Human cooperation by lethal group competition

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Why humans are prone to cooperate puzzles biologists, psychologists and economists alike. Between-group conflict has been hypothesized to drive within-group cooperation. However, such conflicts did not have lasting effects in laboratory experiments, because they were about luxury goods, not needed for survival (“looting”). Here, we find within-group cooperation to last when between-group conflict is implemented as “all-out war” (eliminating the weakest groups). Human subjects invested in helping group members to avoid having the lowest collective pay-off, whereas they failed to cooperate in control treatments with random group elimination or with no subdivision in groups. When the game was repeated, experience was found to promote helping. Thus, not within-group interactions alone, not random group elimination, but pay-off-dependent group elimination was found to drive within-group cooperation in our experiment. We suggest that some forms of human cooperation are maintained by multi-level selection: reciprocity within groups and lethal competition among groups acting together.

The evolution and maintenance of cooperation among unrelated individuals is a fundamental problem in the biological and social sciences. Theoretical conditions favouring cooperation include genetic relatedness among cooperators, situations allowing for direct benefits to the cooperator, and repeated interactions allowing for indirect benefits to the cooperator via reciprocal altruism and reputation building. In absence of these conditions, however, humans show more cooperation than theory predicts. Group structure may be a factor bridging the gap between theory and experiment, but as yet its role in cooperation is a highly debated topic. Recent theory points to a role for inter-group conflicts. The idea is that individuals are engaged in a conflict between personal performance and group performance, causing the emerging levels of cooperation to be a compromise. This is the modern way to view the process of group selection: group structure matters to the extent in which it influences the individual interests.

The question how group conflicts affect decisions of individuals within groups, has received some attention in social psychology, where so-called “team games” are used to identify conditions under which individual or collective rationality prevails. So far, experiments involved non-lethal group competition and failed to show a lasting effect on cooperation. If effects on cooperation were demonstrated, then they were the result of aligning personal interest with group benefit. In this article, we design a repeated “team game” experiment that differs in particular by (I) eliminating groups based on group performance criteria (lethal group competition instead of non-lethal as done in experiments published so far), by (II) making individuals play multiple rounds of the game instead of one-shot games, and by (III) setting the rule that the ultimate winner of the game is the individual in the surviving group with the highest payoff over all rounds. This design causes group competition to be extreme and the conflict of interest for individuals between group performance and personal performance to be as high as possible. To assess the consequences experimentally we explored three versions of the game differing in the way group elimination was executed: elimination of the group with the lowest pay-off (the sum of individual pay-offs), random elimination of a group, and no elimination. Here, we show experimentally that lethal competition by pay-off-dependent group elimination can drive within-group cooperation in humans.

Results

Under the treatment where the poorest group was eliminated, group members on average invested a significant fraction of EMUs in other group members (Figure 1a). Only in the two-group stage of the tournament this average fraction decreased. In subsequent games, the per-individual investment in the first round significantly increased (Figure 2). Individuals contributed increasingly more in the first round of the three games (F₂,₃₅₇ = 11.5,
p < 0.0001), but this increase slowed down as participants approached full contribution in game 3 (Figure 1c). This demonstrates a positive effect of learning on cooperative investment.

To control for elimination based on group pay-off, we performed an additional experiment with random group elimination. Assuming rational decision making among all players, game theory predicts that subjects should refrain from investing in others. This prediction is met in our experiments except in the first few rounds (Figure 1a), but this first-round effect vanished in the two subsequent games (Figure 1b,c). To control for group elimination we performed a final experiment in which no elimination occurred. The mode of elimination affected the mean investment for each of the three games (repeated measures ANOVA; Game 1: F2,22 = 70.8, P < 0.0001; Game 2: F2,22 = 94.1, P < 0.0001; Game 3: F2,22 = 63.9, P < 0.0001). The results of the no-elimination experiment appeared to be statistically indistinguishable from those obtained under random group elimination, (Bonferroni posthoc tests in both comparisons in all three games yielded p > 0.9) and those of both control experiments were statistically different from the experiments involving pay-off based group elimination (Bonferroni posthoc tests in both comparisons in all three games yielded p < 0.0001).

