A cue of kinship promotes cooperation for the public good

Daniel Brian Krupp[a,*], Lisa M. Debruine[b], Pat Barclay[c]

[a]Department of Psychology, Neuroscience and Behavior, McMaster University, Hamilton, ON L8S 4K1, Canada
[b]School of Psychology, University of Aberdeen, Aberdeen AB24 2UB, UK
[c]Department of Neurobiology and Behavior, Cornell University, Ithaca, NY 14853, USA

Abstract

Relatedness is a cornerstone of the evolution of social behavior. In the human lineage, the existence of cooperative kin networks was likely a critical stepping stone in the evolution of modern social complexity. Here we report the results of the first experimental manipulation of a putative cue of human kinship (facial self-resemblance) among ostensible players in a variant of the "tragedy of the commons," the one-shot public goods game, in which group-level cooperation—via contributions made to the public good and the punishment of free riders—is supported at a personal cost. In accordance with theoretical predictions, contributions increased as a function of the "kin density" of the group. Moreover, the distribution of punishment was not contingent on kin density level. Our findings indicate that the presence of a subtle cue of genealogical relatedness facilitates group cooperation, supporting the hypothesis that the mechanisms fostering contemporary sociality took root in extended family networks.
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1. Introduction

Kinship pervades animal social organization, and considerations thereof have greatly enhanced our understanding of cooperation and conflict.[1] Kin selection theory, an extension of Darwinian natural selection that includes the effects of genes on the reproduction of their copies in the bodies of other individuals, provides the principal rationale: The dispensation of benefits to genealogical kin may, under broad conditions, increase the fitness of an allele (Hamilton, 1964, 1975). Familial networks are common among social animals, and many cooperatively breeding vertebrates—*Homo sapiens* chief among them—engage in complex collaborations involving mixed groups of close and distant relations, where benefits are preferentially channeled to kin (Griffin & West, 2003). Given social dilemmas in which free riders can stand to gain more than their altruistic counterparts, cooperative outcomes are nonetheless regularly achieved (Fehr & Fischbacher, 2003). Yet, this kind of altruism remains vulnerable to a tragedy of the commons: a conflict between the group's interest to build and maintain a public good and each individual's interest to withhold or take from this good more than a fair share (Hardin, 1968). The puzzle, then, is how ancestral humans surmounted this vulnerability and how their descendents continue to engineer evermore intricate alliances in the face of it.

[1] *Cooperation* is here defined as a social action that provides a benefit to the recipient, irrespective of the effects of the action on the actor's fitness. Likewise, *conflict* is here defined as a social action that imposes a cost on the recipient, again irrespective of the effects on the actor. Thus, both *altruism* and *mutual benefit* are forms of cooperation, and both *selfishness* and *spite* are forms of conflict. These definitions are typical, albeit inconsistently applied, among evolutionary biologists (West, Griffin, & Gardner, 2007). Those with etymological concerns over the use of the term "cooperation" to include the phenomenon of altruism might wish to substitute the word "helping" in its stead.

A leading explanation is that kin networks served as a precondition to the evolution of larger cooperative groups that began to incorporate nonrelatives (Alexander, 1987; Gardner & West, 2004). Kin selection models of the tragedy of the commons predict that the magnitude of group cooperation will vary with the degree of within-group relatedness (Foster, 2004; Frank, 1998; Hamilton, 1964; West & Buckling, 2004) or "kin density." By virtue of its success, however, high levels of intragroup cooperation could have elevated intergroup competition for resources and could have also supplied unrelated individuals with a niche to exploit by selectively invading the kin groups of undiscriminating altruists and by free riding on group productivity (Grafen, 1984; Hamilton, 1975; Lehmann & Keller, 2006). Initially, unrelated opportunists would acquire a disproportionately large share of the group profits. More-over, they would suffer no indirect loss of fitness by free riding on group productivity, being unrelated to the other members of the group. The upshot of this is an increase in the frequency with which nonrelatives interact. By contrast, altruists in this scenario would suffer a decrement in fitness, both directly and indirectly. Accordingly, selection should have favored discriminative responses to available kinship cues that would make exploitation by nonrelatives difficult.

