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Cooperation in humans: competition between groups and proximate emotions

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Abstract

Understanding the ultimate and proximate mechanisms that favour cooperation remains one of the greatest challenges in the biological and social sciences. A number of theoretical studies have suggested that competition between groups may have played a key role in the evolution of cooperation within human societies, and similar ideas have been discussed for other organisms, especially cooperative breeding vertebrates. However, there is a relative lack of empirical work testing these ideas. Our experiment found, in public goods games with humans, that when groups competed with other groups for financial rewards, individuals made larger contributions within their own groups. In such situations, participants were more likely to regard their group mates as collaborators rather than competitors. Variation in contribution among individuals, either with or without intergroup competition, was positively correlated with individuals' propensity to regard group mates as collaborators. We found that the levels of both guilt and anger individuals experienced were a function of their own contributions and those of their group mates. Overall, our results are consistent with the idea that the level of cooperation can be influenced by proximate emotions, which vary with the degree of intergroup competition.

Keywords: Human; Cooperation; Public good; Economic game; Group competition; Proximate; Emotion; Anger; Guilt

1. Introduction

Explaining cooperative behaviour remains one of the greatest problems for evolutionary biology and the social sciences (Alexander 1987; Hamilton 1964; Maynard Smith & Szathmàry 1995; West, Griffin, & Gardner, 2007a, 2007b). The problem is that cooperative behaviours benefit other individuals, and so can reduce the relative fitness of the performer. Consequently, ceteris paribus, individuals that do not cooperate should be able to out-compete cooperators. Recently, there has been much interest in the suggestion that a major factor selecting for cooperation in humans may have been competition between groups. However, while this idea has been supported by a number of theoretical models, there is a lack of empirical work testing the predictions of this theory (Bowles & Gintis 2004; Boyd, Gintis, Bowles, & Richerson, 2003; De Cremer & Van Vugt 1999; Erev, Bornstein, & Galili, 1993; Gintis 2000, 2003; Gintis, Bowles, Boyd, & Fehr, 2005; Gunnthorsdottir & Rapoport 2006; Hamilton, 1971, 1975; Henrich & Boyd 2001; Henrich et al., 2005; Lehmann, Rousset, Roze, & Keller, 2007; Puurtinen & Mappes 2009; Tan & Bolle 2007; West, Griffin, & Gardner, 2007a, 2007b). This is in stark contrast to other possible factors, such as punishment, which have received considerable empirical attention and support (Boyd et al., 2003; Egas & Riedl, 2008; Fehr & Fischbacher 2003; Fehr & Gachter 2002; Gintis et al., 2005; Haley & Fessler 2005; Hammerstein 2003; Henrich et al., 2005, 2006; Okamoto & Matsumura 2000).

Our aim in this study was to test the prediction that competition between groups leads to higher levels of cooperation. We allowed individuals to play a public goods game (see Methods) for financial rewards, both with and without group competition, to test whether this influenced the level of cooperation. Our without-group-competition treatment corresponded to a standard public goods game. We

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introduced group competition into this game by allocating additional rewards to members of high-performing groups (i.e., those with relatively high cumulative total of contributions in a given round). An advantage of carrying out such experiments with humans, as opposed to other animals, is that we were also able to investigate the underlying emotions that motivate behavior (Gintis et al., 2005). We examined the extent to which cooperation within groups was associated with feelings of guilt and anger and how participants viewed the other players, depending on their relative levels of cooperation and whether these phenomena were influenced by competition between groups.

2. Methods

Full details of the methods can be found in the electronic supplementary material. We conducted a "public goods" game based on standard techniques (Fehr & Gachter 2002) using real monetary rewards as motivation and two treatment conditions: group competition and without group competition. All participants played under both treatments, with the order reversed between sessions. The experiment was programmed and conducted using the z-Tree software (Fischbacher 2007).

2.1. Participants and sessions

A total of 48 undergraduate students from the University of Edinburgh voluntarily participated in the experiment. We conducted three experimental sessions (blocks) with 16 participants each. Each of the 48 participants played two public goods games with six rounds in each game. One game was a standard public goods game (without group competition), and the other game included group competition, with more additional monetary units (MU) being awarded to individuals in the more cooperative groups (see below). We varied the order of these treatments across the three different sessions.

2.2. Game structure

In each round of a session, we randomly allocated each of the 16 participants to one of four groups of four participants. Reputations, which are often suggested as a mechanism for stabilizing the evolution of cooperation (Nowak & Sigmund 1998; Wedekind & Milinski 2000), were not possible because we did not inform participants about the prior behaviour of their group mates. Our design also removed opportunities for reciprocity, another suggested mechanism for stabilizing the evolution of cooperation (Trivers 1971).

