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Original Article

The joint emergence of group competition and within-group cooperation

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ABSTRACT

Between-group conflict and within-group cooperation can be seen as two sides of the same coin, coevolving in a group-structured population. There is strong support for between-group competition facilitating the evolution of human cooperative tendencies, yet our understanding of how competition arises is less clear. We show that groups of randomly assembled individuals spontaneously engage in costly group competition, and that decisions promoting between-group conflict are associated with high levels of within-group cooperation. Remarkably, when groups were given the possibility to compete against other groups, net earnings for individuals were higher than when groups were not allowed to interact. The joint emergence of conflict and cooperation along even weakly defined group boundaries, and the apparent benefits of this strategy, suggest the existence of behavioral biases influencing human social behavior and organization.

1. Introduction

Extensive cooperation among unrelated individuals, as displayed by humans, presents an evolutionary puzzle. Beginning with Darwin, scientists have proposed that aggressive between-group competition is a critical component of human social organization that has been instrumental in shaping cooperative tendencies (Alexander, 1979, 1990, 2006; Boyd & Richerson, 2009; Darwin, 1871; Flinn, Geary, & Ward, 2005; Gat, 2006; Hamilton, 1975; Henrich, 2004). Support for this hypothesis comes from studies showing that violent intergroup conflicts have been frequent and severe enough in primitive human societies to have favored the evolution of individually costly traits that increase a group's success in conflict (Bowles, 2009). Furthermore, experimental studies consistently report that interactions between groups tend to be more competitive than interactions between individuals, a phenomenon known as interindividual–intergroup discontinuity (Wildschut & Insko, 2007). This discontinuity has been reported to extend to aggressive behavior (Meier & Hinsz, 2004). However, the reasons why group-against-group aggression is so common in humans, and rare in other animals, are not well understood (Gat, 2009).

Coalitionary aggression, as displayed by humans, is not simply the sum of individual aggression, but a complicated game of coordination and cooperation along group boundaries. Hence, coalitional aggression may place strong adaptive demands on individuals to acquire and process social information that allows them to make effective decisions (Tooby & Cosmides, 1988). In this respect, empirical evidence suggests that humans possess flexible responses to problems of within-group cohesion and between-group aggression. Specifically, individuals typically treat other groups as benign unless they pose sufficient threat to resources or cultural institutions, at which point individuals are willing to promote inter-group hostilities (Halevy, Bornstein, & Sagiv, 2008; Riek, Mania, & Gaertner, 2006; Sherif, Harvey, White, Hood, & Sherif, 1988) Furthermore, individuals cooperate more with group members under conditions of inter-group competition compared to when competition is absent (Bornstein, Erev, & Rosen, 1990; Burton-Chellew, Ross-Gillespie, & West, 2010; Egas, Kats, van der Sar, Reuben, & Sabelis, 2013; Puurtinen & Mappes, 2009).

Importantly, recent theoretical studies suggest that intergroup hostility and within-group cooperation can select for one another, with hostility spawning direct conflict between groups, and within-group cooperation increasing the group's success in conflicts (Choi & Bowles, 2007; Garcia & van den Bergh, 2011; Lehmann, 2011; Lehmann & Feldman, 2008). That is to say, we can expect that the expression of either within-group cooperation or between-group hostility to facilitate the expression of the other. However, research shows that the two are not necessarily expressed together (Brewer, 1999; Cashdan, 2001; Koopmans & Rebers, 2009; Pan & Houser, 2013). Thus, whilst the two behaviors can be fundamentally linked in an evolutionary sense, individuals appear to show a nuanced response to their social situation that does not take the connection for granted. It is thus clear that there is much left to understand about the links and feedbacks between individual decisions and the emergence of hostile between-group interactions.

The complexity involved in social strategies and intergroup interactions imply that individuals may possess an information-processing system capable of motivating beneficial responses to the social environment. One critical aspect of the social environment that could influence decisions about within-group cooperation and between-group aggression is the variability of cooperation within and between groups. In particular, individually costly group-beneficial behaviors are expected to be

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selected for when within-group variability in cooperativeness is low and between-group variability is high (Okasha, 2006; Price, 1972). It is thus possible that individually costly cooperation and aggression can be influenced by observed levels of variation in cooperativeness within and between groups.

We designed a decision-making experiment that involves choices of both between-group interaction and within-group cooperation. More specifically, we wanted to test i) if individuals decide to promote between-group competition even when competition is costly, ii) if promotion of between-group competition is associated with high level of within-group cooperation, iii) what the consequences of endogenously determined group interactions are on individual and collective welfare, and iv) whether individual changes in behavior are correlated with levels of within- and between-group variability in cooperation. The experiment was designed to limit any influence of reciprocity, reputation, costly signaling or coercion as an attempt to unravel the behavioral biases that may drive the dynamics of social interactions even in a situation of limited information.