One form of kin recognition mechanism, phenotype matching, operates by comparing the phenotypes of potential social partners to mental representations of self or prototypical kin members and using the resultant information to determine a course of action (Sherman, Reeve, & Pfennig, 1997). Experimental manipulations of facial self-resemblance yield context-specific effects on attractiveness and trust that are in line with predictions from kin selection theory. Facial self-resemblance increases trust in an experimental game (DeBruine, 2002), an outcome consistent with the hypothesis that self-resemblance is a cue of kinship, but also consistent with the hypothesis that self-resemblance simply exploits general preferences for "famil-iarity" or "similarity." However, DeBruine (2002) did not find that resemblance to famous familiar faces had any detectable effect on trust in the same game. Moreover, on a familiarity hypothesis, similarity in resemblance should tend to increase the "liking" of a stimulus, irrespective of context. This is not true of kinship cues, however: Consideration of the costs of inbreeding depression would suggest a preference for similar individuals in cooperative contexts, but antipathy for those same individuals in mating contexts. Corroborating the kinship hypothesis, facial self-resemblance increases attributions of the attractiveness of same-sex faces (DeBruine, 2004) and the trustworthiness of opposite-sex faces, but decreases the attractiveness of opposite-sex faces in short-term mating contexts (DeBruine, 2005). Furthermore, judgments of facial similarity appear to be largely in the service of kin recognition. Maloney and Dal Martello (2006) presented a group of participants with pairs of children's faces and asked them to rate the "similarity" of the faces; unbeknownst to these participants, half of the paired pictures were of siblings. A second group of participants was presented with the same set of faces and asked to classify each pair as depicting siblings or not. They found that 96% of the variance in the first group's judgments of the "similarity" of face pairs could be explained by the second group's judgments of kinship; however, differences in age and sex between paired images were not associated with similarity judgments. Together, this is compelling evidence that facial resemblance is a cue of kinship and does not merely activate general preferences for familiarity.

Field data suggest that humans make cognitive and behavioral distinctions between close relatives and others: Although varying considerably in their mappings onto genetic relatedness, linguistic divisions along kinship lines are universally drawn (Brown, 1991; Jones, 2004); magna-nimity and resource exchange are biased to the advantage of kin (Anderson, 2005; Bowles & Posel, 2005; Hames, 1987); and transgressions by nonrelatives are more likely to lead to violent, often fatal, altercations (Chagnon, 1988; Daly & Wilson, 1988). Despite this, there have been no experimental tests of the effects of kinship cues on cooperation in the tragedy of the commons, perhaps because of the difficulty of manipulating kinship without confounding it with the social history of the interacting individuals.

We hypothesized that humans use facial self-resemblance as a cue of relatedness to assist in the dispensation of resources and, as a consequence, promote the public good. To test this, we examined contributing behavior in a "perfect stranger" public goods game (PGG), a four-member cooperative task (Fehr & Gächter, 2002), in response to the facial self-resemblance of ostensible group members. Specifically, we predicted that contributions to the public good would increase as a function of the "perceived" kin density of the group's composition.

Free riding by group members undermines the public good, but punishment directed at these individuals can facilitate cooperative behavior (Fehr & Gächter, 2002; Yamagishi, 1986). The attendant increase in cooperation benefits all group members, but because it can be costly for the punisher to produce, punishment is also a public good that may be subject to the tragedy of the commons (Oliver, 1980). An intuitive reading of kin selection theory might suggest that individuals should be more forgiving toward free-riding kin and more punitive toward unrelated free riders who take advantage of kin, but theoretical models do not find a clear effect of kinship on punishment: In some cases, relatedness may even inhibit its evolution (Boyd & Richerson, 1992; Gardner & West, 2004). However, these models were constructed to examine the evolutionary stability of general punishment strategies and do not directly speak to systems in which punishers could vary their decisions as a function of relatedness to free riders and to the "victims" of free riding. Thus, we made no prediction about the effect, if any, that facial self-resemblance would have on punishment behavior.