In both conditions, groups comprising four participants played the following public goods game. Each participant received an endowment of 20 MU, a fraction of which (0–20 MU) they could contribute to a group investment. Participants kept any MU they did not contribute. For each MU contributed to the investment, each of the four group members earned 0.5 MU. Therefore, investing provided a benefit at the group level (2.0 MU return for each MU invested) but was individually costly (only 0.5 MU return for each MU invested). In the group-competition games, we allowed participants the opportunity to earn additional MUs depending on the combined performance of their group. The groups were ranked according to their sum total of contributions in that round, and the members of the highest-ranked group each received an extra 16 MU. The members of the remaining groups received 8, 4, or 2 according to their group rank.

Following each round, we recorded participants' instantaneous emotional responses to information about their contributions and payoffs, and those of their fellow group mates, in the preceding round. Participants were prompted (on screen) to score their feelings of both anger and guilt on a scale of 0 (no anger or guilt) to 7 (maximum anger or guilt). We thus obtained 12 near instantaneous values of self-reported "anger" and "guilt" for each participant. At the end of the experiment, participants were asked to indicate, on a sliding scale ranging from 0 to 20, whether they viewed their group mates, by treatment, as "collaborators" or "competitors." On screen, the scale was demarcated from 0 (collaborator) to 20 (competitor).

3. Results

3.1. Cooperation—competitors and collaborators

Contributing was costly under the without group-competition treatment, with income a negative function of total contribution (linear regression of total income against cumulative contribution: R^2=0.58, $F_{1,47}$=64.5, p<.0001) but was nonsignificantly correlated with total contribution under group competition (linear regression of total income against cumulative contribution: R^2=0.02, $F_{1,47}$=0.75, p=.39). Thus, on average, the benefits of contributing towards the group's success were negated by the costs of contributing. The presence of group competition resulted in participants contributing more, from the beginning and throughout, despite not earning more (LMM: $F_{1,6.978}$=61.829, p<.000; Fig. 1, Table 1). Overall, 44 out of the 48 participants contributed more in total during the six rounds of group competition, and the differences for the four in the other direction were marginal (difference of 1, 2, 10, and 13 MU over six rounds). Individual contributions also decreased by the final rounds for both treatments (LMM: $F_{5,17.758}$=3.400, p=.025), although there is a suggestion of a significant interaction between the effects of treatment and round (LMM: $F_{5,6.620}$=3.10, p=.09), with Fig. 1 looking like the contributions under group competition are dropping off later (after Round 4). There was no effect of treatment order (LMM: $F_{1,1}$=.669, p=.564) or period (LMM: $F_{1,7.651}$=.058, p=.816), and all other interactions were nonsignificant (Table 1), although our limited sample size (only three sessions) meant that we were unable to thoroughly test these

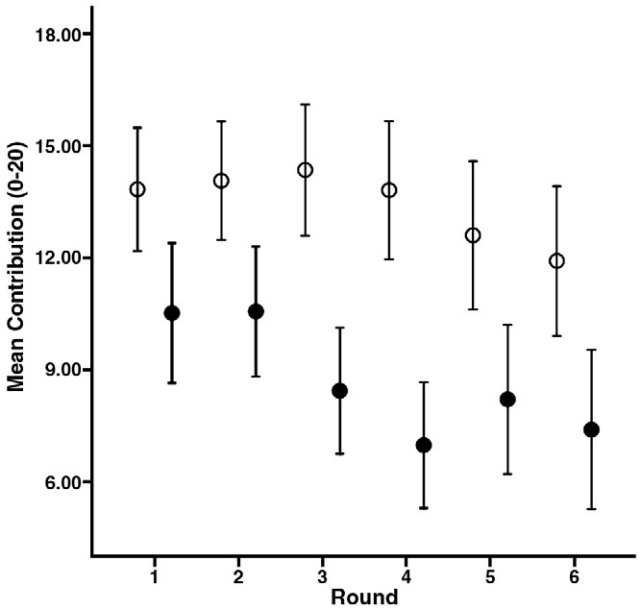

Fig. 1. The effect of group competition. Mean contributions decreased over time but were significantly higher under group competition. Open circles indicate group competition; filled circles, without group competition; lines, 95% confidence intervals.

effects, unless we used individual level data (which gives qualitatively the same results, not included here), which is compromised as players in one session are not independent from the other players in the same session, and therefore, it is better to take the mean levels of cooperation for each session.

Participants reported markedly altered views of their group mates depending on the presence or absence of group competition, with individuals being more likely to view their group mates as collaborators in the group-competition treatment (paired t test: t_{47}=7.13, p<.0001, without-group-competition mean±SE=13.7±0.72; group-competition mean±SE=7.2±0.82, Fig. S1a). In addition, individuals who contributed more to the group-competition public goods game were more likely to see their group mates as collaborators (linear regression: y=13.56−0.048×sum contributions; $F_{1,45.371}$=9.53, p=.003; Fig. S1b).