2. Material and methods

2.1. General experimental procedures

Subjects to the study were recruited from all faculties in the University of Jyväskylä with emails sent to student mailing lists, announcing a study involving playing a game on a computer and a chance to earn money. The game sessions were held in two computer classrooms with 12 computers. Each computer was in a separate cubicle with a cloth covering the entrance. The subjects received instructions to the game on a sheet of paper (English translations of the original instructions in Supplementary Material, available on the journal's website at www.ehbonline.org).

After everyone had read the instructions, the subjects were asked to put on earmuffs to exclude any auditory disturbance, and the experimenter started the computer software. The software first presented a series of questions to make sure that everyone understood the structure of the game. After all the subjects in the session had correctly answered all questions, the game started and ran automatically until the last round. After the last round, the experimenter handed out a questionnaire asking some background information about the subjects (age, sex, etc.), and about motivations for their decisions in the game. After subjects had filled in the questionnaire, they were individually excused and paid in cash the amount of Euros corresponding to their earnings in the whole game session.

2.2. Experimental treatments

We conducted public goods experiments with two treatment conditions. In the Public Goods (PG) treatment, subjects played the basic public goods game with changing group composition between rounds. In the Public Goods with Choice (PGwC) treatment, subjects played a similar public goods game, but also decided how groups divide their earnings. We executed four sessions of the PG treatment and six session of PGwC treatment. Each session had 24 subjects, so altogether 240 subjects participated in the study. Sessions consisted of 30 game rounds. In each round, subjects interacted in groups of four. Between each round, the subjects were randomly reallocated to new groups.

In the PG treatment, each subject received an endowment of 20 money units (MUs) in the beginning of the round. The subjects then decided how to allocate the endowment between a private account and a group project. Each subject made the allocation decision independently, without knowing the decisions of other subjects. After all subjects had made their decision, the total amount of MUs allocated to the group project was doubled by the experimenter and divided equally among the four group members. Subjects were then informed about the allocations and resulting pay-offs of all group members. Following this, the subjects were presented with a comparison of the total amount of MUs allocated to the group project between their own group and another, randomly chosen group. The comparison had no monetary consequences, but previous research has shown that mere comparison between groups elicits higher levels of cooperation (Böhm & Rockenbach, 2013; Burton-Chellew & West, 2012). By incorporating between-group comparisons to both treatments, we control for the group comparison effect. The comparison between groups ended the game round in the PG treatment. The pay-off structure of the PG treatment is a social dilemma where allocating 1 MU to the group project returns 0.5 MUs; thus it is in the material self-interest of any subject to keep all MUs privately, irrespective of how much the other three subjects contributed. Yet, individuals will only earn 20 MUs if all group members keep their MUs privately, whereas individuals can earn $(20 \times 4 \times 2)/4 = 40$ MUs if each group member allocates their 20 MUs to the group project.

The PGwC treatment was similar to the PG treatment, except that subjects made a choice between three options for desired interaction with a randomly chosen out-group: 'separate', 'competition', or 'equal division'. In 'separate', like in the PG treatment, groups would be compared with no monetary consequences. In 'competition', the more cooperative group would win money from the less cooperative group. In 'equal division', earnings would be divided equally between groups, with the more cooperative group giving money to the less cooperative group. 'Equal division' can be seen as a benign complementary option to 'competition'. The exact pay-off of consequences of group interaction types are described in more detail below. The decision about the group interaction type was made simultaneously with the decision on allocating the endowment, and without knowing the decisions of other subjects.

The group decision of the interaction type was determined by simple majority voting, or in case of a tie, by random draw between the tied choices. After all subjects in a group had made their choices, the total allocations to the group project were doubled by the experimenter and divided equally among the four group members. The subjects were then informed about the choices and pay-offs of their group members, and about the interaction type decided by the group. Following this, the groups were paired randomly for interaction, and the type of interaction was determined by the decisions of the paired groups. If both groups had chosen the same interaction type, that interaction was implemented. If the groups had chosen different interaction types, 'competition' dominated over 'separate' and 'equal division', and 'separate' dominated over 'equal division'. This dominance hierarchy was chosen as it mirrors a natural hierarchy of interactions; aggressive interaction requires only one aggressive party, but generosity between parties requires that both parties agree to be generous.

