual covariance between prosociality and attack since these variables were measured from the same individuals. All the models fitted used full-information maximum likelihood (FIML) estimation, assuming that data is missing at random. The fit of the final model, allowing potential sex-specific parameters, to the data was assessed with chi-square test (χ^2 -test, should be non-significant at $\alpha = 0.05$), root mean square error of approximation (RMSEA, should be < 0.1 and non-significant at $\alpha = 0.05$), comparative fit index (CFI, should be >0.95) and standardized root mean square error (SRMR, should be <0.1) (Kline 2016). Analyses were conducted using Mplus 8.0 (Muthén and Muthén 2017).

Results

For males, the direct associations between Parental Harshness and both SVO and Attack were stronger than their indirect associations via Religiosity, Honor Code or Belongingness (Figure 1; Tables 3, S4). Furthermore, there were no direct associations between Religiosity, Honor Code or Belongingness with either SVO or Attack. The results for females, by contrast, showed no significant direct or indirect associations with SVO and Attack involving any measured factor (Figure 1; Tables 4, S5). The level of total ($\chi^2_2 = 19.4$, $p < 0.001$) and direct ($\chi^2_2 = 21.6$, $p < 0.001$) associations among parental harshness and SVO and attack were significantly different between the sexes. This conclusion held when tested separately for SVO (total: $\chi^2_1 = 10.2$, $p = 0.014$; direct: $\chi^2_1 = 5.3$, $p = 0.022$) and Attack (total: $\chi^2_1 = 13.4$, $p < 0.001$; direct: $\chi^2_1 = 15.6$, $p < 0.001$).

There were no sex differences with respect to the indirect associations involving Religiosity, Honor Code and Belongingness ($\chi^2_6 = 2.5$, $p = 0.88$). Furthermore, the estimates of direct associations involving Religiosity, Honor Code or Belongingness with SVO and Attack did not significantly differ between the sexes ($\chi^2_6 = 1.4$, $p = 0.97$). This model also showed an adequate, but not perfect fit to the data ($\chi^2_6 = 10.2$, $p = 0.06$; RMSEA (90% CIs) = 0.10 (0.00, 0.19), $p = 0.13$; CFI = 0.93; SRMR = 0.04).

Discussion

We proposed a hypothesis that harsh parental treatment intensifies a set of individual traits that contribute to success in intergroup conflicts, particularly in males. Our finding supports this hypothesis as harsh parenting was the only factor that was associated with greater prosociality and bellicosity in males, but not in females. Thus our result suggests how harsh parental treatment might have been culturally selected via intergroup competition. These results suggest significant new insights into current theories of cultural selection.

Our new finding that harsh parental treatment is associated with both prosociality and bellicosity might appear surprising. Harsh parenting and increased aggressiveness is well established (Waltes *et al.* 2016; Zhang *et al.* 2017), but associations with certain forms of prosociality are not as clear. Although further studies are necessary to explain this link, we can offer some suggestions by extending the concept of prosociality. Prosociality is typically considered as a valuation of others, and the SVO measure we used assesses how much one values others in relation to oneself in a situation of inter-dependence (Murphy *et al.* 2011b). But higher scores can stem from decreased self-value in addition to an increased value placed on others. Harsh parental punishments and disciplinary practices may thus increase prosociality by coercing individuals to forego self-interest. In line with this view, harsh parenting has been found to increase norm obedience, which often appears as prosocial behaviour (Baumrind 1978; Kandler *et al.* 2016). Further, harsh parenting may diminish the internalization of self-worth (Hardy *et al.* 2010), which can further contribute for the observed increase in SVO. Worth noting is that this form of prosociality, based on decreased self-valuation, may be different from prosociality inspired by valuation of others.

Our result that parental treatment was the only factor associated with bellicosity and prosociality further emphasizes the critical importance of the early years of development in forming long-lasting behavioural tendencies (Klebanov and Travis 2014). Yet, we still expected the mediating factors to play some role. This discrepancy may stem from parental treatment being largely unconsidered in studies that focus on religiosity, honor code or belonging (but see McCullough et al., 2013) and the potential for parental treatment to be instrumental in promoting the effects of these other factors. Thus, parental care may form the foundation for an individual's behavioural tendencies which are later influenced by experiences with religion, honor codes or belonging.

Religions, especially those with beliefs in moralistic, punitive gods, have been shown to associate with increased prosociality (Atkinson and Bourrat 2011; Shariff *et al.* 2016; Bennett and Einolf 2017). Thus religions with punitive gods have argued to be one of the key mechanisms contributing to the emergence of larger complex societies across the globe (Johnson 2005; Norenzayan *et al.* 2016; Purzycki *et al.* 2016). However, to our knowledge, none

of these studies have taken into account the effect of harsh parental treatment, despite the potential for it to mechanistically explain the effects of religiosity on prosociality and cultural evolution. For instance, conservative religions and belief in punishing gods have found to be associated with high rates of child corporal punishment (Prescott 1975; Hoffmann *et al.* 2017; Martinez *et al.* 2017), which our results suggest explain increased prosociality rather than religiosity. That is, the mechanism for the positive association of prosociality and religions might be more directly due to the biological and psychological effects of harsh parental treatment rather than a belief in punishing gods alone. The effect of religious institutions, however, may come from intensifying the cultural evolutionary role of harsh parenting by promoting its use, legitimating the practice and spreading it within and across cultures as part of the religion (Bottoms *et al.* 2004; Simonič *et al.* 2013; Norenzayan *et al.* 2016).

We found a significant gender difference in that the associations between harsh parenting, bellicosity and prosociality were present only in males. This might be due to boys' development being more sensitive to harsh parenting and stressors in childhood (Klabunde *et al.* 2017; Schore, Allan 2017). Yet, this result is expected in light of life history theory, which suggests that increased aggression in response to harsh childhood conditions can be adaptive for males (Wilson and Daly 1985; Belsky *et al.* 1991). This is because harsh environmental conditions in childhood likely predict harsh environment conditions in adulthood, where increased aggression can pay off for males.

Our results support the hypothesis that harsh parenting intensifies a set of individual traits that likely enhance a group's success in intergroup conflicts. The increased bellicosity gives the motivation to attack, and the increased prosociality and norm obedience should contribute for in-group efficiency and decrease free-riding in battle situations (Choi and Bowles 2007; Bowles and Gintis 2011). While there are likely many factors contributing to harsh parenting in post-forager societies, our results together with the supporting evidence presented in the introduction suggest that harsh parenting might have spread worldwide by contributing to success in between-group conflicts. Moreover, the smaller cultural selection pressure of intergroup conflict for forager societies compared to agricultural societies (Turchin *et al.* 2013; Morris 2014) might explain why harsh parenting has not spread in the former but has in the latter.

A certain degree of cautiousness toward our results should be acknowledged. First, our data do not cover all possible adverse childhood experiences that might covary with our measures. For example, socio-economic status has been shown to affect various measures (Steele *et al.* 2014). Furthermore, our sample size is rather small, and retrospective questionnaire studies can hold a relatively large error rate. Finally, the questionnaire on parental harshness assessed participants' childhood from years 5-15 and not from earlier childhood when the largest effects of parenting takes place. Nevertheless, our results are in line with numerous other studies supporting our hypothesis.

Our approach considered one particular model of causal relationship, stemming from harsh parenting to prosociality and bellicosity. Whilst this relationship can be justified by epigenetic effects, animal foster-parenting experiments and human twin-studies, it is only one of many potential causal structures. For example, bellicose children may stimulate harsh parenting, or the effects of parenting may come after socialization. There are also many other factors left unconsidered, such as environmental variation and genetics. Even so, our focus on this singular model can serve as support for our hypothesis by showing that harsh parenting can increase prosociality and bellicosity under a (albeit limited) causal structure.

According to our hypothesis, harsh parental treatment may have recently spread partly via success in warfare due to the bellicose phenotype it produces in men. According to theories, genes that produce the bellicose phenotype should have spread also (Choi and Bowles 2007; Bowles and Gintis 2011). A monoamine oxidase gene (MAO-A), the so called "Warrior-gene", offers an example for a possible gene-culture co-evolutionary relationship that seems to align with our hypothesis. The male carriers of low activity type allele of this gene develop a bellicose phenotype if they are exposed to harsh parenting (Caspi *et al.* 2002; Frazzetto *et al.* 2007), and studies show that it has spread very recently in seven studied populations (Gilad *et al.* 2002; Lea and Chambers 2007) apparently via success in warfare (Lea and Chambers 2007). In addition, harsh parenting and the bellicose phenotype it induces are likely common in these populations (Lea and Chambers 2007; Runyan *et al.* 2010).

Intergroup conflicts have been argued to lead to the evolution of prosocial and cooperative moral systems within groups, which have further led to the selection of other-regarding motives like empathy (Boyd and Richerson 2009; Richerson *et al.* 2016). However, our results suggest that the high selection pressure from intergroup conflicts may have selected for harsh parenting, which is associated with decreased empathy and sympathy (Kanat-Maymon and Assor 2010; Guo and Feng 2017; Narvaez 2017), increased delinquency and aggressiveness (Caspi *et al.* 2002; Waltes *et al.* 2016), and preferences for right-wing authoritarianism and prejudiced dominance systems (Gabriel 2009; Kandler *et al.* 2016). If such harsh values and practices, promoted by harsh parenting, are reflected within institutional functions then the proposed selective effect on other-regarding concerns may be impaired. If, however, between-group cultural selection pressure is reduced, harsh parenting may cease to spread as has happened in many parts of Europe after World War II (Steele *et al.* 2014). This could allow individuals to develop stronger other-regarding concerns and sympathy (Kanat-Maymon and Assor 2010; Guo and Feng 2017; Narvaez 2017), which may better support prosociality based on regard for others rather than strict obedience.

Taken together, we tested our hypothesis that harsh parental treatment intensifies group-beneficial prosocial and bellicose norms that can contribute to success in intergroup conflicts. We found support for this hypothesis, as harsh parenting was associated with increased prosociality and bellicosity in males. In addition, our hypothesis suggests an explanation for why harsh parenting has

proliferated only after the shift to agriculture when cultural selection pressure due to warfare increased. Further, our result together with supporting studies suggests that the proposed large culture evolutionary consequences of a belief in moralizing gods may be better explained by the developmental consequences of harsh parenting practices that take place within these groups.