3.2. Emotions—guilt and anger

In the group-competition treatment, participants reported a nearly significant lower level of guilt (mean±SE values were 0.76±0.14 for group competition and 0.98±0.15 for without group competition; paired t test on participant means over six rounds: t_{47}=1.9, p=.06), and a nonsignificantly lower level of anger (mean±SE values were 1.50±0.19 for group-competition and 1.71±0.21 for without group-competition treatment; paired t test on participant means over six rounds: t_{47}=1.1, p=.295). Further analysis (Table S1) showed that these differences were influenced primarily by participants' own contributions and those of their group mates, and not by the treatment itself (with or without group competition). Specifically, participants felt angrier when they had contributed relatively more than their group mates (LMM: $F_{1,469.086}$=104.36, p<.000; Fig. S2a). In contrast, participants felt guiltier when they had contributed relatively less than their group mates (LMM: $F_{1,497.214}$=93.48, p<.000; Fig. S2b). The interaction term between own and others' mean contribution was also significant for both anger and guilt (LMM: anger: $F_{1,469.902}$=21.49, p<.000; guilt: $F_{1,507.293}$=35.98, p<.000; Table S1).

4. Discussion

We allowed individuals to play a public goods game in groups, with or without competition between groups. As predicted by theory, we found higher levels of cooperation when there was competition between groups (Fig. 1). The higher level of cooperation in this treatment was associated with a significant tendency for individuals to regard their group mates as collaborators rather than competitors (Fig. S1a). In addition, even when controlling for this effect of treatment, individuals who had a greater tendency to view their group mates as collaborators, also contributed more to the public goods game (Fig. S1b). Reviewing the emotions participants reported during the games, we found that individuals felt (a) more angry when they contributed relatively more than their group mates (Fig. S2a), and (b) more guilty when they contributed relatively less than their group mates (Fig. S2b). Overall, these results are consistent with the idea that cooperation is facilitated by proximate emotions such as guilt, anger, and perceptions of common purpose within the group (collaborators or competitors).

Participants varied in their levels of cooperation and in their views of their group mates. Probst, Carnevale, & Triandis (1999) showed that individuals that scored higher for individualism (were more competitive in general) were

Table 1
Linear mixed model analysis of individual contributions

Source	Test statistic	*p value*
Intercept	$F_{1,1.002}$=382.567	.032
Round	$F_{5,17.758}$=3.400	.025
Order	$F_{1,1}$ =.669	.564
Period	$F_{1,7.651}$ =.058	.816
Round×order	$F_{5,10.255}$=.929	.501
Round×period	$F_{5,12.763}$=1.263	.338
Order×period	$F_{1,6.978}$=61.829	.000
Round×order×period	$F_{5,6.620}$=3.101	.091
Random (session)	Z=0.487	.626
Repeat (AR1 diagonal)	Z=2.970	.003
Repeat (AR1 rho)	Z=1.146	.252

Linear mixed model with an autoregressive covariance structure for the repeated effect (6 rounds×2 treatments; subject=session). The interaction between order and period is equivalent to the effect of Treatment (group competition versus without group competition). Degrees of freedom are approximated by the model fitting procedure. Values shown for the main effects and the significant interaction between Order and Period are from the final model. Values for the non-significant interactions are from when the term was removed from the model.

less likely to contribute in a standard public dilemma and more likely to contribute under group competition. It would appear that these more competitive individuals value relative success, either at the individual level, or the group level, that is, they are sensitive to the scale of competition that is operating at the time. Consistent with this, West et al. (2006) showed that competition within groups leads to lower levels of cooperation. Regarding a possible role of emotions, De Cremer and Van Vugt (1999) showed a positive correlation between the extent to which individuals identified with their group and their level of cooperation, and that these could both be manipulated by emphasizing the perceived saliency of their group and the importance of the group's performance to the study's aims and objectives (reviewed by Bornstein 2003). In support of this, both Puurtinen and Mappes (2009) and this study (Fig. S1a) found that group competition led to individuals being more likely to identify their group mates as collaborators rather than competitors.

Our results agree with several previous studies that have shown how group competition can lead to higher levels of cooperation and lower levels of free-riding, both in laboratory (Baron 2001; Bornstein & Erev 1994; De Cremer & Van Vugt 1999; Gunnthorsdottir & Rapoport 2006; Nalbantian & Schotter 1997; Probst et al., 1999; Puurtinen & Mappes 2009; Tan & Bolle 2007) and field (Erev et al., 1993) settings. However, from a mechanistic perspective, it is hard to say if our participants contributed more under group competition because they either believed that this would make them more money (even though on average it had no effect), or because they were strongly motivated by a sense of competition and wanted their group to "win" (Nalbantian & Schotter 1997). It has been shown that individuals are prepared to pay a premium just to increase the chances of their group's success, even when this is costly for themselves (Bornstein & Erev 1994; Probst et al., 1999), and this has been explained as either rational behaviour with a utility function that incorporates the success of others (Baron 2001; Probst et al., 1999) or the result of mistaken beliefs, such as the "voter's illusion" and the "self-interest illusion," whereby people believe that their cooperation will make others cooperate, or that it is actually in their financial self-interest to cooperate, respectively (Baron 2001). Overall, this suggests that people operate a rule of thumb which values relative success at either the individual or group level, depending on the level of competition. From an ultimate perspective, this may have been adaptive in the past as members of relatively successful groups may have gained benefits, either directly through increased access to mates and resources, or indirectly through the increased fitness of their relatives (Boyd et al., 2003; Lehmann & Feldman 2008; West et al., 2007a, 2007b). It is also clear that learning plays a role, with increased "training" leading to fewer "mistakes" from the narrow self-interest point of view (Baron 2001).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.evolhumbehav.2009.07.005.

