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Original Article

No unique effect of intergroup competition on cooperation: non-competitive thresholds are as effective as competitions between groups for increasing human cooperative behavior

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ABSTRACT

Explaining cooperation remains a central topic for evolutionary theorists. Many have argued that group selection provides such an explanation: theoretical models show that intergroup competition could have given rise to cooperation that is costly for the individual. Whether group selection actually did play an important role in the evolution of human cooperation, however, is much debated. Recent experiments have shown that intergroup competitions do increase human cooperation, which has been taken as evidence for group selection as a mechanism for the evolution of cooperation. Here we challenge this standard interpretation. Competitions change the payoff structure by creating a threshold effect whereby the group that contributes more earns an additional prize, which creates some incentive for individuals to cooperate. We present four studies that disentangle competition and thresholds, and strongly suggest that it is thresholds – rather than competitions per se – that increase cooperation. Thus, prior intergroup competition experiments provide no evidence of a unique or special role for intergroup competition in promoting human cooperation, and shed no light on whether group selection shaped human evolution.

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1. Introduction

Humans are exceptional in the extent to which they are willing to cooperate with unrelated others at costs to themselves (Melis & Semmann, 2010; Rand & Nowak, 2013). This high rate of cooperative behavior presents an evolutionary puzzle (Nowak, 2006): how can natural selection favor individual sacrifice? There are a number of explanations for why individuals are willing to make sacrifices to provide benefits to non-kin. For example, theories of reciprocal altruism and direct reciprocity (Axelrod & Hamilton, 1981; Delton, Krasnow, Cosmides, & Tooby, 2011; Nowak & Sigmund, 1992; Trivers, 1971) demonstrate how evolution can favor cooperation when individuals interact repeatedly. Indirect reciprocity and reputation models (Barclay, 2006; Boyd & Richerson, 1989; Leimar & Hammerstein, 2001; Nowak & Sigmund, 2005; Ohtsuki, Hauert, Lieberman, & Nowak, 2006) demonstrate that cooperation can evolve via third parties rewarding one individual's generosity toward another. And models of dynamic population structures, where individuals can choose whom to interact with, also allow the

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evolution of cooperation (Perc & Szolnoki, 2010; Santos, Pacheco, & Lenaerts, 2006; Skyrms & Pemantle, 2000)—a prediction that is borne out in social networks observed in the real world (Wu, Ji, He, Du, & Mace, 2015) as well as those constructed in the laboratory (Barclay & Raihani, 2016; Rand, Arbesman, & Christakis, 2011; Shirado, Fu, Fowler, & Christakis, 2013). These various mechanisms for the evolution and maintenance of cooperation all explain apparent self-sacrifice via long-run self-interest.

There is another mechanism for the evolution of cooperation that has been particularly controversial, in part because it does not require that cooperation be payoff-maximizing for individuals: group (or "multi-level") selection via intergroup competition. Theoretical models show that if cooperative groups out-compete non-cooperative groups, there are conditions under which selection for cooperation at the level of the group can outweigh selection for selfishness at the level of the individual, and cooperation can evolve despite being costly to individuals. Critically, this group-level selection process requires competition between groups, whether such competition is built directly into the payoff structure of the model (e.g., agents make decisions about whether to fight in competitions) (Choi & Bowles, 2007; García & van den Bergh, 2011) or operates via the model's evolutionary dynamic (e.g., successful groups divide, eliminating other groups in the process; or groups compete and replace each other) (Boyd, Gintis, Bowles, &



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Richerson, 2003; Gintis, 2000; Traulsen & Nowak, 2006; Wilson & Sober, 1994). Either way, it is intergroup competition that is driving the evolution of cooperation in these models.

While it is clearly theoretically possible for competition between groups to lead to the evolution of cooperation, it is much less clear whether the conditions needed for group selection were actually met over human evolution. What is contested, therefore, is not whether group selection is theoretically possible, but rather whether (and to what extent) group selection actually contributed to the evolution of human cooperation (Boyd et al., 2003; Burnham & Johnson, 2005; Burton-Chellew, Ross-Gillespie, & West, 2010; Fehr, Fischbacher, & Gächter, 2002; Gintis, Bowles, Boyd, & Fehr, 2003; Sterelny, 1996; West, El Mouden, & Gardner, 2011; West, Griffin, & Gardner, 2007; Wilson & Sober, 1994). In recent years, some researchers have attempted to shed light on this empirical question—for example, by examining anthropological evidence to estimate relevant parameters like levels of mortality in intergroup conflicts and variance between groups (Bell, Richerson, & McElreath, 2009; Bowles & Gintis, 2011; Bowles, 2009).