The pay-off consequences of the group interaction types were as follows: In 'separate', the groups were compared with no consequences to the pay-offs. In 'equal division', the total earnings between the two groups were leveled. Each member of the group that had earned more lost an equivalent of one-eighth of the difference in the total investments of the groups, and each member of the group that that had earned less gained an equal amount of MUs. After 'equal division', the average earnings between groups were thus equal, but pay-off differences within groups were not altered. In 'competition', each member of the group that had earned more gained an equivalent of one-half of the difference in the total investments of the groups, and each member of the group that that had earned less lost an equal amount of MUs. Negative earnings were not allowed. In case some group member did not have enough tokens to cover the losses, other members of the group covered the losses the player was not able to pay. If total losses exceeded total earnings of the group, the group lost all tokens earned during the game round. The winning group could win only as many tokens as the losing group held. Additionally, when competition was implemented, 1 MU was deducted from all subjects in both groups as a cost of group competition (no deduction was made for subjects holding zero tokens). The cost of group competition signifies the costs involved with intergroup aggression, and results in 'competition' being less profitable than 'separate' or 'equal division' when allocations to the group project are the same (see below).

The pay-off structure in the PGwC treatment is such that in any one round, the best allocation decision is to allocate the whole endowment to the private account. Allocating everything to the private account is clearly the best option in both 'equal division' and 'separate' group interaction types: allocating 1MU to the group project returns only 0.375 MU in 'equal division' and 0.5 MU in 'separate'. In 'competition' allocating 1 MU to group project returns 1 MU (0.5 MU from the group project *plus* 0.5 MU from the other group), making personal income independent of the allocation decision (see also Puurtinen & Mappes, 2009). Allocating to the group project thus never has a positive return. Because a subject cannot be certain which group interaction type will be implemented, the best choice is to allocate everything to the private account.

The best choice of group interaction type depends on the allocation decisions made by the subjects in each group. 'Equal division' is the best choice when the out-group allocates more to the group project and also chooses 'equal division', as this results in transfer of MUs to the group of the focal individual. For 'competition' to be the best choice, the total allocations in the focal individual's group need to be more than 2 MU greater than the allocations of the competing group to offset the personal 1 MU cost of group competition. The explicit cost of group competition, together with the random assortment of subjects into groups on each round, renders the expected pay-off from 'competition' to be less than from either 'equal division' or 'separate' (assuming identical allocations to the group project). Pay-off from 'equal division' can be either larger or smaller than pay-off from 'separate', depending on the allocation decisions of subjects in each group. However, the expected pay-off does not differ between the two interaction types. The combination of choices in any one round that maximizes the expected net income is thus to allocate nothing to the group project and to choose either 'equal division' or 'separate' as the type of group interaction.

Some researchers express concern about the validity of generalizing the results of such economic games to reality, chiefly owing to observed differences between behaviors in and out of games and due to contextual variation (Levitt & List, 2007a, 2007b). However, all empirical approaches have their limitations and it is only in the use of complementary approaches that the predictions of theory can be scrutinized. In this regard, it is important to consider the virtues of lab experiments in controlling the influence of exogenous factors, creating situations that are relevant to theory but not easily found in nature, manipulating only the factors of interest, and providing direct observation of the decision-making process (Falk & Heckman, 2009; Levitt & List, 2007a, 2007b). In this respect, our experiment provides a sound test for the existence of behavioral biases, independent of confounding influences that come from reputation, reciprocity and communication. We are able to focus explicitly on decisions about within- and between-group interactions in a simple system that is free from social institutions and other externalities. Importantly, we have also limited individual access to information about the likely consequences of group interaction by forcing them to make group-interaction decisions simultaneously with cooperative decisions. Thus, we can infer that any tendencies regarding the inter-group interaction decision were independent of inter-group assessment. In general, the qualitative patterns observed in lab experiments are typically considered to be reliable, and controlled experiments are considered necessary for empirical testing of scientific hypotheses (Falk & Heckman, 2009; Levitt & List, 2007a, 2007b).

2.3. Statistical analyses

To assess the effect of treatment (PG vs. PGwC) on average investments and net earnings, we fit full and reduced models with SPSS MIXED procedure using maximum likelihood estimation, and compare the fit of the models with likelihood ratio tests. Response variables are session means for investment and net earnings for each game period. Sessions are defined as subjects, and game period is a repeated measure with first-order autoregressive moving average covariance structure. In the full model, we included treatment (PG vs. PGwC), game period (covariate), and treatment by game period interaction as fixed effects. Parameters for the final model were estimated with restricted maximum likelihood.