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Electronic Supplementary Material

1. FULL METHODS

We conducted a 'public goods' game based on standard techniques (Fehr and Gachter 2002) using real monetary rewards as motivation and two treatment conditions: group-competition and without group-competition. All participants played under both treatments, with the order reversed between sessions. The experiment was programmed and conducted using the z-Tree software (Fischbacher 2007).

1.1 Participants and Sessions

A total of 48 undergraduate students from the University of Edinburgh voluntarily participated in the experiment. We recruited participants by means of posters distributed across the science campus and an email sent to all 1st year science students. We conducted three experimental sessions (blocks) with 16 participants each.

At the beginning of each session, we randomly allocated participants (by card draw) to computer consoles. Participants were, by means of a raised hand, able to summon demonstrators to clarify procedural points if necessary. Apart from that, no communication was permitted. Before each game, the participants proceeded at their own pace through an on-screen demonstration (available from the authors upon request), which explained the rules and structure of the game. Participants then worked through a brief on-screen comprehension test to confirm their

understanding of the rules and the payoff structure, and their ability to successfully compute their own and their groupmates' payoffs. The session did not begin until every subject had successfully completed the comprehension test.

Each of the 48 participants played two public goods games with 6-rounds in each game. One game was a standard public goods game (without group-competition) and the other game included group-competition, with more additional monetary units (MU) being awarded to individuals in the more cooperative groups (see below). We varied the order of these treatments across the three different sessions. Participants played the first 6-round game without knowing that they would play a second game afterwards. We informed participants at the start of the session that the game would last for 6 rounds, then after round 6, we informed them, by on-screen instructions, that they would repeat another 6-round game, but this time with different rules, which we then explained accordingly, again on-line. Participants were informed that there would be no more games after these additional rounds. We waited for all the participants to confirm, on-line, that they understood the new rules before starting the new game. The experiments typically lasted around 60 minutes and the mean, private, payout was £29.

1.2 Game Structure

In each round of a session, we randomly allocated the 16 participants to one of four groups of four participants. The game was played via interactions with a personal computer console, allowing participants to make their decisions anonymously and simultaneously. Reputations, which are often suggested as a mechanism for stabilizing the evolution of

cooperation (Nowak and Sigmund 1998; Wedekind and Milinski 2000), were not possible because we did not inform participants about the prior behaviour of their groupmates. Our design also removed opportunities for reciprocity, another suggested mechanism for stabilizing the evolution of cooperation (Trivers 1971). At the end of each round participants were informed (on-screen) about their own contribution and those of their groupmates, and their own payoff, in MU, plus their running total success, in MU, for the whole game.

In both conditions, groups comprising four participants played the following public goods game. Each subject received an endowment of 20 MU, a fraction of which (0-20 MU) they could contribute to a group investment. Participants kept any MU they did not contribute. For each MU contributed to the investment, each of the four group members earned 0.5 MU. Therefore, investing provided a benefit at the group level (2.0 MU return for each MU invested), but was individually costly (only 0.5 MU return for each MU invested). In the group-competition games, we allowed participants the opportunity to earn additional MU's depending on the combined performance of their group. The groups were ranked according to their sum total of contributions in that round, and the members of the highest ranked group each received an extra 16 MU. The members of the remaining groups received 8, 4, or 2 according to their group rank.
Following each round, we recorded participants' instantaneous emotional responses to information about their contributions and payoffs, and those of their fellow groupmates, in the preceding round. Participants were prompted (on-screen) to score their feelings of both anger and guilt on a scale of 0 (no anger or guilt) to 7 (maximum anger or guilt). We thus obtained 12 instantaneous values of self-reported 'anger' and 'guilt' for each subject.

After the experiment, participants were asked to indicate, on a sliding scale ranging from 0 to 20, whether they viewed their groupmates, by treatment, as 'collaborators' or 'competitors'. On-screen the scale was demarcated from 0 (collaborator) to 20 (competitor).