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Table 1. A likelihood ratio test of a metric invariance (i.e. factor loadings) between the sexes.

Factor	χ^2	df	p
Parental Harshness	7.37	8.00	0.50
Religiosity	2.66	2.00	0.26
Honor Code	8.43	6.00	0.21
Un-Belonging	12.20	6.00	0.06

Table 2. Congeneric reliability estimates with 95% confidence intervals and factor determinacy scores (FD) for males and females

	Males				**Females**			
	Congeneric Reliability				Congeneric Reliability			
Factor	**L-CI**	**Est**	**U-CI**	**FD**	**L-CI**	**Est**	**U-CI**	**FD**
Parental Harshness	0.80	0.85	0.90	0.94	0.89	0.92	0.95	0.98
Religiosity	0.90	0.94	0.98	0.97	0.92	0.94	0.97	0.98
Honor Code	0.82	0.86	0.91	0.93	0.76	0.82	0.87	0.91
Un-Belonging	0.88	0.91	0.94	0.96	0.87	0.91	0.94	0.96

Table 3. For males, the point estimates (with 95% CI) for linear associations between Parental Harshness and SVO or Attack, decomposed into total, direct and indirect effects. Estimates for the direct associations of Religiosity, Honor Code and Belongingness are also given. Confidence Intervals are bootstrapped with 5000 draws. Bold cases indicate significant associations.

Males	SVO			Attack		
	L-CI	**Est**	**U-CI**	**L-CI**	**Est**	**U-CI**
Parental Harshness						
Total effect	**6.4**	**10.7**	**15.6**	**0.3**	**0.8**	**1.3**
Total indirect	-6.5	-1.3	3.0	-1.2	-0.4	0.3
Indirect effects via						
Religiosity	-1.2	-0.2	0.3	-0.1	0.0	0.2
Honor Code	-1.7	-0.2	0.4	-0.1	0.0	0.1
Un-Belonging	-5.7	-0.9	3.6	-1.2	-0.3	0.2
Direct effect	**4.7**	**12.0**	**20.4**	**0.4**	**1.2**	**2.1**
Religiosity						
Direct effect	-2.5	-0.8	0.8	-0.2	0.1	0.4
Honor Code						
Direct effect	-5.4	-1.8	1.9	-0.5	-0.1	0.4
Un-Belonging						
Direct effect	-3.6	-0.6	2.4	-0.7	-0.3	0.2

Table 4. For females, the point estimates (with 95% CI) for linear associations between Parental Harshness and SVO or Attack, decomposed into total, direct and indirect effects. Estimates for the direct associations of Religiosity, Honor Code and Belongingness are also given. Confidence Intervals are bootstrapped with 5000 draws.

Females	SVO			Attack		
	L-CI	**Est**	**U-CI**	**L-CI**	**Est**	**U-CI**
Childhood harshness						
Total effect	-2.4	1.6	4.7	-0.6	-0.2	0.2
Total indirect	-3.0	-0.7	1.7	-0.4	-0.1	0.3
Indirect effects via						
Religiosity	-1.0	0.2	1.3	-0.2	0.0	0.1
Honor Code	-1.5	-0.3	0.6	-0.1	0.0	0.1
Un-Belonging	-2.7	-0.6	1.7	-0.3	0.0	0.3
Direct effect	-2.3	2.2	5.8	-0.6	-0.2	0.3
Religiosity						
Direct effect	-2.0	-0.3	1.5	-0.2	0.1	0.3
Honor Code						
Direct effect	-6.4	-2.3	1.8	-0.6	0.0	0.6
Un-Belonging						
Direct effect	-4.0	-0.9	2.2	-0.5	-0.1	0.4

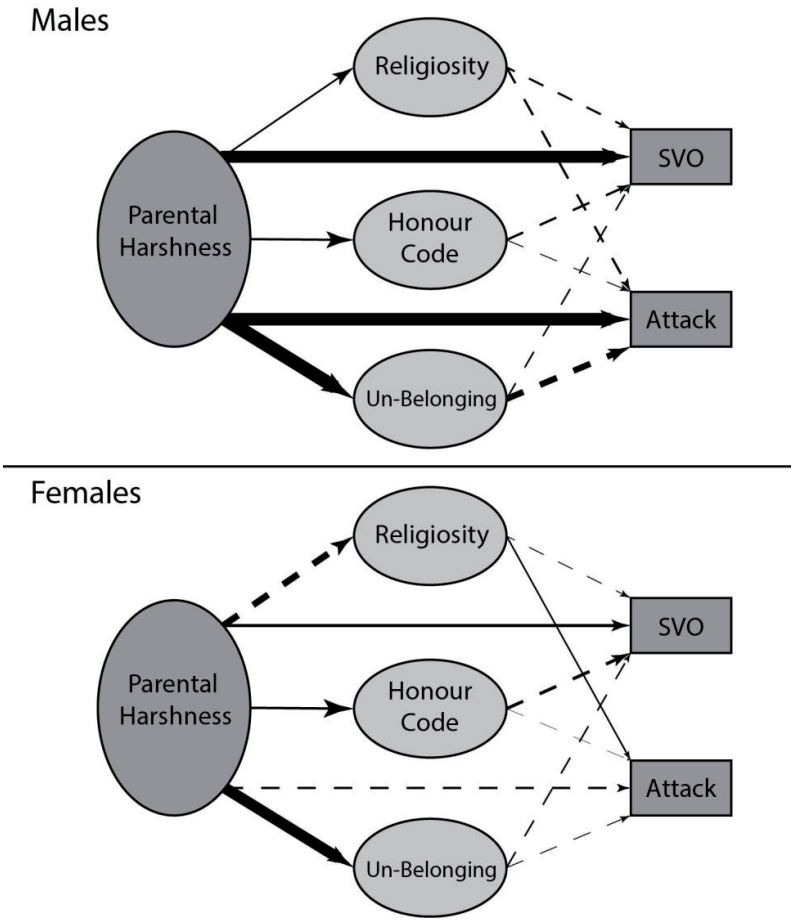

Figure 1. Path diagrams for direct and indirect effects of Parental Harshness on SVO and Attack, separated by sex. Solid lines represent positive associations and dashed lines represent negative associations. Lines are weighted by their standardized coefficient (Supplementary Tables S4, S5).

SUPPLEMENTARY INFORMATION

Human cooperation in groups: variation begets variation

Van den Berg P, Molleman L, Junikka J, Puurtinen M & Weissing FJ

CONTENTS

1. Results for all subcategories of response to heterogeneity

It may be argued that the classification of 'response to heterogeneity' in the main text of our experiment is somewhat crude. Even individuals that only contributed more in case of more heterogeneity in peer contributions in one of the three comparisons (and contributed equally in the other two cases) are classified as 'positive responders'. Similarly, an individual that only contributed less in case of more heterogeneity in peer contributions in one case, was classified as 'negative responders'. To investigate to what extent these seemingly small differences between weakly negative and weakly positive individuals are meaningful, we analysed the relationship between response to heterogeneity and cooperation tendency when considering all subcategories of individuals (as they are shown in Fig. 2 in the main text). Figure S1 shows that even the marginally positive and negative individuals have quite different cooperation tendencies.

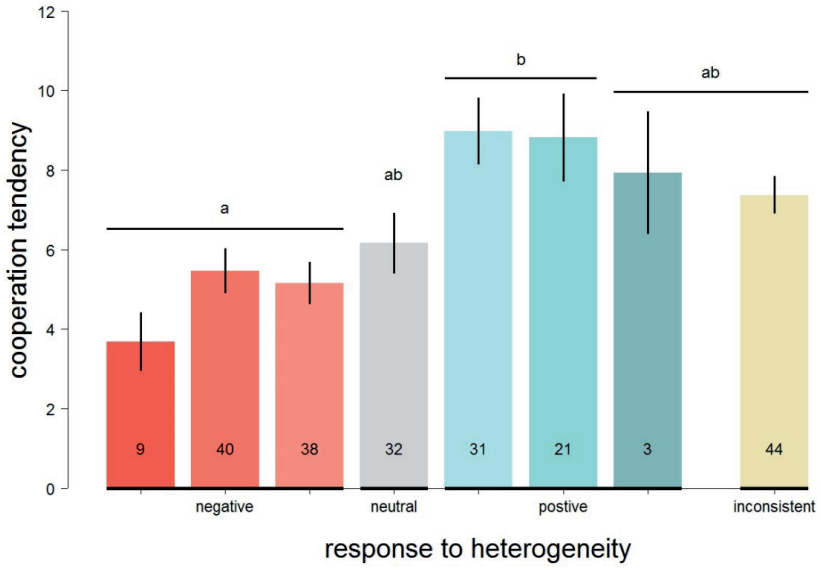

Figure S1. Response to heterogeneity in peer contributions is associated with cooperation tendency, even when the response to heterogeneity is weak. Bars show the average and SEM of contributions over ten rounds of a public goods game, where group composition was randomised before every round. The same data as in Fig. 3 of the main text are shown, but the 'negative' and 'positive' categories are further subdivided by degree of negativity or positivity, as in Fig. 2 of the main text. Negative responders to information are further subcategorised by whether they contributed less in response to increasing heterogeneity in one, two, or all three situations. Similar subcategories were made for positive responders to heterogeneity. The darker bars (furthest removed from the 'neutral' bar) show the most extreme responders, whereas the lighter bars (next to the 'neutral' bar) show the individuals that only responded positively or negatively to increased heterogeneity in one case, and responded neutrally in both other cases. Letters (**a** and **b**) indicate significant differences (Tukey HSD test); all bars indicated with **a** are significantly different from all bars indicated with **b**, whereas bars indicated with **ab** are not significantly different from either. Numbers at the bottom of each bar indicate the number of subjects falling in this category.