Factors affecting individual investments to group project in the PGwC-treatment were analyzed by fitting full and reduced models with SPSS MIXED using maximum likelihood estimation, and comparing the fit of the models with likelihood ratio test. In the models, individuals are defined as subjects, and game period is a repeated measure with first-order autoregressive moving average covariance structure. Session is included as a random factor (random intercept). Fixed factors were individual's vote for group interaction type (equal division, isolate, or competition), game period, and the interaction between vote and game period. Parameters for the final model were estimated with restricted maximum likelihood.

We analyzed the effect of within- and between-group variability in allocations on individual voting behavior in the PGwC-treatment with a generalized linear mixed model using SAS 9.4 (SAS Institute). We used a binomial response distribution with a logit link function for whether or not an individual voted 'competition'. The within-group standard deviation of allocations and the standard deviation of total allocations between groups in the game period preceding a vote were used as predictors. Consequently, the first game period was not included in the analysis. Game period was treated as a repeated measure within individual subjects, and autocorrelation was accounted for with a first-order autoregressive moving average covariance structure. Additionally, we used planned polynomial contrasts to test for a linear relationship between game period and competition vote. Parameters were estimated by residual pseudo-likelihood. We allowed each session to have a separate intercept by including it as a random factor, but the variance due to session was estimated to be zero and session was thereby removed from the final model. The degrees of freedom were calculated using the methods of Kenward and Roger (1997). We excluded individuals that expressed unconditional voting behavior from this analysis.

3. Results

Looking at the decisions about group interaction we find that, contrary to the expectations of rational pay-off maximizing strategy, 'competition' was the most frequent choice for group interaction in the PGwC treatment (60.3% of all choices made by the subjects). In the first game round, 'equal division', 'separate', and 'competition' were chosen approximately equally often, but in later game rounds 'competition' became the most frequent choice (Fig. 1A). Choices for 'equal division' and 'separate' were approximately equally common throughout the game (20.5% and 19.2% of all choices, respectively), with the frequency of both declining as the game proceeded. 'Competition' was also the most frequently implemented type of interaction, due to both the high frequency of choices for 'competition', and the dominance of competition over the other two interaction types (Fig. 1B). 'Separate' was implemented relatively frequently in the first rounds of the game, with frequency declining towards the end of the game. 'Equal division' was implemented sporadically throughout the game, due to both the low frequency of choices and to the subordination of 'equal division' to the other types of group interaction.

Looking at the relationship between decisions about within-group cooperation and group interaction, we find that the allocations to the group project in the PGwC-treatment differed depending on the type of group interaction chosen by the subject (Fig. 2, Table 1). When choosing 'compete', subjects allocated on average 14.3 MU to the group project, and this level stayed nearly constant throughout the game.

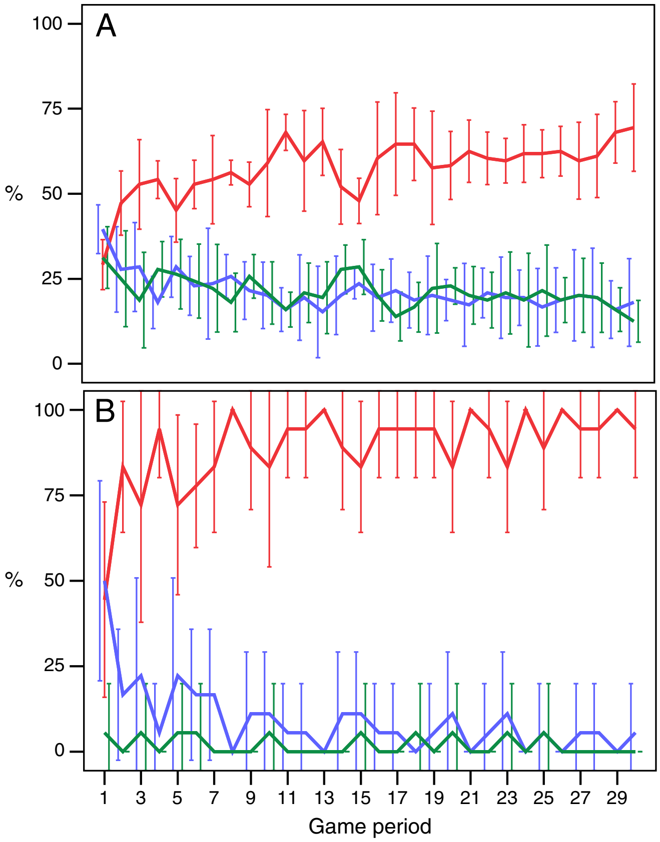

Fig. 1. Frequencies (%) of choices for different types of group interaction (A) and the frequency of implemented group interaction types (B) in the PGwC-treatment. Lines indicate the mean of the six replicate sessions, and the error bars indicate 95% parametric confidence interval. Red: competition; blue: separate; green: equal division.