2. Methods

Participants were recruited from an introductory psychology participant pool. They were photographed on arrival under the pretense that they were to participate, with students at other universities, in an online study of investment decisions. After this, they completed a distracter questionnaire and were scheduled to return approximately 1 week later to participate in the PGG. In the ensuing week, one of their images was used to create digital composites ("morphs") for the self-resemblance manipulation (DeBruine, 2002). During the second session, participants played the PGG and provided demographic information. We took pains to make this scenario believable: One of the experimenters (D.B.K.) made a mock phone call prior to play to confirm that the "other" laboratories involved were ready to begin. Participants were included only if their morphs were appropriately realistic (e.g., no conspicuous or odd features) and if they appeared to understand the task, both assessed before data analysis. Two participants were removed from the analysis because they indicated in postexperiment feedback that they were somewhat skeptical of the experimental manipulation, but there is no indication that any of the remaining participants believed that they were not interacting with real people.

2.1. Public goods game

Forty participants (20 women, 20 men) were each given an endowment (in Canadian dollars) of $10 at the beginning of each of four rounds and within their groups made simultaneous decisions to contribute any whole-dollar portion of that amount toward the public good. They were assured that they would not know the other participants and would interact with group members only once, performing the task with four different groups. Ostensible group members changed every round, code names were used, and preprogrammed strategies were designed to emulate cooperators (randomly contributing $7, $8, or $9) or free riders (randomly contributing $0, $1, or $2). Contributions were multiplied by a factor of 2 and divided evenly among all group members, so that a contribution of $1 earned a return of 50¢ to the contributor and to each other group member. Self-interest dictates that participants should keep their endowments to the detriment of group profits, hence the "tragic" element of the PGG. The order of kin density levels was counterbalanced such that each was presented an equal number of times in the first round. Participants were told in advance that they would receive their earnings from one of the rounds, selected at random.

Displayed on each participant's screen were images of the faces of the three ostensible other players in the group, matched on sex and "race" (East Asian, South Asian, or European descent). All images were morphs. Morphs fell into two categories: "self-resembling," composed of the participant's own face and an unknown face (the "base identity"), or "stranger," composed of two unknown faces. Fig. 1 depicts an example of this manipulation. Participants were presented with three levels of kin density: one round with 0 self-resembling morphs (k_0), two rounds with 1 self-resembling morph (k_1), and one round with 2 self-resembling morphs (k_2). In one of the k_1 rounds, the self-resembling morph was programmed to free ride; in all other rounds, the free rider was a stranger morph. A new set of three faces was used in each round to reduce the effects of previous interaction. Table 1 summarizes the kin density and role information for each round.

PGG instructions were displayed to the participants, as well as two questions to ensure that they understood the task. Participants were able to contribute any whole-dollar amount of their endowment. Once they had contributed, their earnings (based on their own contributions and the "contributions" of the other group members) were displayed, as well as the contributions made by each ostensible group member. To investigate the effects of nepotism on responses to free riding by kin and nonrelatives, participants were then

Fig. 1. Facial resemblance manipulation. The shape and color information of an unknown face (a "base identity"; left) and a "family face" (center) were blended in a 60:40 ratio to create a composite face (right). See Methods for further details.

Table 1
Ostensible player roles and morph types

Kin density level	Cooperator 1	Cooperator 2	Free rider
0	Stranger	Stranger	Stranger
1C	Self-resembling	Stranger	Stranger
1F	Stranger	Stranger	Self-resembling
2	Self-resembling	Self-resembling	Stranger

In each round, participants were presented with two cooperators and one free rider. Both the proportion of self-resembling faces (kin density level) and the role of these faces (cooperator or free rider) were varied in the experiment.

given the option of allocating punishments, in whole dollars, to any of the other group members: For every $1 spent by the punisher, the punished recipient incurred a penalty of $3. To simulate punishment behavior among group members, participants who contributed <$3 were automatically punished by the preprogrammed strategies: A contribution of $2 was punished $3; a contribution of $1 was punished $6; and a contribution of $0 was punished $9. This would give participants the impression of greater consensus among the other group members about what constitutes free riding because smaller contributions were punished more steeply, as has been found elsewhere (Fehr & Gächter, 2002). The punishments they received from the preprogrammed strategies and their updated earnings were then displayed; however, participants were not told which group members punished them.