Round-to-round changes in the fraction investment may depend on elimination events: (I) the phase before the first elimination, (II) the phase in between the first and second eliminations, and (III) the phase after the second elimination. Such dependencies cannot be detected in the treatments involving random group elimination and no elimination due to the low investment overall. In the treatment with lethal group elimination, however, we found statistical evidence that investments declined significantly after the second elimination event (Table 1) but not after the first (Table 1), except for game 2 where significant declines were found after both elimination events. Also, we observed decreasing investment with rounds in phase I and phase III, but not in phase II (Fig. 1). Comparison of these features across games (Fig. 1a–c) suggests no differences except for a decline in phase I that was less pronounced in the last game than in the previous games.

**Discussion**

We found that cooperation only emerged under pay-off-dependent group elimination. Thus, it is not group elimination per se that drives
human cooperation in our experiment. Because we observed no cooperation in the two control treatments, other mechanisms favouring cooperation, such as rewarding or punishment in response to the mean contribution of others in the group, can be ruled out.

We claim that the effect of pay-off-dependent group elimination on cooperation within groups is independent of most details of our together-alone game. Our game differs from the well-known public goods game in that (I) the investor does not receive any return from his own investment, (II) the subjects accumulate EMUs over rounds of the game, and (III) only one group member receives payoff at the end of the game. Whereas rule (III) is implemented to strengthen the conflict of individual interest between the subject and its group, rules (I) and (II) are rooted in biology. There are many examples of cooperation where the individual contributing to a public good does not or cannot benefit from the public good to the same extent as others in the group – in the extreme, individuals may die when performing the cooperative act\(^1\). It is also quite common that the condition of individuals depends on the returns from cooperative behaviour such that individuals with high returns have more to invest the next time this behaviour is invoked.

Our experimental results are generally in agreement with Bowles’ review\(^2\) on inter-group conflict and group extinction in humans. Bowles\(^3\) pointed out that group competition promotes within-group cooperation most strongly when the group members gain in equal measures from outcompeting another group. This element in his theoretical framework, called reproductive levelling, is not present in our game. Our results, however, imply that such reproductive levelling is not a necessary condition for within-group cooperation to emerge, as long as there are more than two groups competing with each other (note that cooperation is high until the two-group stage of the tournament, probably because participants start thinking more about their personal interest of winning the game by cooperating less). Thus, human cooperation may result from pay-off dependent  

**Methods**

The “together-alone” game. Repeated “team games” were played with 12 individuals, placed in 4 groups of 3 subjects each. The subjects remain part of the same group over all rounds of the game. Within the group subjects make decisions in a social dilemma situation. Every subject received an endowment of 100 experimental money units (EMUs). In every round of the game subjects had to decide how much of their EMUs they invest in helping the other (anonymous) subjects in their group. This investment was multiplied by a factor, arbitrarily set to 1.5, and then equally divided over the other two subjects. EMUs not invested in helping the other (anonymous) subjects in their group. The result of each round of the game (i.e. EMUs not invested plus EMUs received from help by the other two group members) formed the starting point for the next. Thus, each subject accumulated EMUs over all rounds of the game. This game is played for a number of rounds unknown to the subjects. Each subject receives information on total EMUs of its group members at the end of each round, and the winner of the game is the one that has accumulated most EMUs over all rounds.

We introduce pay-off-dependent group elimination by involving four groups in a game, and subsequently eliminating the group with lowest total EMUs (i.e. “your group loses, you die”) at the end of three arbitrarily chosen rounds. This treatment is called the group competition treatment. After each round subjects received information about the investments of the other subjects in their group, as well as the

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**Author contributions**

M.E. designed experiments, analysed data and wrote the paper; R.K. and X.v.d.S. performed experiments; E.R. supervised experiments; and M.W.S. designed experiments and wrote the paper.

**Additional information**

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**Competing financial interests:** The authors declare no competing financial interests.

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