When choosing 'separate', subjects allocated on average 6.6 MU, with allocations decreasing as the game proceeded. When choosing 'equal division', subjects allocated on average only 3.3 MU.

To study the effects of being able to choose group interaction type on the level of cooperation and net earnings, we compare the two treatment conditions. The level of within-group cooperation (i.e., allocations to the group project) was significantly higher in the treatment with a choice of group interaction type (PGwC) than in the treatment without choice (PG; see Table 2). In PGwC, average allocations to the group account remained at approximately 10 MU throughout the game, whereas in PG the allocations started at a lower level and declined as the game proceeded (Fig. 3A). The higher level of cooperation in PGwC compared to PG was due to high allocations from subjects that chose 'competition' in PGwC. Thus, provided that the costs of between-group competition remain moderate, and that competition is based on production of goods, the possibility to engage in direct between-group competition can have positive social consequences. However, when competition is based on non-productive conflict expenditures, competition between groups can also drastically reduce social efficiency (Abbink, Brandts, Herrmann, & Orzen, 2010, 2012; Leibbrandt & Sääksvuori, 2012).

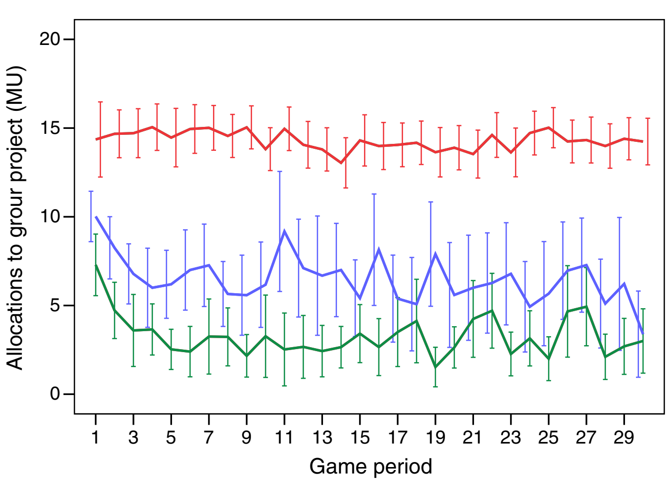

Fig. 2. Allocations to the group project depending on the choice of group interaction type in the PGwC-treatment. Lines indicate the mean of individual allocation decisions, and the error bars indicate 95% parametric confidence interval. Red: competition; blue: separate; green: equal division.

The higher level of cooperation in PGwC also resulted in higher net earnings in PGwC compared to PG (Fig. 3B, Table 3), despite the 1 MU cost of group competition that was deducted from each subject when group competition was implemented. In PGwC, the average net earnings per round were 29.5 MU, showing no temporal trend of decrease or increase. In PG, the average net earnings per round were 25.6 MU, showing a rather constant decline from around 27 MU in the first rounds and declining to close to 24 MU by the end of the game. Note that subjects earn 20 MU per round when there are no contributions to the group project.

Looking at the behavior of individual subjects, only 9 out of the 144 subjects (6.25%) in the PGwC treatment consistently chose only one type of group interaction (eight subjects always chose 'competition' and one always chose 'equal division'). The remaining 135 subjects changed their preferred type of group interaction once or more. Changes in the choice for group interaction type happened 1604 times, which is 38.4% of consecutive choices.

Finally, there was a significant negative effect of within-group variability ($F_{1,3809} = 14.11$, $P < 0.001$; Fig. 4A) and a significant positive effect of between-group variability ($F_{1,3664} = 18.24$, $P < 0.001$; Fig. 4B) in allocations to the group project on the probability that an individual voted for 'competition'. All else being equal, every additional MU to the standard deviation of allocations within group decreased the odds of voting for 'competition' by 5%, whilst increases in the standard deviation of allocations between groups increased the odds of voting for 'competition' by 2%. Additionally, there was a significant effect of game period on voting for 'competition' ($F_{28,\ 3470} = 2.17$, $P < 0.001$). Planned polynomial contrasts indicated that the probability an individual voted for 'competition' increased significantly over subsequent game periods ($F_{1,\ 351.7} = 15.22$, $P < 0.001$; Fig. 1A). All else being equal, an individual was 65% more likely to vote for 'competition' in the final game period than in the second game period.