An additional 40 participants, matched on sex and "race," were recruited as controls yoked to participants in the experimental condition. These yoked controls played the PGG with the same preprogrammed strategies and faces, and in the same presentation order of rounds as their experimental counterparts. Thus, the only methodological difference between participants in the experimental and yoked control conditions was whether any face was self-resembling. Difference scores were computed by subtracting the contributions and punishments of yoked controls from the contributions and punishments of their experimental counterparts in each round. Participants were assigned to conditions in the order that they participated: The first participant of each pair was assigned to the experimental condition, and the next available participant matching this individual on sex and "race" was assigned as the yoked control.

2.2. Stimuli

Morphs were produced in the same manner as in previous studies of facial self-resemblance (DeBruine, 2002), using custom image manipulation software (Tiddeman, Burt, & Perrett, 2001). Briefly, 12 stimuli were created for each participant in the experimental condition by blending the shape and color of a "family face" with 1 of 12 individual "base identities" of the same sex and "race." The participant's face was used as the family face for the four self-resembling stimuli, while an unknown

face of the same sex and "race" as the participant was used as the family face for four of the eight stranger stimuli, and a second unknown face was used as the family face for the other four stranger stimuli. The morphs consisted of 40% of the shape and color of the family face and 60% of the shape and color of the base identity; hair, clothing, and background remained the same as the base identity. The unknown base identities that were morphed with the participant's face and the two stranger family faces were alternated among participants in order to counterbalance the base identities associated with self-resemblance versus nonresemblance.

2.3. Statistical methods

Repeated-measures analysis of covariance (ANCOVA) was used to test the linear trend for the contributions analysis: The dependent variable was the mean difference in dollar amounts contributed to the public good between participants in the experimental condition and their yoked controls; the independent variable was the kin density level (0, 1, or 2 self-resembling faces); and the covariate was the mean difference between experimental participants and their yoked controls in amounts contributed across rounds (irrespective of kin density level). Repeated-measures ANCOVA was also used to generate the omnibus F statistic for the punishment analysis: The dependent variable was the mean difference in dollar amounts spent on punishment between participants in the experimental condition and their yoked controls; the independent variable was the kin density level and role of the self-resembling face (cooperator vs. free rider); and the covariate was the mean difference between experimental participants and their yoked controls in amounts spent on punishment across rounds (irrespective of kin density level).

Several of our a priori hypotheses pertaining to contributions, from Foster (2004), Frank (1998), Hamilton (1964), and West and Buckling (2004), generated directional or "one-sided" predictions. Relevant analyses were thus modified by multiplying the probability of calculating the test statistic under the null hypothesis (i.e., .5 if the means were distributed in the predicted pattern) by the P value associated with the statistic itself. This method maintains the probability of committing a Type I error at the .05 level if the null hypothesis is true (Howell, 1997).

3. Results

Averaging across experimental and control groups, participants contributed $5.08 and spent $1.59 on punishment per round. Contributions in the two k_1 rounds were averaged because participants would have no reason to regard them differently at the contribution stage of each round, and F statistics were generated using ANCOVA. Following theoretical models, we predicted that contribution means (μ) would increase with the level of the relatedness
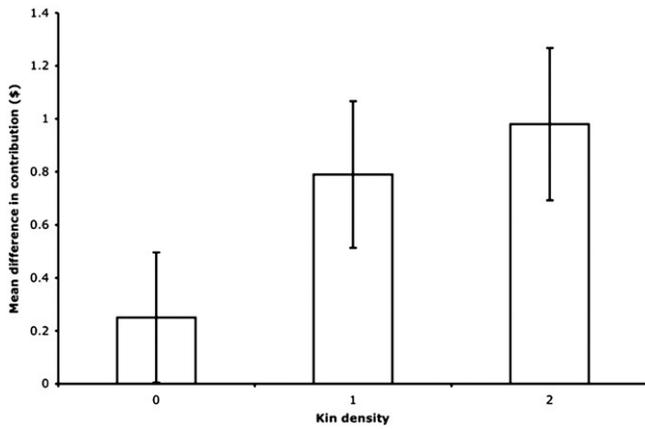
Fig. 2. Contributions to the public good as a function of perceived kin density. Mean difference (±S.E.M.) in dollar amounts contributed to the public good by participants in the experimental condition minus their yoked controls across kin density levels (number of self-resembling morphs of the experimental participant in each group). If there is no effect of kin density level, mean differences should approach zero.