2. Results using other measures of general cooperation tendency

In our experiment, we measure general cooperation tendency by taking the average of subjects' contributions in ten consecutive one-shot rounds of a PGG. This is in principle a valid way to measure general cooperation tendency, because individuals are playing one-shot games; information from earlier rounds is not relevant when deciding how much to contribute. However, one may argue that the outcomes of earlier rounds may still have influenced subjects in their decisions. Therefore, we here check whether our results still hold when only considering the first interaction round (when individuals have no information whatsoever about the decisions of others). Figure S2*a* shows that this is indeed the case.

An alternative (and independent) measure of general cooperation tendency is the 'unconditional contribution' that individuals entered in the second part of the experiment. This unconditional contribution was used in the single round of PGG that was played in groups of four after the second part of the experiment. From each group, three randomly chosen subjects automatically contributed their unconditional contribution, and the remaining subject made their corresponding conditional contribution. Figure S2*b* shows that if this measure is used, the same pattern still emerges. This strongly suggests that the observed pattern is robust.

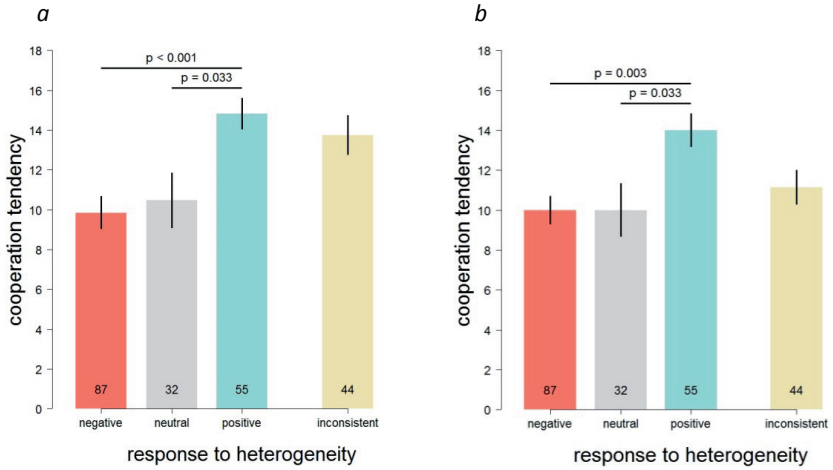

Figure S2. Response to heterogeneity in peer contributions is associated with cooperation tendency, also when using other measures of cooperation tendency. Bars show the average and SEM of contributions when considering (*a*) only the first PGG in the first part of the experiment, and (*b*) 'unconditional contributions' in the second part of the experiment. Statistically significant differences between types are indicated (Tukey HSD), except for differences between inconsistent responders and any of the other groups. Numbers at the bottom of each bar indicate the number of subjects falling in the respective category.

3. Overview of statistics

This section gives an overview of the statistical methods that were used in the study.

Factors affecting average contribution
We constructed a linear mixed model to determine which factors influence the response contribution levels when only considering the three pairs of cases that have equal average peer contribution, but different heterogeneity in contributions. We used a stepwise backwards elimination approach (Zuur *et al.*, 2009*), starting with a full model that contains as predictor variables the average peer contribution (the three levels are modelled as categorical factors), heterogeneity in peer contribution (including 'high heterogeneity' and 'low heterogeneity' as factors), and their interaction. Also, we included 'individual' as a random factor. The final model included both average peer contribution and heterogeneity in peer contribution as predictor variables, but not their interaction. We conclude that both average peer contribution and heterogeneity in peer contributions have a significant (respectively positive and negative) effect on response contributions. A summary of the final model is given below:

	Estimate	Std. error	t-value	P-value
(Intercept)	4.7951	0.3428	13.989	<0.001
heterogeneity in peer contributions	-0.9021	0.2348	-3.842	<0.001
average peer contribution (10)	3.5711	0.2876	12.418	<0.001
average peer contribution (13.33)	5.3142	0.2876	18.479	<0.001

In summary, average response contributions increase with average peer contributions, but decrease with increasing heterogeneity in peer contributions. This is consistent with earlier results.

Recent experiments indicate that the outcome of past social interactions in an experimental session may affect unrelated future cooperation decisions (Peysakhovich and Rand, 2015**). For our experiment, this may lead to the expectation that subjects who experienced higher average levels of cooperation in the first part of the experiment would contribute more to the public good in the second part. However, an extended regression analysis including peer cooperation levels in part 1 of the experiment reveal that they had no significant effect on public good contributions in part 2. There was a small yet significantly positive effect of the average cooperation levels in the stable groups (rounds 11-25; see Section 4 of this Supplementary Information), but including this factor in the regression analysis did not alter our main conclusions; both average peer contribution and heterogeneity in peer contributions have on average a significant (respectively positive and negative) effect on response contributions.

*Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM. 2009. Mixed Effects Models and Extensions in Ecology with R. Springer (New York).
** Peyshakhovich A, Rand D. 2015 Habits of virtue: creating norms of cooperation and defection in the laboratory. *Management Science* (forthcoming)

Factors affecting the incidence of extreme contributions
To determine which factors influence the incidence of extreme contributions we constructed a mixed-effects logistic regression model both for the incidence of contributions of 0 and the incidence of contributions of 20. We used a stepwise modelling approach, as described for the linear mixed model above, and included the same predictor variables in the first step. The final model for **contributions of 0** contained average peer contribution, heterogeneity in peer contributions, and their interaction as predictors:

	Estimate	Std. Error	z-value	P-value
(Intercept)	-0.6805	0.2617	-2.600	0.009
heterogeneity in peer contributions	0.8905	0.2718	3.276	0.001
average peer contribution (10)	-2.5345	0.3317	-7.642	<0.001
average peer contribution (13.33)	-2.5948	0.3346	-7.754	<0.001
average (10) * heterogeneity	0.7127	0.4164	1.712	0.087
average (13.33) * heterogeneity	0.8907	0.4179	2.131	0.033

The final model **for contributions of 20** contained average peer contribution and heterogeneity in peer contributions as predictors:

	Estimate	Std. Error	z-value	P-value
(Intercept)	-14.3402	1.5627	-9.177	<0.001
heterogeneity in peer contributions	1.9519	0.4378	4.458	<0.001
average peer contribution (10)	2.5724	0.7352	3.499	<0.001
average peer contribution (13.33)	6.4348	0.8979	7.166	<0.001

In summary, heterogeneity in peer contributions affects the incidence of extreme contributions in both ways; it has a positive effect on both the frequency of contributions of 0 and the frequency of contributions of 20. Average contribution also had an effect in both cases, but in opposite directions.

Effect of exclusion of unresponsive individuals

For the results presented in this study, individuals that were completely unresponsive (always made the same contribution, regardless of peer contributions) were excluded from the analysis. These were in total 22 subjects (8.8%); 21 unconditional free-riders (always contributing 0), and one unconditional cooperator (always contributing 20). The exclusion of these individuals from our analysis does not affect our conclusions. Their inclusion would increase the frequency of response contributions of 0 and 20 with the same amount for each combination of peer contributions (resulting in the same amount of extra red and blue in each bar of Fig. 1). Since all unresponsive individuals would have been classified as 'neutral responders to heterogeneity' (resulting in a larger 'neutral' group in Fig. 2), their exclusion does not affect the differences in cooperation tendency that we observe between positive and negative responders to heterogeneity (see Fig. S3).

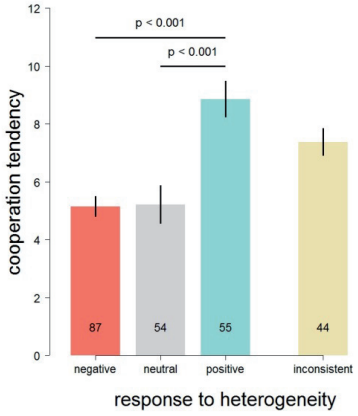

Figure S3. Response to heterogeneity in peer contributions is associated with cooperation tendency, also when including unresponsive individuals in the analysis. Bars show the average and SEM of contributions. Statistically significant differences between types are indicated (Tukey HSD), except for differences between inconsistent responders and any of the other groups. Numbers at the bottom of each bar indicate the number of subjects falling in the respective category.

4. Details of the experimental set-up

The current experiment was part of a larger experiment that was designed to test the effects of positive assortment on cooperation in human groups. Here, we give a full description of the entire experimental set-up.

At the start of each session, all subjects received written instructions that were also read aloud by one of the experimenters (full instructions are included in chapter 4 of the Supplementary Materials). Individuals did not know that the experiment was designed to test the effects of assortment or information about assortment in the first rounds of the experiment, or that the first rounds were used to measure general cooperation tendency for the current study.

As described in the main text, subjects first anonymously interacted in a Public Goods Game (PGG) for 10 rounds in groups of four, with changing group compositions in each round. The average contribution in these ten rounds was used as a measure of individual cooperation tendency in this study.

After the first 10 rounds, subjects played another 15 rounds of the PGG. This part was designed to test the effects of assortment and information about assortment. Each session was assigned to one of three treatments: *i)* assortment with information, *ii)* assortment without information, and *iii)* no assortment. Prior to this part, subjects received new instructions relevant to the treatment of their session. In the assortment treatments (*i* and *ii*), subjects were assorted in groups of four based on their decisions in the first 10 rounds of the PGG; the individuals that contributed most were grouped together, as were the individuals that contributed least, and the individuals that were in between. Individuals then played 15 more rounds of the PGG in these assorted groups, with fixed group membership over all rounds. In treatment *i*, individuals were made aware of the assortment regime, and were told in which group they were to be assorted (*i.e.*, they had information about the general cooperation tendency of their fellow group members). In treatment *ii*, individuals did not have this information, and were only told that

they would now interact in fixed groups. In treatment *iii*, individuals were grouped randomly, and were only told that they would now interact in fixed groups.

After these 15 rounds, the second part of the current study ensued: individuals were asked how much they would contribute in various situations with different contributions of fellow groups members (as explained in the main text).