4. Discussion

The results demonstrate that a competitive environment at the group level readily emerges from decisions made by individual subjects. Furthermore, the decision to act competitively toward other groups coincided with the decision to cooperate with group members. Importantly, individuals had greater net earnings in populations that adopted this strategy compared to the control sessions in which competitive interactions were prohibited. Apparently, people can be comfortable with making decisions promoting between-group competition and are ready to invest to the success of their own group, even when such investments reduce payoffs relative to their own group members. Such behavioral predispositions may underlie the well-known tendency for humans to form a social environment that is characterized by persistent inter-group competition and within-group cooperation. The question that remains, however, is how and why do individuals approach a strategy of joint within-group cooperation and between-group competition?

Theoretical studies have demonstrated that simple genetic polymorphisms coding for within-group cooperation and between-group conflict can coevolve (Choi & Bowles, 2007; Garcia & van den Bergh, 2011; Lehmann, 2011; Lehmann & Feldman, 2008). We show that a

Table 1
Analysis of factors affecting individual investments in the PGwC treatment. V = group interaction vote ('equal division', 'isolate', or 'compete'), P = game period (covariate), *D* = difference in the deviances of the compared models, *df* = difference in the number of parameters of the compared models, *P* = P-value associated with the observed *D* and *df*, calculated from the chi-square distribution.

Factors			−2 Log Likelihood
V, P, V*P			25861.76
V, P			25884.05
V			25893.65
P			28411.52
Null (intercept)			28412.93
	D	*df*	*P*
V, P, V*P vs. V, P	22.32	2	<0.001
V, P vs. V	9.56	1	0.002
V vs. Null	2519.28	2	<0.001

The final model estimated with REML had estimated repeated measures covariance parameters (s.e): diagonal 32.92 (1.38), rho .95 (.01), phi .43 (.02). Estimated variance for Session (random intercept) was 2.33 (1.74).

dynamic interdependence between cooperation and conflict can also exist on the behavioral level, even with anonymous interactions in ephemeral groups. In other words, the joint expression of these traits in a population need not be the result of frequency dependent selection on fixed individual types, but rather cognitive features that allow individuals to strategically respond to the social environment. Studies that associate behavior in economic games with experience of real-world intergroup conflict consistently support the notion that individuals have flexible social motivations that promote group welfare at individual expense during or following periods of intergroup violence. Israeli senior citizens showed a greater willingness to reward cooperators and punish defectors during the Israel-Hezbollah war compared to periods before and after (Gneezy & Fessler, 2012), whilst individuals from Georgia, Sierra Leone and Burundi that experienced war showed lasting prosocial motivations years following the conflict (Bauer, Cassar, Chytilová, & Henrich, 2014; Voors et al., 2012).

Although intergroup conflict can select for cooperation along multiple evolutionary pathways including multilevel selection (Bowles, 2006, 2009), cultural selection (Bowles, Choi, & Hopfensitz, 2003; Boyd & Richerson, 2009; Gintis, 2003b), and individual benefits from building coalitions (Gintis, Smith, & Bowles, 2001; Nowak & Sigmund, 2005), these explanations take group competition as a given. Competition need not be overtly aggressive in nature, and human groups frequently treat one another as benign (Brewer, 1999; Cashdan, 2001; Halevy et al., 2008; Koopmans & Rebers, 2009; Pan & Houser, 2013) and even seek mutually beneficial interactions such as trade. Nevertheless, it appears that when the nature of group interactions is such that the gains of one group (and consequently the benefits to its constituent individuals) equate to the losses of another, individuals are willing to invest toward aggressive competition (Halevy et al., 2008; Riek et al., 2006; Sherif et al., 1988). In a similar fashion, our experiment detected an individual preference for competitive intergroup interactions over a balanced prosocial alternative. Although a more extensive range of group interaction options may have yielded different results (and hence we cannot claim that competitive interactions will always be approached), it is clear that there is some bias toward promoting competition. Evolutionarily speaking, selection for this bias is likely dependent on sufficient levels of cooperation within the group, lest aggression result in self-destruction.

We found that the individual tendency to vote for 'compete' was associated with information from the previous round. In particular, the probability an individual was willing to promote competition increased when within-group variability in cooperation was low and between-group variability in cooperation was high. Importantly, people behaved this way despite groups being restructured in each round, and the potential for experience in one round to accurately predict the next thus being limited. These results, and the deviation from rational expectations, suggests that the motivation to vote for 'competition' stems from an adaptive information-processing system that allows individuals to recognize the special social conditions under which otherwise disadvantageous traits are beneficial. Specifically, both within-group cooperation and between-group aggression are costly behaviors that can become adaptive when there is sufficiently small trait variation within groups and sufficiently large trait variation between groups (Bowles, 2006, 2009; Price, 1972). The levels of within- and between-group variability are likely in a dynamic state of flux in complex social environments, and therefore it could be expected that individuals will benefit from tracking this information by attending to environmental cues. Such individuals may better optimize their cooperative and hostile behaviors compared to individuals that are ignorant of variability or that are less effective at processing the information.