cue or perceived kin density; that is, $\mu(k_0)<\mu(k_1)<\mu(k_2)$. As expected, there was a positive linear trend in contributions as a function of kin density [Fig. 2; $F(1,38)=4.02$, $p=.026$, one sided]. At the highest kin density level (k_2), participants in the experimental condition contributed 21% more to the public good than did yoked controls ($t_{39}=2.01$, $p=.026$, one sided). Free riding, measured by the amount of punishment a participant received as a response to low contributions,[2] was significantly lower among experimental participants than among yoked controls ($t_{39}=2.33$, $p=.013$, one sided). Participants in the experimental condition were not indiscriminately more cooperative than yoked controls, as the two did not differ significantly in amounts contributed in the k_0 round ($t_{39}=0.46$, $p=.648$).

Although three of eight stranger morphs were free riders, while only one of four self-morphs was a free rider, learning to associate the probability of free riding with a certain facial type cannot explain our results, as this would have affected the control participants equally. Moreover, learning to associate the probability of free riding with a certain face type *in interaction with* the experience of one's own face also cannot explain our results: Participants in the experimental condition contributed more than yoked controls in each of Rounds 1–4 (range, $0.50–0.83) and did not contribute more over time. If anything, over the four rounds, the slope of the mean difference in amounts contributed between participants in the experimental and yoked control conditions is slightly, although not significantly, negative [linear trend, $F(1,39)=0.18$, $p=.677$].

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[2] We use the amount of punishment received as an index of a participant's degree of free riding because punishment was an automatic computer response to contributions of <$3. Since participants were guaranteed to be punished at these contribution levels, they would be more likely to construe their own behavior as free riding.

Punishment of free riders neither increased nor decreased significantly as a function of kin density level [Fig. 3; omnibus ANCOVA, $F(2.278,86.569)=1.33$, $p=.270$, Greenhouse–Geisser correction]. Furthermore, there was no significant difference between punishment directed at the free-riding self-resembling morph versus the free-riding stranger morph in the two types of k_1 rounds ($t_{39}=1.28$, $p=.209$), or between yoked controls and their experimental counterparts in punishment directed at the free-riding self-resembling morph ($t_{39}=0.70$, $p=.486$).

4. Discussion

We show that group cooperation can be advanced by a subtle manipulation of facial self-resemblance whose impact, we propose, derives from the fact that it was a cue of kinship in ancestral environments. Participants were less likely to free ride, contributing more to the public good, when exposed to greater levels of "perceived kin density." There was no effect of perceived kin density on the distribution of punishment, a finding that is consistent with a self-report study of punitive sentiments in hypothetical scenarios (O'Gorman, Wilson, & Miller, 2005). This is perhaps because kinship concerns do not inspire punitive sentiments (Boyd & Richerson, 1992; Gardner & West, 2004). Alternatively, the tendency to cooperate may itself be a cue of relatedness (Dawkins, 1976; Grafen, 1985); if so, it can perhaps overwhelm any effect of facial self-resemblance at the punishment stage. Finally, nepotistic biases may be tempered by the personal and public nature of the allocation of punishment that, unlike contributions to the group, is directed to a particular recipient; punishment may thus
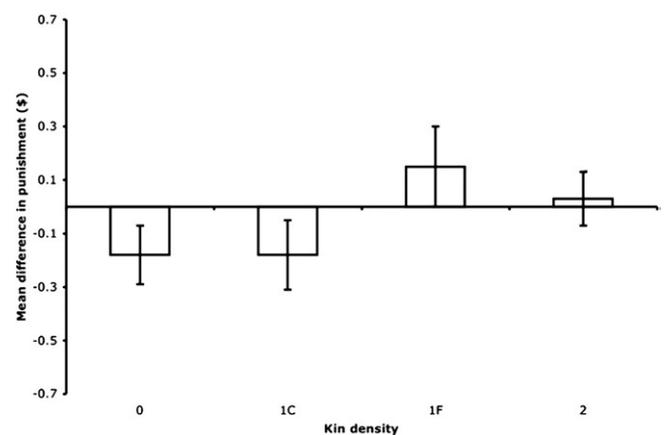