To demonstrate that the results described in the main text of this study were not affected by the assortment regimes described above, we show our results separately for each treatment in Fig. S3 bel

i: assortment, info *ii*: assortment, no info *iii*: control

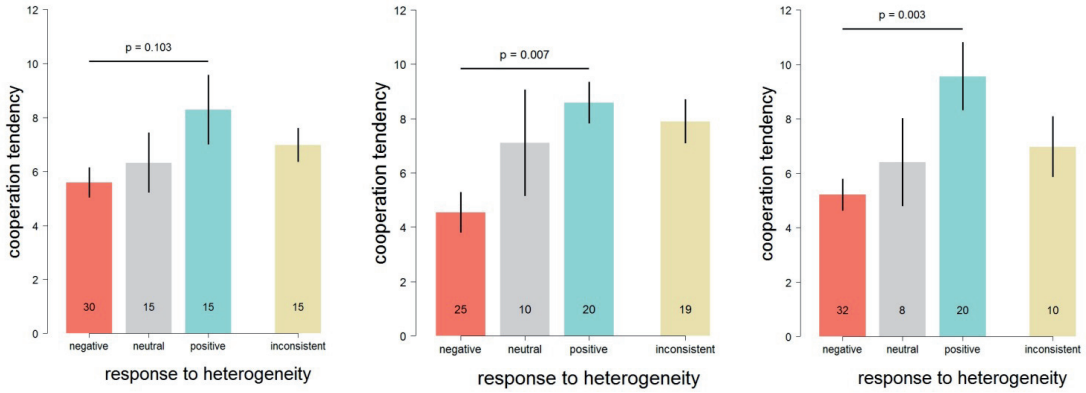

Figure S4. Response to heterogeneity in peer contributions is associated with cooperation tendency independent of experimental treatment. Bars show the average and SEM of contributions over 10 rounds of a public goods game, where group composition was randomised before every round, separately for individuals who had earlier experienced treatments *i* (assortment with information), *ii* (assortment without information) and *iii* (control; no assortment). All three graphs show the *P*-value of a Tukey HSD test, comparing the cooperation tendency of negative and positive individuals. Only for the subset of individuals that were in treatment *i*, response to heterogeneity does not significantly predict general cooperation tendency, but even in this case the effect is in the same direction as the overall pattern. Numbers at the bottom of each bar indicate the number of subjects falling in the respective category.

5. Experimental instructions

Below, the experimental instructions are shown that subjects received at the start of the session. Those instructions were read aloud by one of the experimenters.

Introduction

Welcome to this experiment!

This session will last for approximately one hour. During the session it is **not allowed to talk** or communicate with the other participants. If you have a question, please raise your hand and one of us will come to you to answer it.

In this experiment you will play a game in which you can earn points. After the experiment, these points will be converted into real money (50 points = 1€). The amount you earn depends on your decisions and the decisions of others. At the end of the experiment, you are asked to fill out a Questionnaire.

The money you earn will be paid to you in cash individually in the reception room. **Please stay seated at the end of the session** until your desk number is called. We will not inform any of the other participants about your earnings.

Instructions

In this experiment you will play a game. The game is subdivided in rounds. First, you will play a block of **10 rounds**. At the beginning of each round, the participants in the room are randomly divided into four groups of four players. Group members are anonymous, so you will not know who the other members are, and the other members will not know who you are. The **groups are randomly formed in the beginning of each new round**. This means that you are in a different group in every round. After the first block of 10 rounds, you will receive new instructions on the computer screen for the rest of the experiment.

Progress of the game:

1. At the start of a round, you are given 20 points.
2. Next, you decide how many points (0-20) you contribute to a group project, and how many points you keep for yourself. At the same time, the other three members of your group make their decision about the use of their points.
3. After all group members have made their decision, all points contributed to the group project are summed, and the game organizer doubles this number of points.
4. The doubled number of points is divided equally among the group members (irrespective of how much they contributed to the group project)**.**
5. The points you earn in a round will be stored in the computer memory. These points cannot be used in following rounds. At the end of each round, you are informed about the contributions and earnings in your group. When a new round begins, new groups are formed and you are given another 20 points to start with.
6. After ten rounds, the first block of rounds is over, and new instructions will be given on the computer screen.

Your points after a round:

The points you keep for yourself
plus
the points you earn from the group project

Group project – Example 1

All 4 players contribute 20 points to the group project: 80 points in total.

The number of points in the group project is doubled to 160 (2x80) points.

The points from the group project are divided equally among the four players: 40 points for each.

At the end of the round, each player has earned 40 points.

Group project – Example 2

Three players (A, B and C) contribute 20 points to the group project; one player (D) contributes 0 points. Hence, in total 60 points are contributed to the group project.

The number of points in the group project is doubled to 120 (2×60) points.

The points from the group project are divided equally among the four players; 30 points for each.

In this round, players A, B and C obtain 30 points (zero points kept for themselves *plus* 30 points earned from the group project), and player D obtains 50 points (20 points D kept for himself *plus* 30 points from the group project).

Supplementary Information – Chapters III and IV

Contents

Justification to remove cases

To ensure the reliability of our data, we removed those participants (53 males and 40 females) who did not read the rather complex instructions of Stage Two and were thus likely not able to understand the conditions of the game and whose attack and defense decisions consequently were thus more or less random. The removed participants, who managed to read the instructions of approximately 3000 words and pass the comprehension questions in less than 25 seconds, form a distinctive spike in the histogram visualizing the time participants used to read the instructions for part two (Figure S1 and S2). Figure S1 presents the overall data, and figure S2 the fine scale histogram which stands as the grounds to remove participants that used less than 25 seconds to read the instructions.

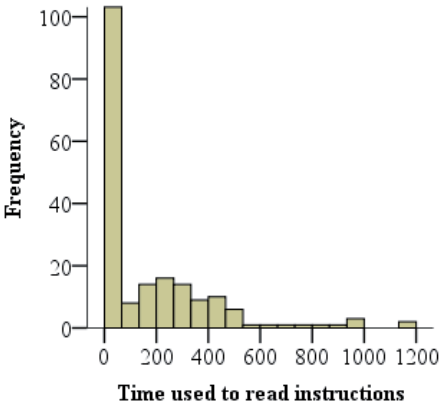

Figure S1. Histogram of time participants used to read the instructions.

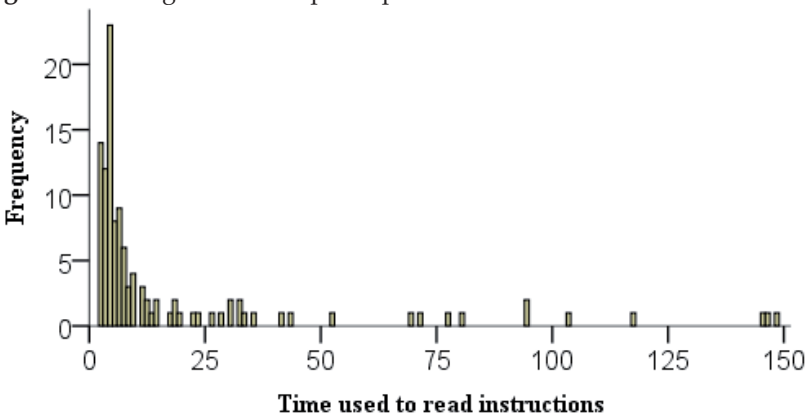

Figure S2. Fine-scale histogram of time participants used to read the instructions. Bar width is 1 second. Participants who used under 25 second to read the instructions and get through the comprehension questions were excluded from the main analysis.

Results with the full data set (Chapter III)

The analyses used here are identical with the corresponding results in the article. Please refer to the main article for a description of statistical methods.

1. Motivations of Attacks

Patterns in the whole data set were similar to those in the restricted case used in the article.

1.1 Attack decisions' sensitivity to defense

Attack decisions were not sensitive to defence for both genders, as the within-subject estimates did not differ for males ($F_{2.77,351.28} = 0.25$, $p = 0.844$) or females ($F_{2.47, 350.67} = 0.79$, $p = 0.498$), nor were there interactive effects of defence and treatment for males ($F_{8.30, 351.28} = 1.01$, $p = 0.392$) or females ($F_{8.84,350.67} = 1.16$, $p = 0.321$).

1.2. Motivations to attack

The average contributions to Public and Private Attack accounts differed between treatments for both genders, but in a different manner for each (Figure S3; Males: $F_{3,127} = 9.03$, $p < 0{,}001$; Females: $F_{3,119} = 5.43$, $p = 0.002$). In males, attack contributions did not differ between Public Goods and Private Goods treatments, nor within the Public and Private accounts within the Trade-off treatment (Figure S3 and Table S1). Whereas contributions to both Public and Private attack accounts in the Trade-off treatment were significantly smaller than when they were the only options in Public Good and Private Good treatments. In females, contributions between Public Good treatment and contributions to Public Good and Private Good accounts in Trade-off treatment did not differ from each other (Figure S3 and Table S1). Whereas contributions to these three accounts were all significantly smaller than contributions in Private Good treatment.

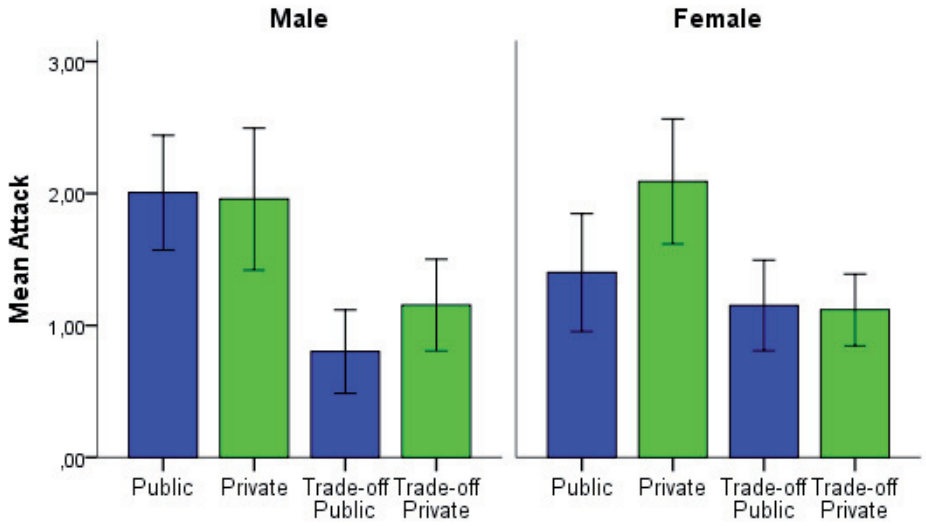

Figure S3. Mean attack contributions across three treatments, separated by gender. Blue bars represent contributions to the Public Good attack accounts and green bars contributions to the Private Good attack account. Error bars indicate +/- 2 standard errors.