1.3 Statistical Analyses

Participants of the same session interact with each other and thus are not independent, so to test whether the treatments affected the level of contributions, we took the mean level of contributions for each session in each round of each treatment (N = 3 sessions x 2 treatments x 6 rounds = 36). These contributions were treated as a continuous variable, as by taking the means of the contributions, which are proportional by nature, the data were normally distributed. Rounds were treated as an ordinal variable. The six rounds by two treatments were treated as a repeated effect with Session as the subject variable in a linear mixed model (LMM) with an auto-regressive 1^{st}-order covariance structure (AR(1)). A paired T-test, based on each participant's mean levels of emotion over the 6 rounds, was used to assess if participants changed their views of their groupmates by treatment. Whilst this method takes account of the correlation between responses from the same individuals, it unfortunately does not take into account that participants from the same session may be correlated in their responses. A linear mixed model (LMM) with the six rounds by two treatments treated as a repeat effect with participant as the subject and an auto-regressive 1^{st}-order covariance structure (AR(1)) was fitted to the complete data set to test for the effects of participants' contributions and the contributions of their groupmates in each round. Again, whilst this method takes account of the correlation between responses from the same individuals, it unfortunately does not take into account that participants from the same

session may be correlated in their responses. All statistics were performed using either JMP, version 7.0.1 (SAS Institute Inc.) or SPSS, version 16.0 (SPSS inc).

Table S1: Linear Mixed Model analysis of *in-situ* emotional values reported for own and others' contributions.

	Anger		Guilt	
Source	Test Statistic	*p-value*	Test Statistic	*p-value*
Intercept	$F_{1,349.663} = 13.899$	0.000	$F_{1,439.663} = 0.068$	0.795
Treatment	$F_{1,498.759} = 0.323$	0.570	$F_{1,520.000} = 0.599$	0.439
meanOther	$\mathbf{F_{1,457.536} = 18.189}$	**0.000**	$\mathbf{F_{1,497.214} = 93.484}$	**0.000**
Contribution	$\mathbf{F_{1,469.086} = 104.362}$	**0.000**	$F_{1,510.537} = 0.002$	0.968
Treatment * meanOther	$F_{1,466.167} = 0.744$	0.389	$F_{1,503.427} = 0.043$	0.835
Treatment * Contribution	$F_{1,480.533} = 0.619$	0.432	$F_{1,512.923} = 0.051$	0.805
meanOther * Contribution	$\mathbf{F_{1,469.902} = 21.489}$	**0.000**	$\mathbf{F_{1,507.293} = 35.975}$	**0.000**
Treatment * meanOther * Contribution	$F_{1,473.051} = 0.504$	0.478	$F_{1,508.832} = 0.079$	0.779
Random (Participant)	Z = 4.142	0.000	Z = 4.137	0.000
Repeat (AR1 diagonal)	Z = 14.078	0.000	Z = 15.418	0.000
Repeat (AR1 rho)	Z = 4.835	0.000	Z = 2.024	0.043

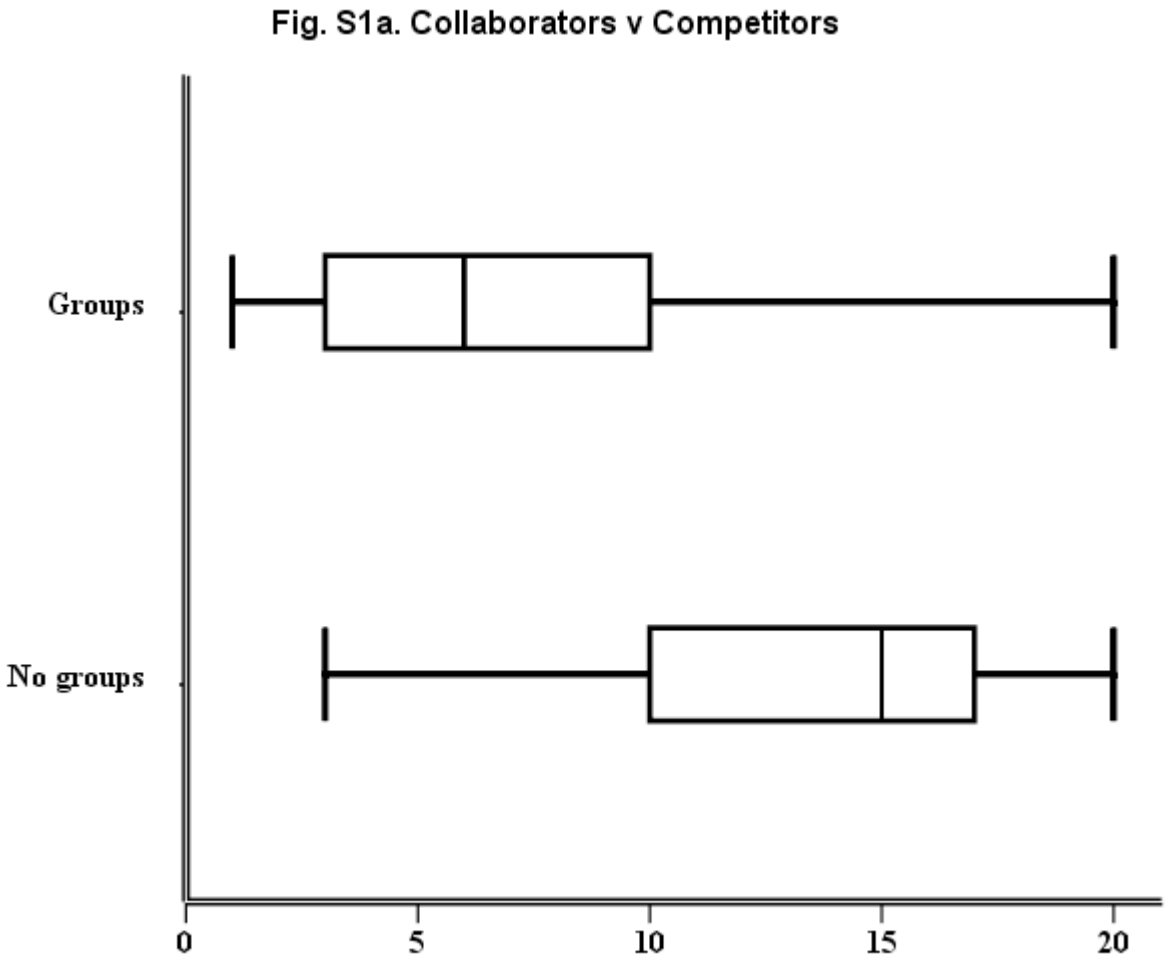
Linear mixed model with an autoregressive covariance structure for the repeated effect (6 rounds x 2 treatments; subject = Participant). "meanOther" is the mean contribution of the other three participants in the participant's group. Degrees of freedom are approximated by the model fitting procedure.