Another possible explanation is that individuals are motivated to choose 'compete' out of psychological biases that operate within the context of the game and not out of social adaptations. Firstly, individuals may choose the competitive option to psychologically protect themselves from the disappointment of making a poor decision (Larrick, 1993). Because competitive inter-group interactions dominate over the other options, it is more likely to occur. Thus, individuals may vote for competition and behave cooperatively because they would feel poorly if they were to do otherwise and competition was to occur (as could be expected). This explanation is supported by a post-game questionnaire, in which 35/144 individuals answered an open-ended question about their motivation for voting 'compete' by stating that "it was going to happen anyway" or "because others were doing it". Additionally, competition may have seemed a safer option for those that wanted to cooperate, as in competition the marginal per capita return of allocations to the group project was 1 (0.5 in 'isolate' and 0.375 in 'equal division'), and the personal 1MU cost of group competition can be considered fairly low. Further, it is also possible that individuals chose 'compete' as it was the more interesting option. However, as we found that decisions to choose 'competition' were influenced by observations about variability within and between groups, it seems likely that the decisions about group interactions were strategic, with the aim of increasing individual or group success.

Aside from the explanations discussed above, there are several important mechanisms that could influence willingness to promote intergroup competition, but cannot be addressed with the current study design. Firstly, internalized cultural norms and previous experience with conflict may play large roles in an individual's response to the game (Bauer et al., 2014; Bowles et al., 2003; Boyd & Richerson, 2009; Gintis, 2003a; Gneezy & Fessler, 2012; Voors et al., 2012). Of important note, the subjects of our study share a cultural background and had not experienced violent conflict. Studies across cultures, experience and context are critical for determining whether there is any variation in the motivation to promote intergroup competition. Secondly, populations can reach a characteristic state (such as that which we found) through the

Table 2
Analysis of factors affecting mean investments to the group project. T = treatment (PG vs. PGwC), P = game period (covariate), *D* = difference in the deviances of the compared models, *df* = difference in the number of parameters of the compared models, *P* = P value associated with the observed *D* and *df*, calculated from the chi-square distribution.

Factors			−2 log-likelihood
T, P, T*P			989.61
T, P			995.55
T			996.61
P			1009.01
Null (intercept)			1009.90
	D	*df*	*P*
T, P, T*P vs. T	7.00	2	0.021
T, P vs. T	1.06	1	0.303
T vs. Null	13.29	1	<0.001

The final model estimated with REML had estimated repeated measures covariance parameters (s.e.): diagonal 4.08 (1.17), rho .97 (.02), phi .71 (.08).

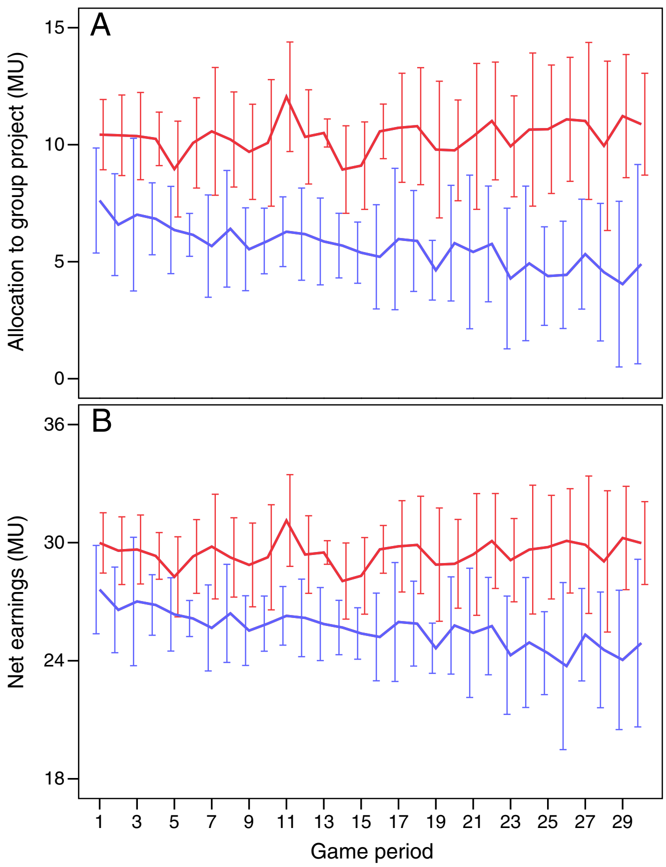

Fig. 3. Cooperation and net earnings in the PGwC and PG treatment conditions. (A) The mean level of cooperation was higher in the treatment with choice of group interaction type (PGwC, red line) than in the treatment without choice (PG, blue line). (B) Net earnings were also higher in PGwC than in PG. Lines indicate the mean of the replicate session means, and the error bars indicate 95% parametric confidence interval.