Table S1. Contrast Results (K Matrix) for repeated measure ANOVA of attack contributions to public and private accounts between treatments.

		Gender	Difference (Estimate)	Std. Error	Sig.
Public only	Private only	Female	0.69	0.28	0.014
		Male	-0.05	0.29	0.868
	Public trade off	Female	-0.25	0.29	0.386
		Male	-1.20	0.29	< 0.001
	Private trade off	Female	-0.32	0.29	0.264
		Male	-0.94	0.29	0.001
Private only	Public trade off	Female	-0.90	0.28	0.002
		Male	-1.14	0.30	< 0.001
	Private trade off	Female	-0.97	0.28	0.001
		Male	-0.83	0.29	0.005

2. *Association of In-group and Out-group prosociality*

Associations between ISVO and OSVO were similar in the full data set and the restricted case. In-group Social Value orientation (ISVO) was positively associated with Out-group Social Value Orientation (OSVO, Figure S4, Table S2). Yet, on average subjects allocated less money to out-group than in-group members according to a one-sample t-test of ISVO-OSVO against zero (Figure S4; Males: t_{96}=4.92, p < 0,001; Females: t_{93} =6.59, p < 0,001).

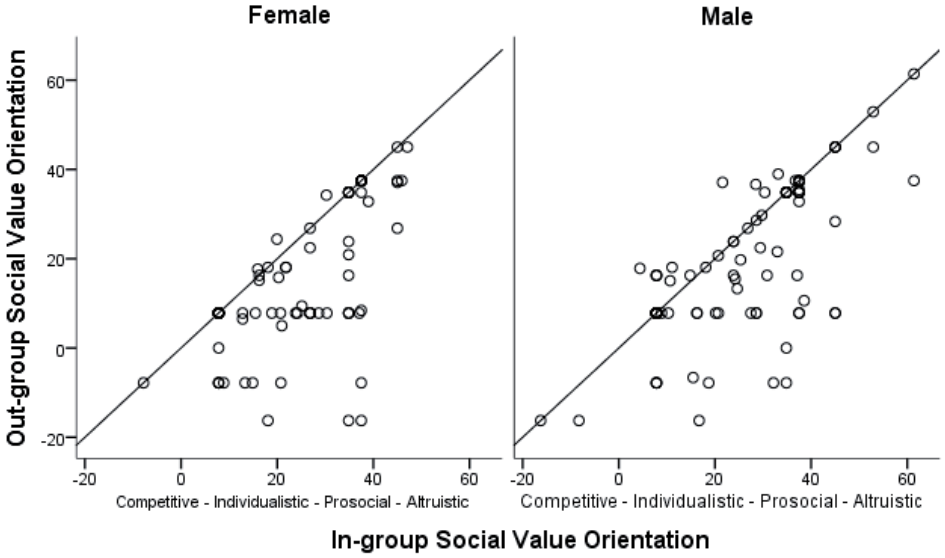

Figure S4. The relationship between Social Value Orientation toward in-group members and out-group members with the whole data. The diagonal line represents the span of equal SVOs.

3. SVOs associations with attack and defence

For males, the strong associations of Social Value Orientation measures with attack and defense contributions were present also for the whole data set, but were weaker (Figures S5, S6 and Table S2).

The consistent association of prosociality measures and attack separately for public and private goods were also present for the whole data in each measurement (2-tailed significant Pearson correlations are marked by * for p < 0.05 and ** for p < 0.001. ISVO Public: r = 0.57*; ISVO Private: r = 0.52**; OSVO Public: r = 0.52**, OSVO Private: r = 0.65**; SSVO Public: r = 0.47*, SSVO Private: r = 0.49**). For females, with the restricted data set, there were no significant correlations between attack and SVOs but with the whole data set there emerged a weak significant positive association between attack and ISVO (r = 214*) and SSVO (r = 217*, Figures 5, 6; Table 2). In addition, with the whole

data set there emerged a weak positive association between OSVO and defense (r = 0.229*).

However, for those who did not read the instructions (passed the instructions and comprehension questions in less than 25 sec) there were no significant correlations between any SVO measure and attack values for both genders (Pearson 2-tailed correlations for Males ISVO – Attack: 0.117; p = 0.402. OSVO – Attack: 0.250; p = 0.071. SSVO: 0.221; p = 0.112. For Females ISVO - Attack: 0.282; p = 0.077. OSVO – Attack: 0.143; p = 0.380. SSVO: 0.212; p = 0.188).

The associations between SVO measures and attacks for those males who read the instructions were strong, but there were no associations with those who did not read the instructions. This further implies that they contributed to Attack Accounts randomly and suggests that those who passed the instructions in less than 25 seconds should be removed from the analysis.

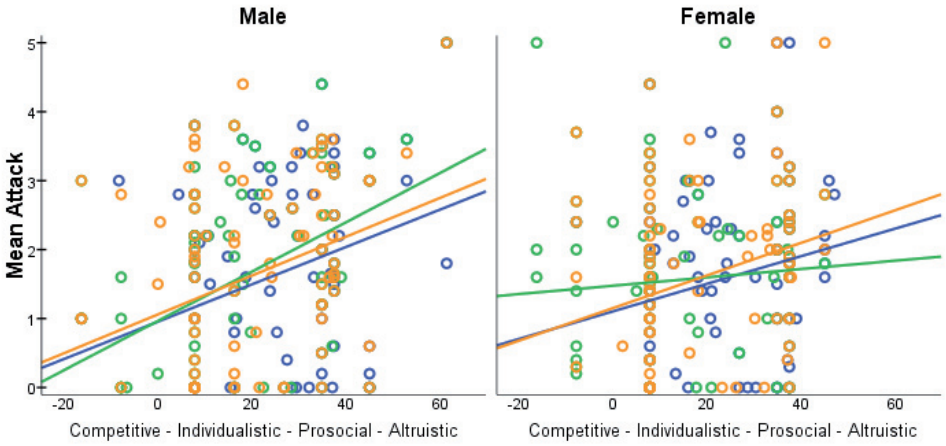

Figure S5. Associations between Social Value Orientations and mean attack contribution (blue: In-group Social Value Orientation, green: Out-group Social Value Orientation, orange: Standard Social Value Orientation).

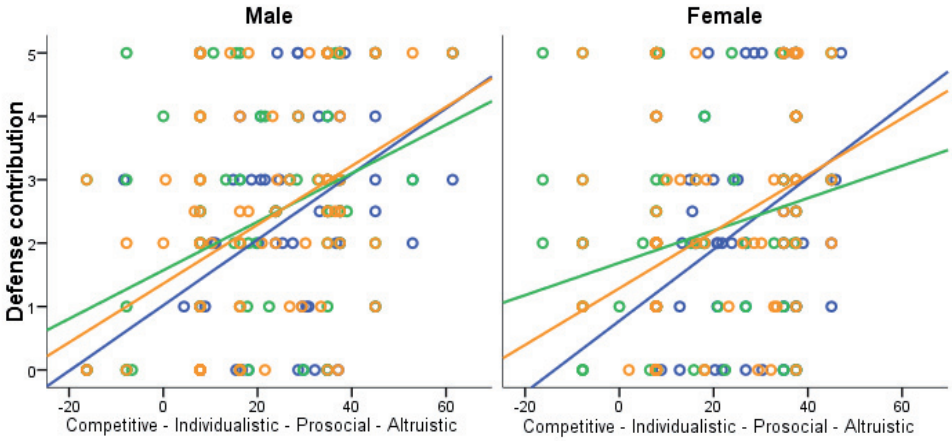

Figure S6. Association between Social Value Orientations and mean defense contributions (blue: In-group Social Value Orientation, green: Out-group Social Value Orientation, orange: Standard Social Value Orientation).

Table S2. Pearson Correlations (2-tailed) of mean attack contributions, mean defense contributions and SVO measures (ISVO: In-group Social Value Orientation, OSVO: Out-group Social Value Orientation, SSVO: Standard Social Value Orientation) for the whole data. Results for males (n = 98) are above the diagonal and females (n = 94) below. Significant correlations are marked by * for $p < 0.05$ and ** for $p < 0.001$.

	Attack	**Defense**	**ISVO**	**OSVO**	**SSVO**
Attack		0.47**	0.29**	0.44**	0.33**
Defense	0.45**		0.41**	0.35**	0.41**
ISVO	0.21*	0.44**		0.69**	0.75**
OSVO	0.08	0.23*	0.66**		0.82**
SSVO	0.27**	0.37**	0.72**	0.73**	

4. in-group preference - Attacking

Results for the effect of in-group preference (ISVO minus OSVO) and ISVO on attack contributions are similar in the whole data set and the data in the article. ISVO positively affects attack contributions (standardized $\beta = 0.41$, $t = 4.15$, $p < 0.001$), and in-group preference was associated with a lower tendency to attack (standardized $\beta = -0.32$, $t = -3.29$, $p = 0.001$). For females, neither ISVO (standardized $\beta = 0.19$, $t = 1.80$, $p = 0.076$) nor in-group preference (standardized $\beta = 0.09$, $t = 0.85$; $p = 0.399$) predicted attack contributions as they did for the data in the article.

Pooling Treatments (Chapter IV)

We justify the pooling of treatments in Chapter IV because there are no significant differences in any measured scale between the treatments (Table S3). This test includes component scales for honour code not used in the final analysis (we used only the street scale).

Table S3. ANOVA results for between-treatment differences in all measured scales.

Factor	**F**	**p**
Attack	1.86	0.162
Defense	0.19	0.825
SVO	1.61	0.200
Parental Harshness	0.02	0.978
Un-Belonging	1.08	0.343
Honour Code (street)	2.53	0.083
Honour Code (revenge)	1.30	0.274
Honour Code (forgive)	0.77	0.467
Religiosity	0.48	0.623
Sexuality	0.18	0.839

Full Results for Structural Equation Models (Chapter IV)

Table S4. Structural equation model results for males. Fully standardized solutions (β_{STDYX}) are also given for structural parameters.