Figure legends.

Fig. S1. (a) Subjects were more likely to view their groupmates as collaborators under group-competition and as competitors without group-competition. (b) Subjects that viewed their groupmates more as collaborators under group-competition also contributed more in total under group-competition (filled circles = without group-competition, open circles = group-competition, solid line is significant regression for group-competition, dashed-line is non-significant without group-competition).

Fig S2. (a) Anger increases, whereas (b) guilt decreases, with relative contribution to the group project, and there is no significant effect of treatment. Filled circles and dashed-line (no group-competition), empty circles and solid-line (group-competition).

Figure S1. (a) and (b)



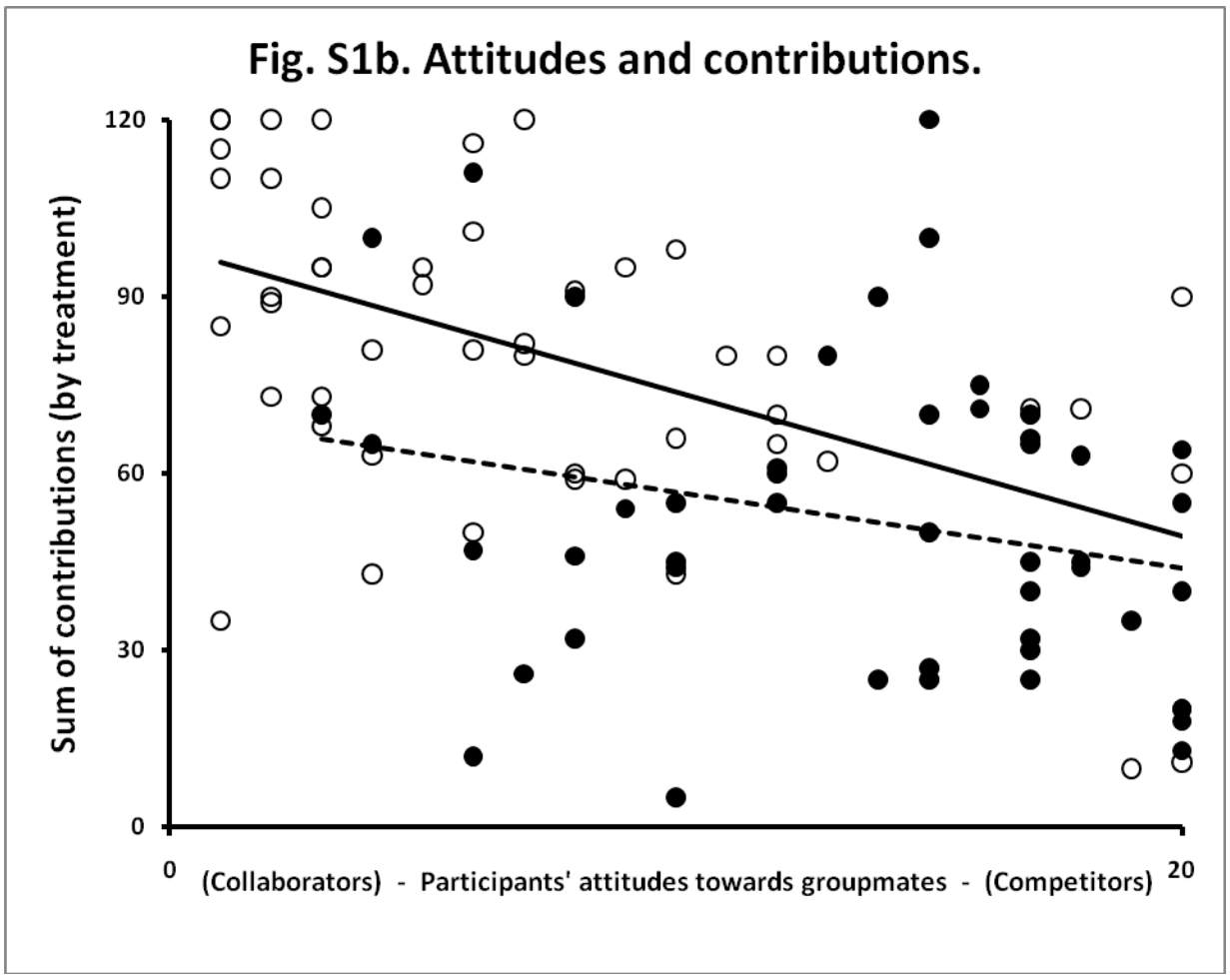
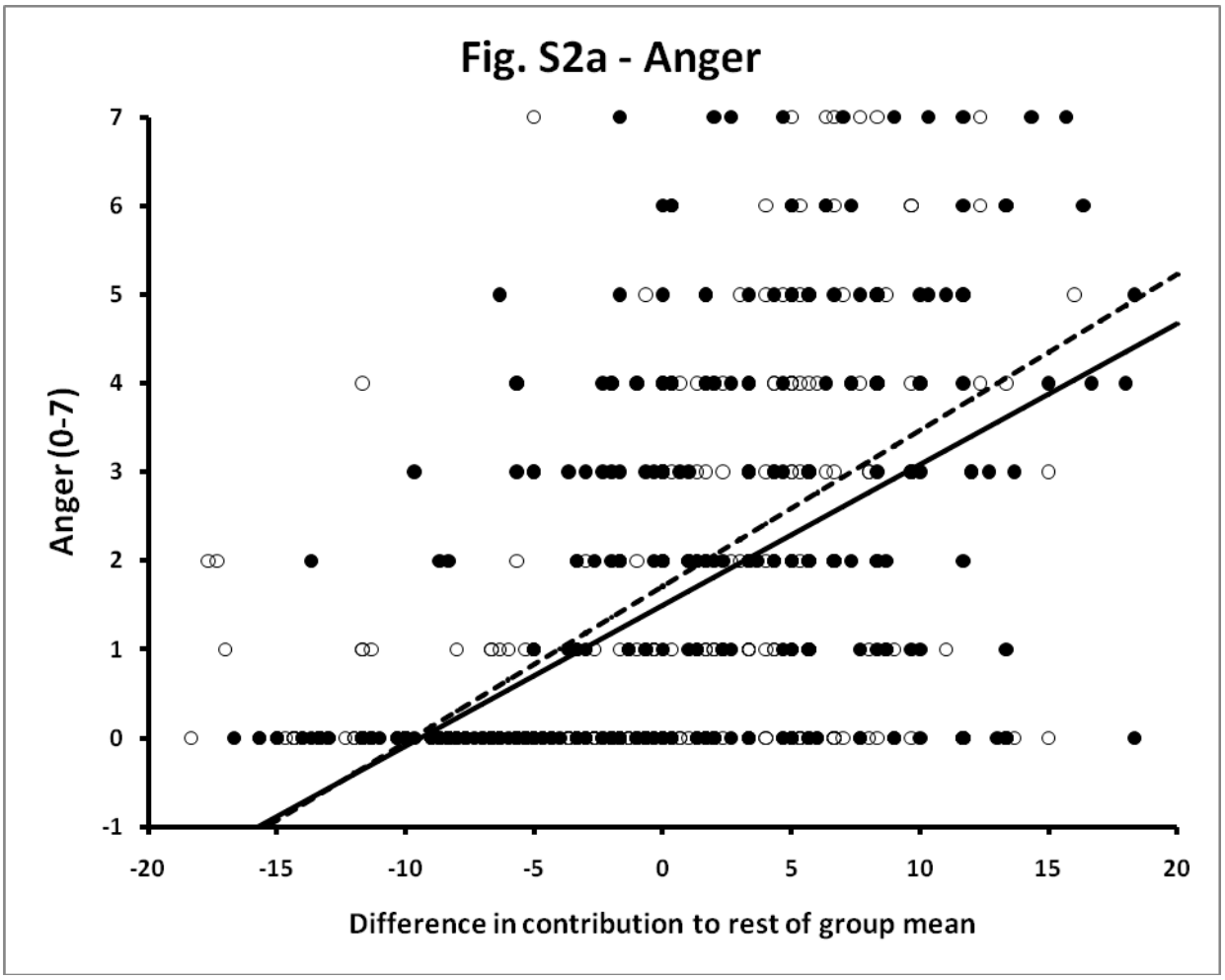