Laboratory experiments have also been used to investigate the impacts of between-group competition on within-group cooperation, both using real-world conflicts between real groups (Gneezy & Fessler, 2012; Silva & Mace, 2015; Voors et al., 2012) and in-lab competitions between artificially constructed groups (Bornstein, Gneezy, & Nagel, 2002; Cárdenas & Mantilla, 2015; Erev, Bornstein, & Galili, 1993; Gunnthorsdottir & Rapoport, 2006; Puurtinen & Mappes, 2009; Sääksvuori, Mappes, & Puurtinen, 2011; Tan & Bolle, 2007). Typically, these experiments have found that between-group competitions do increase within-group cooperation (but see Silva & Mace, 2015). These results have been interpreted as evidence that intergroup competition did in fact play a role in the evolution of human cooperation via group selection (e.g., Puurtinen & Mappes, 2009; Sääksvuori et al., 2011).

Here, we challenge this interpretation of prior intergroup competition studies. Specifically, we point out that previous studies do not necessarily provide evidence of a specific or unique effect of group competitions on cooperation. Adding group competition to a cooperation game can also introduce a second factor that influences cooperation-threshold effects (Archetti & Scheuring, 2012). Studies in which groups compete over a prize manipulate not only the presence of intergroup competition, but also whether a non-linearity exists in an individual's payoff function: the group that contributes more (i.e., crosses a contribution threshold) wins a prize that is shared equally by that group's members. Because such thresholds mean that contributing increases the probability that one's group, and thus oneself, will earn this prize, contributing in the presence of a threshold can sometimes be self-interested, and it is possible that the threshold alone is what drives increased cooperation. If so, adding a threshold should increase cooperation regardless of the whether or not group competition is involved. Thus, previous intergroup competition experiments confound competition and thresholds, and do not necessarily provide any evidence of a specific causal role of intergroup competition on within-group cooperation (as compared to other thresholds).

Across four studies, we de-confound competition and thresholds for the first time. We ask whether introducing competition between artificial groups has an independent causal effect on cooperation in laboratory experiments, above and beyond the effect of adding a threshold. We do this by comparing Public Goods Game (PGG) contributions in (i) control PGGs that do not involve interacting with other groups, (ii) PGGs that add a competitive, zero-sum threshold in which a prize is won by one of two competing groups (as is typical in PGG experiments on intergroup competition), and (iii) PGGs that add a threshold that is not zero-sum and not competitive, such that group members all receive a prize if their total contribution is high enough to surpass a threshold (without causing another group to not receive a prize).

If the results of previous group competition studies were driven specifically by group competition, we should observe greater contributions in PGGs with competitive zero-sum thresholds than standard PGGs or PGGs with non-zero-sum thresholds, because competitions contain both a threshold and a zero-sum competition. If, on the other hand, thresholds were sufficient to account for previous results, we should observe that competitive and non-competitive thresholds both elicit equal cooperation, and elicit more cooperation than control PGGs.

2. General methods and materials

2.1. Participants

Across four studies, we recruited 2828 participants from Amazon's Mechanical Turk (Amir & Rand, 2012; Horton, Rand, & Zeckhauser, 2011) (53% male, mean age = 34 years). Participants were only permitted to take part in one study and were excluded from all other studies once they had participated.

2.2. Procedure

In each of the four studies we (i) assigned subjects to groups; (ii) provided the instructions for a single one-shot public goods game (PGG) (in which subjects made one cooperation decision); (iii) assigned subjects to an experimental condition (through which we manipulated the threshold structure of the PGG), and then measured (iv) cooperation in the PGG and (v) attitudes toward in-group and out-group members. The four studies all proceeded in this order, although the experimental conditions differed.

Specifically, we began each experiment by assigning participants to groups of size 10. We then asked participants to read instructions and answer comprehension questions about both the PGG and its threshold structure (see Appendix for full instructions and comprehension questions). In the PGG, each participant started with 30 monetary units and decided how much to contribute to their group's public good, in increments of 5 units (units were converted to pay at a rate of 1 unit per cent). All contributions to the public good were doubled and then distributed equally among the group's 10 participants, independent of their individual contributions; thus, contributing nothing was payoff-maximizing for the individual. On top of this basic PGG structure, we varied across conditions (i) whether there was the possibility of earning an additional prize if the group contributed a sufficient amount, and (ii) the precise form of this threshold (as described in more detail below).

After making their contribution decisions, participants answered several questions designed to investigate their regard for members of their own group, and of other groups. Specifically, participants reported how happy they would be if (i) an in-group and (ii) an out-group member (a) lost and (b) won money in a future study. We then computed participants' regard for in-group members (happiness if an in-group member won money, minus happiness if an in-group member lost money), and the same for out-group members. See Appendix for details.

Participants received a show-up fee immediately after finishing the study. Then, after all data were collected, we grouped participants to-gether and calculated their payoffs, which were paid as "bonuses" through Mechanical Turk. These studies were approved by the institutional review board at Yale University. All participants consented prior to participation.

3. Study 1

3.1. Methods

In our first study, we manipulated the threshold structure of the PGG across three experimental conditions: control PGG (standard PGG game), Competition (a threshold PGG game involving a zero-sum competition with another group), or Social Threshold (a threshold PGG game involving a non-competitive *comparison* to another group). (See Appendix for exact instructions).

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