Variable		β	S.E.	β_{STDYX}	z	p
SVO						
	Parental Harshness	**11.96**	**3.50**	**0.53**	**3.42**	**0.001**
	Religiosity	-0.80	0.77	-0.09	-1.04	0.299
	Honour Code	-1.82	1.83	-0.10	-0.99	0.320
	Un-Belonging	-0.63	1.36	-0.07	-0.47	0.642
Attack						
	Parental Harshness	**1.16**	**0.32**	**0.55**	**3.68**	**< 0.001**
	Religiosity	0.09	0.14	0.10	0.66	0.508
	Honour Code	-0.07	0.19	-0.04	-0.35	0.728
	Un-Belonging	-0.25	0.17	-0.27	-1.47	0.142
Religiosity						
	Parental Harshness	0.19	0.25	0.08	0.77	0.440
Honour Code						
	Parental Harshness	0.13	0.15	0.10	0.88	0.381
Un-Belonging						
	Parental Harshness	**1.40**	**0.25**	**0.60**	**5.54**	**< 0.001**
Residual Covariance						
	SVO with Attack	**6.53**	**2.25**	**0.37**	**2.91**	**0.004**

Table S5. Structural equation model results for females. Fully standardized solutions (β_{STDYX}) are also given for structural parameters.

Variable		β	S.E.	β_{STDYX}	z	p
SVO						
	Parental Harshness	2.22	1.86	0.14	1.20	0.231
	Religiosity	-0.26	0.85	-0.04	-0.31	0.758
	Honour Code	-2.31	1.98	-0.14	-1.16	0.245
	Un-Belonging	-0.90	1.47	-0.07	-0.61	0.543
Attack						
	Parental Harshness	-0.16	0.19	-0.10	-0.83	0.405
	Religiosity	0.05	0.11	0.07	0.48	0.634
	Honour Code	-0.01	0.26	-0.01	-0.04	0.966
	Un-Belonging	-0.05	0.20	-0.04	-0.23	0.816
Religiosity						
	Parental Harshness	**-0.61**	**0.18**	**-0.29**	**-3.39**	**0.001**
Honour Code						
	Parental Harshness	0.11	0.13	0.11	0.83	0.405
Un-Belonging						
	Parental Harshness	**0.64**	**0.17**	**0.49**	**3.82**	**< 0.001**
Residual Covariance						
	SVO with Attack	**6.06**	**2.93**	**0.29**	**2.07**	**0.038**

Questionnaire scales

To achieve metric invariance we needed to remove from analyses item 5 in un-Belonging and items 2, 5 and 10 in Honour Code that had largest non-invariance between the sexes.'

Parental Harshness:
1. How often did a parent or other adult in the household make you feel that you were loved, supported, and cared for? (RC)
2. How often did a parent or other adult in the household swear at you, insult you, put you down, or act in a way that made you feel threatened?
3. How often did a parent or other adult in the household express physical affection for you, such as hugging, or other physical gestures of warmth and affection? (RC)
4. How often did a parent or other adult in the household push, grab, shove, or slap you?
5. How often would you say that a parent or other adult in the household behaved violently toward a family member or visitor in your home?
6. How often would you say there was quarreling, arguing, or shouting between your parents?
7. How often would you say there was quarreling, arguing, or shouting between a parent and you?
8. How often would you say there was quarreling, arguing, or shouting between a parent and one of your siblings
9. How often would you say there was quarreling, arguing, or shouting between your sibling(s) and you?
10. How often would you say you were neglected while you were growing up, that is, left on your own to fend for yourself?

Belonging:
1. I feel disconnected from the world around me.
2. Even around people I know, I don't feel that I really belong.
3. I feel so distant from people.
4. I have no sense of togetherness with my peers.
5. I don't feel related to anyone.
6. I catch myself losing all sense of connectedness with society.
7. Even among my friends, there is no sense of brother/sisterhood.
8. I don't feel I participate with anyone or any group

Honour Street Code:

1. Sometimes, you have to fight to uphold your honor or put someone in his or her place.
2. When someone insults you or harms you, it's up to you to handle it yourself.
3. You have to convince people that you're not a "chump" or a "sucker."
4. When people disrespect you, you sometimes must use violence to teach them not to.
5. People will take advantage of you if you don't let them know how tough you are.
6. People do not respect a person who is afraid to fight physically for his/her rights.
7. It is important to show others that you cannot be intimidated.
8. People tend to respect a person who is tough and aggressive.
9. If a person wants to be your enemy, you should treat them like an enemy.
10. Sometimes you need to threaten people in order to get them to treat you fairly.

Religiosity:

1. I am closely connected to and involved in my religion
2. I am an active member of religious organization
3. I am a religious person.

Instructions of the experiment

General Instructions

Welcome to our study

This study is conducted in collaboration of the VU Amsterdam (Dr. Hannes Rusch), The Netherlands, and the University of Jyväskylä (Jaakko Junikka, MSc), Finland.

Participation in this study takes about 45 minutes. For completing the study you will receive a participation fee of $2.50. On top of your participation fee, you can earn up to $12.50 extra depending on your decisions in the study, the decisions of other participants, and random events.

PLEASE NOTE: This is an economic decision study.

This means: This study does not involve any kind of deception. You will be fully informed about the consequences of your decisions for your extra earnings and we pay you exactly as described in the course of the study. Also, whenever we speak of 'other participants' in the course of this study, this refers to real participants of the study; that means: Your decisions will affect your earnings and also the earnings of other people participating in this study.

At the end of the study, you will receive a 'study completion code'. Please enter this code in the respective field at MTurk. After we have verified your completion of the study, you will receive your participation fee. Later, when we have collected all decisions from all participants, we will calculate your extra earnings and pay them to you as a bonus payment.

In case you have any questions about the study, please feel free to contact:

Jaakko Junikka.

Final note:

You are welcome to participate in this study one time. In case you try to participate multiple times, we will not approve your completion of any of these trials and you will not be paid.

General notes on the structure and payment mechanism of this study:

This study has three main parts, followed by a questionnaire section. In the three main parts, you will be making a series of decisions that can affect your extra earnings and potentially also the earnings of other participants.

Although you will be making a series of decisions, eventually only one decision will determine your entire extra earnings from this study. After we have collected all decisions from all participants, we will randomly determine which decision this is. We use this payment mechanism in this study, because we want you to think through every decision you make in the following as if it were the only decision you make in the entire study.

So please note:

Your entire extra earnings from this study are determined by one randomly chosen decision. And since you do not know which decision this will be, you should really think through all of the following decisions carefully: Any of them could be the one determining your entire extra earnings.

After you have made your decisions in the three main parts, a questionnaire section will follow. In that section we ask you for your personal views on a number of questions to which there are no right or wrong answers. Your extra earnings do not depend on the answers you give here. To be eligible for receiving the participation fee, however, you also need to complete the questionnaire section.

The consequences that your decisions have on your own extra earnings and possibly also on the extra earnings of other participants will be fully explained before you make your decisions.

All amounts stated are US-Dollars.

Depending on your own decisions, the decisions of other participants, and on which decision is eventually chosen randomly to be paid out, you can earn between $0.00 and $12.50 extra in the following.

Group formation:

For PART 1 and the subsequent PART 2 of this study, you and three other randomly chosen participants form a group of four. This group will be referred to as 'your group' from now on. Your group will be randomly matched with another group of four randomly chosen participants. That group will be referred to as 'the other group'.

PART 1 (Common for all three Treatments)

You will now make six decisions about how you would like to split a given amount of money between you and the other three members of your group.

For each of these six decisions you will have nine possible allocations to choose from.

If one of the following decisions is chosen to determine your extra earnings, you will receive the amount that you allocate to yourself and each of the three other members of your group will receive the amount that you allocated to your group members.

Example:

In this example, a participant has decided to allocate $1.70 to herself and will earn $1.70 extra if this decision is eventually chosen to be paid out. Each of the other three members of her group will receive $1.18 in this case.

Comprehension question

In following you will make decisions about how to split certain amounts of money between you and ...

- ... three randomly chosen members of the other group. (1)
- ... the three other members of your own group. (2)

PART 1, continued

Again, you will now make six decisions about how you would like to split a given amount of money.

This time, however, you will split the money between you and three randomly chosen members of the other group, i.e. the group which your group is matched with for PART 1 and PART 2.

For each of these six decisions you will have nine possible allocations to choose from.

If one of the following decisions is chosen to determine your extra earnings, you will receive the amount that you allocate to yourself and each of the three randomly chosen members of the other group will receive the amount that you allocated to them.

Comprehension question

In following you will make decisions about how to split certain amounts of money between you and ...

- ... three randomly chosen members of the other group. (1)
- ... the three other members of your own group. (2)

PART 2 (Public Good Treatment)

Thank you for completing PART 1 of the study.

In the following PART 2 you are still grouped with the same three other participants as before, and your group is still matched with another group of four participants.

For PART 2, the members of the other group are endowed with $10.00 each.

You, and the other members of your group, are endowed with $5.00 each.

What the other group decides in this part:

The members of the other group make the following decision:

Their group has a group account G. Each of them also has a private account. Of their $10.00, they can invest up to $5.00 into their group's account G.

All the money which they do not invest into account G remains in their private accounts. As a result of the decisions of the four members of the other group, there will be between $0.00 and $20.00 in their group account G.

What you and your group members decide in this part:

In the following, you will make five investment decisions, one for each of the following cases.

CASE 1) There is no money in the other group's account G.
CASE 2) There are $1-$5 in the other group's account G.
CASE 3) There are $6-$10 in the other group's account G.
CASE 4) There are $11-$15 in the other group's account G.
CASE 5) There are $16-$20 in the other group's account G.

You, and the other members of your group, will each make the following decision for each of the five cases:

Each one of you has two accounts into which you can invest: Account A, and a private account. You can freely distribute your $5.00 between your two accounts. The other three members of your group can also distribute their $5.00 between their own two accounts.

How earnings are calculated if this part of the study is chosen to be paid out:

Once everyone has made their decisions about how to invest their endowments, earnings are calculated as follows:

The actual size of the other group's account G is determined by adding up all the investments into account G by the members of the other group. Then, the respective decisions which you and the other members of your group made for that particular size of account G are used for all subsequent calculations.