Fig. S1b. Attitudes and contributions.
Sum of contributions (by treatment)
120
90
60
30
0
0
(Collaborators) - Participants' attitudes towards groupmates - (Competitors)
20

Figure S2. (a) and (b)



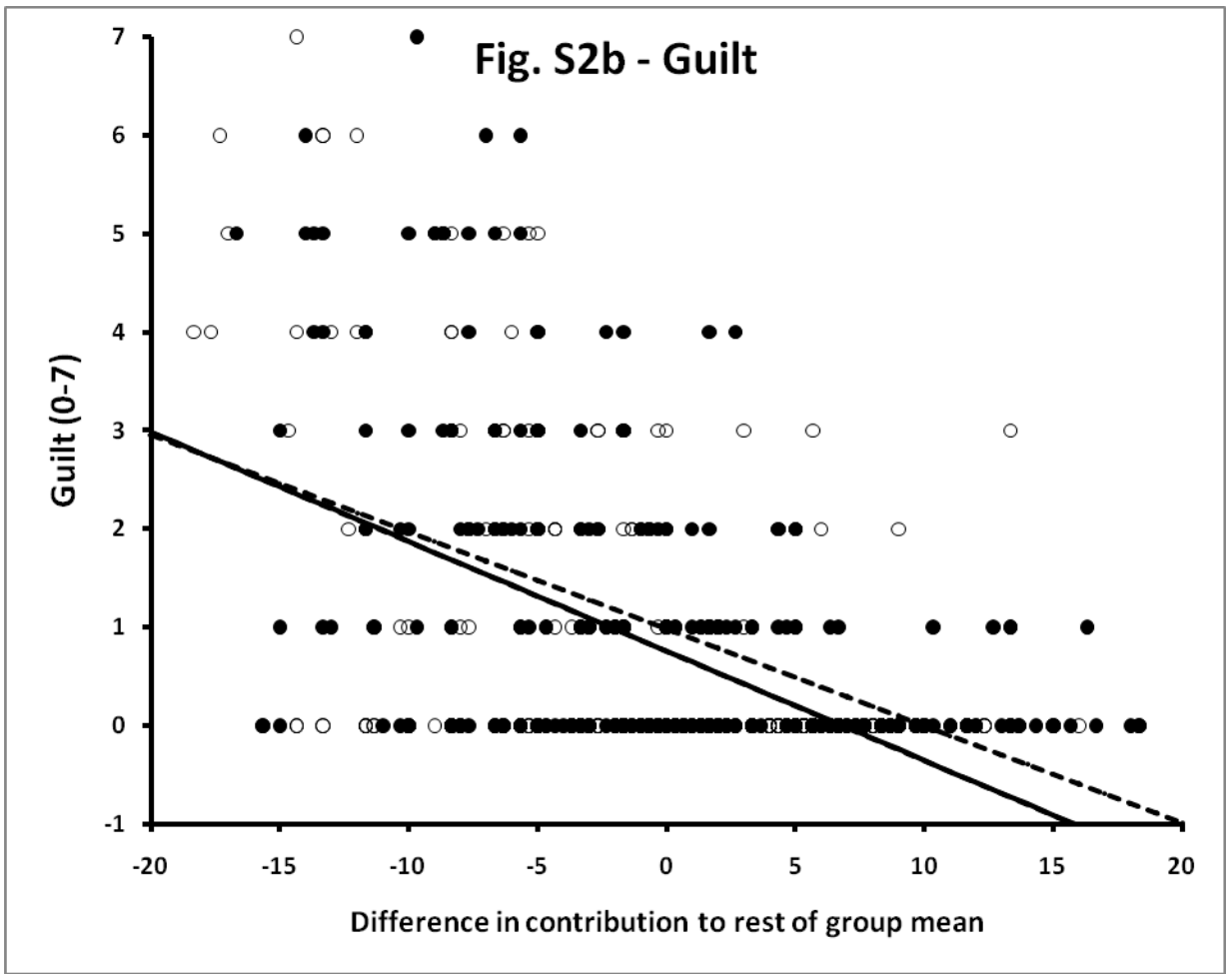


Fig. S2b - Guilt
Guilt (0-7)
7
6
5
4
3
2
1
0
-1
-20
-15
-10
-5
0
5
10
15
20
Difference in contribution to rest of group mean