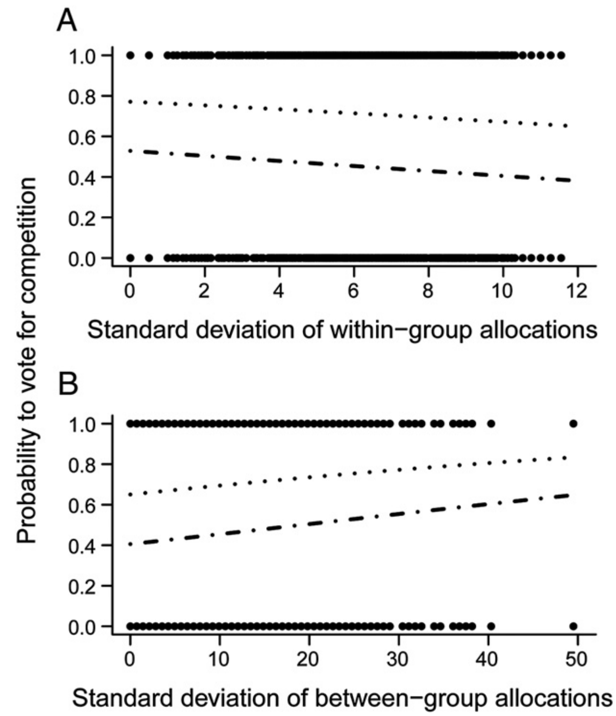

Fig. 4. The predicted relationship between (A) within-group and (B) between-group variability in allocations to the group project on the probability of voting for competition for game period 2 (dashed line) and game period 30 (dotted line). The values for between-group variability (in figure A) and within-group variability (in figure B) are held constant at the mean for the relevant game period.

network-level phenomena of behavioral flow. Fowler and Christakis (2010) experimentally showed that cooperative behavior can spread in a population because individuals model their behavior on the actions of others, and that this mechanism can allow cooperative behavior to cascade through a population even in anonymous and temporary groups. However, an experiment that is capable of reliably detecting whether inter-group hostility behaviors flow through a network requires a control that limits the shared experience between individuals, which is not satisfied by our completely random grouping structure.

Overall, we conclude that both cooperation and between-group hostility can emerge in a group-structured population, even when group boundaries are weak, as the result of individual level actions. That is, the basic conditions provided by our experiment are sufficient for behavioral flexibility to generate a population state based on cooperation and conflict. Importantly, it may be that imposing a condition in which improving individual payoffs could come at the direct expense of members in other groups established a sufficient threat for individuals to promote competitive group interactions over the alternatives. Even so, this competitive state appears to have the effect of maintaining high levels of within-group cooperation. Whilst it is possible that cultural norms or the existence of distinct behavioral types in the population may well play a role in real-life interactions and the evolution of human social behavior, the controls of our experiment and the rapid emergence of a competitive environment suggest that the proximate driving force behind this phenomenon operated at the level of the game. However, it remains unclear whether the biases we detected have an adaptive function directly related to dealing with a complex social environment. Thus, the true nature of behavioral motivations in the context of group-structured populations characterized by numerous social dilemmas remains elusive. Yet, ultimately, our understanding of human social behavior and organization must fully integrate psychological mechanisms that control behavior with the ecological and evolutionary forces that both shape and are shaped by such a system.

Table 3
Analysis of factors affecting mean net earnings. T = treatment (PG vs. PGwC), P = game period (covariate), *D* = difference in the deviances of the compared models, *df* = difference in the number of parameters of the compared models, *P* = P-value associated with the observed *D* and *df*, calculated from the chi-square distribution.

Factors	−2 log-likelihood
T, P, T*P	983.72
T, P	989.05
T	990.90
P	999.66
Null (intercept)	1001.29

	D	*df*	*P*
T, P, T*P vs. T	7.18	2	0.028
T, P vs. T	1.85	1	0.174
T vs. Null	10.39	1	0.001

The final model estimated with REML had estimated repeated measures covariance parameters (s.e): diagonal 4.13 (1.22), rho .97 (.01), phi .73 (.08).

Supplementary materials

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.evolhumbehav.2014.11.005.

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