The total of all A accounts for you and your group members are summed. We call this total 'S'.

The relative contribution, called a, which you have made to S through your A account is determined.

For example:

Assume that you have invested $1 in your A account. Also assume that S amounts to $10 (just meaning that the sum of all A accounts of your group is $10). Then the relative contribution of your A account is a = $1/$10 = 0.10.

The other group's account G is set off against your A account in the following way:

For every $1 in the other group's account G, your A account is reduced by your relative contribution a x $1.

In the example: Assume that there are $5 in account G. Then, your A account is reduced by 0.10 x $5 = $0.50. The A accounts of your group members are reduced in the same way, also depending on their relative contributions to S. As a result of this offsetting, the balance of your A account can be negative (in the case that G > S), zero (in the case that G = S), or positive (if G < S). All accounts that have a negative or zero balance after offsetting are closed and have no further consequences.

Finally, your returns from your accounts are calculated like this:

Private account: All the money that you have invested in your private account is yours.

Account A: If your account A has a positive balance, this amount is doubled and deducted in equal shares from the private accounts of the members of the other group. This means: For every $1 remaining in your A account, $0.50 are deducted from each of the private accounts of the other group's members, resulting in a total $2 reduction of the earnings of the other group. These $2 are then equally distributed within your group.

That means for every $1 remaining in your A account after offsetting, you receive $0.50 and every other member of your group also receives $0.50.

Examples

Below you see two example calculations of the earnings of the members of your group given their respective investment decisions and the amount the other group invested into their group account G.

Example 1

Other group Account G amounts to $6.00

Your group	Member 1	Member 2	Member 3	Member 4
Investment Account A	5	4	2	0
Investment Private Account	0	1	3	5
Sum of all A accounts	S = 11			
Relative contribution a	5/11 = 0.45	4/11 = 0.36	2/11 = 0.18	0/11 = 0.00
Account A after offsetting	5 - 6 x 0.45 = 2.30	4 - 6 x 0.36 = 1.84	2 - 6 x 0.18 = 0.92	0.00
Earnings from own A account	0.50 x 2.30 = 1.15	0.50 x 1.84 = 0.92	0.50 x 0.92 = 0.46	0.00
Earnings from other A accounts	0.50 x (1.84 + 0.92) = 1.38	0.50 x (2.30 + 0.92) = 1.61	0.50 x (2.30 + 1.84) = 2.07	0.50 x (2.30 + 1.84 + 0.92) = 2.53
Earnings from Private Account	0.00	1.00	3.00	5
Total earnings	$2.53	$3.53	$5.53	$7.53

Example 2

Other group Account G amounts to $2.00

Your group	Member 1	Member 2	Member 3	Member 4
Investment Account A	5	4	2	0
Investment Private Account	0	1	3	5
Sum of all A accounts	S = 11			
Relative contribution a	5/11 = 0.45	4/11 = 0.36	2/11 = 0.18	0/11 = 0.00
Account A after offsetting	5 - 2 x 0.45 = 4.10	4 - 2 x 0.36 = 3.28	2 - 2 x 0.18 = 1.64	0.00
Earnings from own A account	0.50 x 4.10 = 2.05	0.50 x 3.28 = 1.64	0.50 x 1.64 = 0.82	0.00
Earnings from other A accounts	0.50 x (3.28 + 1.64) = 2.46	0.50 x (4.10 + 1.64) = 2.87	0.50 x (4.10 + 3.28) = 3.69	0.50 x (4.10 + 3.28 + 1.64) = 4.51
Earnings from Private Account	0.00	1.00	3.00	5
Total earnings	$4.51	$5.51	$7.51	$9.51

Comprehension question

Assume that there is more money in the other group's account G than your group invested in their A accounts in total, that means: assume G > S. In this situation, what will you earn through your investments in your A account?

- I will earn 0.5 times my investment in A and every other member of my group will also earn 0.5 my investment in A. In addition I will earn extra money through my group members' investments in their A accounts. (1)
- If G > S then all A accounts of my group's members are closed and will not produce any earnings. (2)

Comprehension question

The other group will lose $2 for every $1 remaining in any of the A accounts of your group after offsetting.How are these $2 distributed among the members of your group?

- I will receive the entire $2. (1)
- Each member of my group will receive $0.50. (2)

PART 2 (Private Good Treatment)

Thank you for completing PART 1 of the study. In the following PART 2 you are still grouped with the same three other participants as before, and your group is still matched with another group of four participants.

For PART 2, the members of the other group are endowed with $10.00 each.

You, and the other members of your group, are endowed with $5.00 each.

What the other group decides in this part:

The members of the other group make the following decision: Their group has a group account G. Each of them also has a private account. Of their $10.00, they can invest up to $5.00 into their group's account G. All the money which they do not invest into account G remains in their private accounts. As a result of the decisions of the four members of the other group, there will be between $0.00 and $20.00 in their group account G.

What you and your group members decide in this part:

In the following, you will make five investment decisions, one for each of the following cases.

CASE 1) There is no money in the other group's account G.
CASE 2) There are $1-$5 in the other group's account G.
CASE 3) There are $6-$10 in the other group's account G.
CASE 4) There are $11-$15 in the other group's account G.
CASE 5) There are $16-$20 in the other group's account G.

You, and the other members of your group, will each make the following decision for each of the five cases: Each one of you has two accounts into which you can invest: Account A, and a private account. You can freely distribute your $5.00 between your two accounts. The other three members of your group can also distribute their $5.00 between their own two accounts.

How earnings are calculated ***if this part of the study is chosen to be paid out*****:**

Once everyone has made their decisions about how to invest their endowments, earnings are calculated as follows: The actual size of the other group's account G is determined by adding up all the investments into account G by the members of the other group. Then, the respective decisions which you and the other members of your group made for that particular size of account G are used for all subsequent calculations.

The total of all A accounts for you and your group members is summed. We call this total 'S'. The relative contribution, called a, which you have made to S through your A account is determined.

For example: Assume that you have invested $1 in your A account. Also assume that S amounts to $10 (just meaning that the sum of all A accounts of your group is $10). Then the relative contribution of your A account is a = $1/$10 = 0.10.

The other group's account G is set off against your A account in the following way:

For every $1 in the other group's account G, your A account is reduced by your relative contribution a x $1. In the example: Assume that there are $5 in account G. Then, your A account is reduced by 0.10 x $5 = $0.50. The A accounts of your group members are reduced in the same way, also depending on their relative contributions to S. As a result of this offsetting, the balance of your A account can be negative (in the case that G > S), zero (in the case that G = S), or positive (if G < S). All accounts that have a negative or zero balance after offsetting are closed and have no further consequences.

Finally, your returns from your accounts are calculated like this:

Private account: All the money that you have invested in your private account is yours.

Account A: If your account A has a positive balance, this amount is doubled and deducted in equal shares from the private accounts of the members of the other group. This means: For every $1 remaining in your A account, $0.50 are deducted from each of the private accounts of the other group's members, resulting in a total $2 reduction of the earnings of the other group. Of these $2, you receive $1.50. The remaining $0.50 are not paid to anyone.

That means for every $1 remaining in your A account after offsetting, you receive $1.50.

Examples

Below you see two example calculations of the earnings of the members of your group given their respective investment decisions and the amount the other group invested into their group account G.

Example 1

Other group Account G amounts to $6.00

Your group	Member 1	Member 2	Member 3	Member 4
Investment Account A	5	4	2	0
Investment Private Account	0	1	3	5
Sum of all A accounts	S = 11			
Relative contribution a	5/11 = 0.45	4/11 = 0.36	2/11 = 0.18	0/11 = 00
Account A after offsetting	5 - 6 x 0.45 = 2.30	4 - 6 x 0.36 = 1.84	2 - 6 x 0.18 = 0.92	0.00
Earnings from own A account	1.50 x 2.30 = 3.45	1.50 x 1.84= 2.76	1.50 x 0.92= 1.38	0.00
Earnings from Private Account	0	1	3	5
Total earnings	$3.45	$3.76	$4.38	$5.00

Example 2

Other group Account G amounts to $2.00

Your group	Member 1	Member 2	Member 3	Member 4
Investment Account A	5	4	2	0
Investment Private Account	0	1	3	5
Sum of all A accounts	S = 11			
Relative contribution a	5/11 = 0.45	4/11 = 0.36	2/11 = 0.18	0/11 = 00
Account A after offsetting	5 - 2 x 0.45 = 4.10	4 - 2 x 0.36 = 3.28	2 - 6 x 0.18 = 0.92	0.00
Earnings from own A account	1.50 x 2.30 = 3.45	1.50 x 1.84 = 2.76	2 - 2 x 0.18 = 1.64	0.00
Earnings from Private Account	0	1	3	5
Total earnings	$6.15	$5.92	$5.46	$5.00

Comprehension question

Assume that there is more money in the other group's account G than your group invested in their A accounts in total, that means: assume G > S. In this situation, what will you earn through your investments in your A account?

- I will earn 1.5 times my investment in A. (1)
- If G > S then all A accounts of my group's members are closed and will not produce any earnings. (2)

Comprehension question

The other group will lose $2 for every $1 remaining in your A account after offsetting.How are these $2 distributed among the members of your group?

- I will receive $1.50 and the remaining $0.50 will not be paid to anyone. (1)
- Each member of my group will receive $0.50. (2)

PART 2 (Trade-off Treatment)

Thank you for completing PART 1 of the study.

In the following PART 2 you are still grouped with the same three other participants as before, and your group is still matched with another group of four participants.

For PART 2, the members of the other group are endowed with $10.00 each. You, and the other members of your group, are endowed with $5.00 each.

What the other group decides in this part:

The members of the other group make the following decision: Their group has a group account G. Each of them also has a private account. Of their $10.00, they can invest up to $5.00 into their group's account G. All the money which they do not invest into account G remains in their private accounts. As a result of the decisions of the four members of the other group, there will be between $0.00 and $20.00 in their group account G.

What you and your group members decide in this part:

In the following, you will make five investment decisions, one for each of the following cases.

CASE 1) There is no money in the other group's account G.
CASE 2) There are $1-$5 in the other group's account G.
CASE 3) There are $6-$10 in the other group's account G.
CASE 4) There are $11-$15 in the other group's account G.
CASE 5) There are $16-$20 in the other group's account G.

You, and the other members of your group, will each make the following decision for each of the five cases: Each one of you has three accounts into which you can invest: Account A, Account B, and a private account. You can freely distribute your $5.00 between your three accounts. The other three members of your group can also distribute their $5.00 between their own three accounts.

How earnings are calculated if this part of the study is chosen to be paid out:

Once everyone has made their decisions about how to invest their endowments, earnings are calculated as follows: The actual size of the other group's account G is determined by adding up all the investments into account G by the members of the other group. Then, the respective decisions which you and the other members of your group made for that particular size of account G are

used for all subsequent calculations. The total of all A accounts and all B accounts for you and your group members are summed. We call this total 'S'.

The relative contributions, called a and b, which you have made to S through your A account and through your B account are determined.

For example:

Assume that you have invested $1 in your A account and $2 in your B account. Also assume that S amounts to $10 (just meaning that the sum of all A and all B accounts of your group is $10). Then the relative contribution of your A account is a = $1/$10 = 0.10, and the relative contribution of your B account is b = $2/$10 = 0.20.

The other group's account G is set off against your A account and your B account in the following way: For every $1 in the other group's account G, your A account is reduced by your relative contribution a x $1 and your B account is reduced by your relative contribution b x $1.

In the example: Assume that there are $5 in account G. Then, your A account is reduced by 0.10 x $5 = $0.50 and your B account is reduced by 0.20 x $5 = $1.
The A and B accounts of your group members are reduced in the same way, also depending on their relative contributions to S. As a result of this offsetting, the balances of your A and your B accounts can be negative (in the case that G > S), zero (in the case that G = S), or positive (if G < S). All accounts that have a negative or zero balance after offsetting are closed and have no further consequences.

Finally, your returns from your accounts are calculated like this:

Private account: All the money that you have invested in your private account is yours.

Account A:

If your account A has a positive balance, this amount is doubled and deducted in equal shares from the private accounts of the members of the other group.

This means: For every $1 remaining in your A account, $0.50 are deducted from each of the private accounts of the other group's members, resulting in a total $2 reduction of the earnings of the other group. These $2 are then equally distributed within your group. That means for every $1 remaining in your A account after offsetting, you receive $0.50 and every other member of your group also receives $0.50.
Account B:

If your account B has a positive balance, this amount is doubled and deducted in equal shares from the private accounts of the members of the other group.

This means: For every $1 remaining in your B account, $0.50 are deducted from each of the private accounts of the other group's members, resulting in a total $2 reduction of the earnings of the other group. Of these $2, you receive $1.50. The remaining $0.50 are not paid to anyone. That means for every $1 remaining in your B account after offsetting, you receive $1.50.

Examples

Below you see two example calculations of the earnings of the members of your group given their respective investment decisions and the amount the other group invested into their group account G.

Example 1
Other group Account G amounts to $6.00

Your group	Member 1	Member 2	Member 3	Member 4
Investment Account A	0	1	5	0
Investment Account B	0	1	0	5
Investment Private Account	5	3	0	0
Sum of all A and B accounts	S = 12			
Relative contribution a	0/12 = 0.00	1/12 = 0.08	5/12 = 0.42	0/12 = 0.00
Relative contribution b	0/12 = 0.00	1/12 = 0.08	0/12 = 0.00	5/12 = 0.42
Account A after offsetting	0.00	1 - 6 x 0.08 = 0.52	5 - 6 x 0.42 = 2.48	0.00
Account B after offsetting	0.00	1 - 6 x 0.08 = 0.52	0.00	5 - 6 x 0.42 = 2.48
Earnings from own A account	0.00	0.50 x 0.52 = 0.26	0.50 x 2.48 = 1.24	0.00
Earnings from other A accounts	0.50 x (0.52 + 2.48) = 1.50	0.50 x 2.48 = 1.24	0.50 x 0.52 = 0.26	0.50 x (0.52 + 2.48) = 1.50
Earnings from Account B	0.00	1.5 x 0.52 = 0.78	0.00	1.5 x 2.48 = 3.72
Earnings from Private Account	5.00	3.00	0.00	0.00
Total earnings	$6.50	$5.28	$1.50	$5.22

Example 2

Other group Account G amounts to $2.00

Your group	Member 1	Member 2	Member 3	Member 4
Investment Account A	0	1	5	0
Investment Account B	0	1	0	5
Investment Private Account	5	3	0	0
Sum of all A and B accounts	S = 12			
Relative contribution a	0/12 = 0.00	1/12 = 0.08	5/12 = 0.42	0/12 = 0.00
Relative contribution b	0/12 = 0.00	1/12 = 0.08	0/12 = 0.00	5/12 = 0.42
Account A after offsetting	0.00	1 - 2 x 0.08 = 0.84	5 - 2 x 0.42 = 4.16	0.00
Account B after offsetting	0.00	1 - 2 x 0.08 = 0.84	0.00	5 - 2 x 0.42 = 4.16
Earnings from own A account	0.00	0.50 x 0.84 = 0.42	0.50 x 4.16 = 2.08	0.00
Earnings from other A accounts	0.50 x (0.84 + 4.16) = 2.50	0.50 x 4.16 = 2.08	0.50 x 0.84 = 0.42	0.50 x (0.84 + 4.16) = 2.50
Earnings from Account B	0.00	1.5 x 0.84 = 1.26	0.00	1.5 x 4.16 = 6.24
Earnings from Private Account	5.00	3.00	0.00	0.00
Total earnings	$7.50	$6.76	$2.50	$8.74

Comprehension question

Assume that there is more money in the other group's account G than your group invested in their A and B accounts in total, that means: assume G > S. In this situation, what will you earn through your investments in your A and B accounts?

- I will earn 1.5 times my investment in B and 0.5 my investment in A, plus additional money through my group members' investments in their A accounts. (1)
- If G > S then all A and B accounts of my group's members are closed and will not produce any earnings. (2)

Comprehension question

The other group will lose $2 for every $1 remaining in any of the A accounts of your group after offsetting.How are these $2 distributed among the members of your group?

- I will receive the entire $2. (1)
- Each member of my group will receive $0.50. (2)

Comprehension question

The other group will lose $2 for every $1 remaining in your B account after offsetting.How are these $2 distributed among the members of your group?

- I will receive $1.50 and $0.50 will not be paid to anyone. (1)
- Each member of my group will receive $0.50. (2)

PART 2, continued (Common for all the three treatments)

For the following decision you are still grouped with the same three other participants as before, and your group is still matched with another group of four participants. However, the group roles are now reversed: You, and the other members of your group, are endowed with $10.00 each. The members of the other group are endowed with $5.00 each.

What you and your group members decide in this part:

Your group has a group account G. Each member of your group also has a private account. Of your $10.00, you can invest up to $5.00 into your group's account G. All the money that you do not invest into account G remains in your private account. As a result of the decisions of you and the other three members of your group, there will thus be between $0.00 and $20.00 in your group's account G.

What the other group's members decide in this part:

Each member of the other group has two accounts into which they can invest: Account A, and a private account. They can freely distribute their $5.00 between their two accounts. How earnings are calculated if this part of the study is chosen to be paid out: Once everyone has made their decisions about how to invest their endowments, earnings are calculated as follows:

The total sum of all A accounts of the other group is calculated by adding up all investments of the other group's members into their A accounts. We call this

total S. Your group's account G is offset against S by substracting G from S. If your group's account G is larger than or equal to S, meaning that S - G is negative or zero, you are paid the amount which you invested in your private account.

If, however, S is larger than G, a positive amount L = S - G remains after offsetting. Then, for every $1 of L each of your group's members (you included) lose $0.50 from your private accounts. This money your group loses is distributed among the members of the other group.

Examples

Below you see two example calculations of the earnings of the members of your group given their respective investment decisions and the amount the other group invested in total into their A.

Example 1
Other group S, that is the sum of all A accounts, amounts to $10.00

Your group	Member 1	Member 2	Member 3	Member 4
Investment Account G	0	1	2	0
Investment Private Account	5	4	3	5
Fixed in Private Account	5	5	5	5
Earnings from Private Account	5+5 = 10	4+5 = 9	3+5 = 8	5+5 = 10
Losses after offsetting G and S	-0.50 x (10 - 3) = -3.50	-0.50 x (10 - 3) = -3.50	-0.50 x (10 - 3) = -3.50	-0.50 x (10 - 3) = -3.50
Total earnings	$6.50	$5.50	$4.50	$6.50

Example 2
Other group S, that is the sum of all A accounts, amounts to $10.00

Your group	Member 1	Member 2	Member 3	Member 4
Investment Account G	4	2	3	1
Investment Private Account	1	3	2	4
Fixed in Private Account	5	5	5	5
Earnings from Private Account	1+5 = 6	3+5 = 8	2+5 = 7	4+5 = 9
Losses after offsetting G and S	-0.50 x (10 - 10) = -0.00	-0.50 x (10 - 10) = -0.00	-0.50 x (10 - 10) = -0.00	-0.50 x (10 - 10) = -0.00
Total earnings	$6.00	$8.00	$7.00	$9.00

Comprehension question

Depending on the total amount S invested by the other group into their A accounts and your group's account G it is possible that you lose money from your private account after offsetting. In which case do you lose money?

- Only if S is larger than G I lose money from my private account. (1)
- Irrespective of how large G is, I will lose $0.50 for every $1 of S, so I always lose money. (2)

PART 3 (Common for all three Treatments)

For the following PART 3, all group memberships are rescinded.

That means: There are no groups anymore.

Just like in PART 1, you will now make six decisions about how you would like to split a given amount of money.

This time, you decide about how to split the money between you and one other randomly chosen participant of this study.

For each of these six decisions you will have nine possible allocations to choose from. If one of the following decisions is chosen to determine your extra earnings, you will receive the amount that you allocate to yourself and a

randomly chosen other participant will receive the amount that you allocated to 'the other'.

Comprehension question

In following you will make decisions about how to split certain amounts of money between you and …

- ... one randomly chosen other participant of this study. (1)
- ... the three other members of your own group. (2)