Fig. 3. Costly punishment of free riders as a function of perceived kin density. Mean difference (±S.E.M.) in dollar amounts spent on punishment of free riders by participants in the experimental condition minus their yoked controls across kin density levels (number of self-resembling morphs of the experimental participant in each group). If there is no effect of kin density level, mean differences should approach zero. Kin density levels 1C and 1F refer to the k_1 rounds with the cooperating self-resembling morph and the free-riding self-resembling morph, respectively.

entail reputational consequences (Barclay, 2006). Further theoretical and empirical research is needed to tease out the correct account.

Although we demonstrate an increase in cooperation at the level of the group as a function of kin density, we cannot, at this stage, deduce the psychological mechanisms underpinning this change. Relatedness may enhance human cooperation through perceptions of greater trustworthiness, through an inclination to promote the group's success or to embody local group-beneficial norms, or as a by-product of a desire to benefit specific group members. This raises a much discussed problem about the evolution and maintenance of cooperation (Fehr & Fischbacher, 2003; Hagen & Hammerstein, 2006): What functional and proximate motivations promote cooperation, and how can they be distinguished from one another? Strides have been made in recent years (e.g., Barclay, 2006; DeBruine, 2002; Fehr & Fischbacher, 2004; Fehr & Gächter, 2002; Haley & Fessler, 2005; Henrich et al., 2005; Kiyonari, Tanida, & Yamagishi, 2000; Kurzban, DeScioli, & O'Brien, 2007; Milinski, Semmann, & Krambeck, 2002), and we expect better resolution in short order.

In our study, facial self-resemblance affected cooperation in an artificial laboratory setting among complete strangers and in the absence of presumably much more reliable kinship cues, such as maternal–perinatal association and childhood coresidence (Lieberman, Tooby, & Cosmides, 2007; Wolf, 1993). In light of this, we believe that our results are impressive. Nevertheless, the claims we make are modest. If human cooperative alliances routinely comprised genealogical kin, there would have been a concomitant increase in competition among unrelated groups over resources, as well as an incentive for unrelated opportunists to join as a result of raised group profits (Grafen, 1984; Hamilton, 1975; Lehmann & Keller, 2006), thereby increasing the frequency with which nonrelatives came into contact with one another. This may have provided the selective impetus for the evolution of mechanisms of interfamilial conflict (Chagnon, 1988; Daly & Wilson, 1988) and cooperation (Alexander, 1987; Bowles, 2006; Boyd, Gintis, Bowles, & Richerson, 2003; Trivers, 1971) that attenuate outright threats to group survival, as well as discourage opportunistic exploitation as the interests of individuals are increasingly shared with those of relatives and nonrelatives alike. Thus, extant complex forms of cooperation and competition can be rooted in the evolutionary history of the extended family. To be sure, we do not offer here a complete account of the evolution of human cooperation, as we are still left without knowing the ecological determinants of ancestral environments that led to the realization of such a scenario among humans specifically.

Our results were predicted by several theoretical models (Foster, 2004; Frank, 1998; Hamilton, 1964; West & Buckling, 2004). Yet, we know of only one experimental manipulation of kinship or a putative cue thereof in the context of a tragedy of the commons—specifically, the effect of relatedness on the production of costly iron-scavenging agents (siderophores) in a pathogenic bacterium (Griffin, West, & Buckling, 2004). This is surprising, given that genetic relatedness is thought by many theorists to be a dominant force in social evolution. Of course, there are other routes to the evolution of cooperation besides genealogical kinship. Indeed, kinship need not play a part in cooperative ventures where it is in the actor's own direct or indirect interests to contribute to the group's welfare. It is thus probable that some good portion of apparently "altruistic" behavior is, in fact, mutually beneficial for both the group and the individual actor, as cooperative individuals can improve their own fitness prospects by augmenting the competitiveness of their group (Griffin & West, 2003; Lehmann & Keller, 2006; West et al., 2007). In any case, our results provide empirical support for the notion that the tragedy of the commons is mitigated, at least in part, by the opportunity for collaboration among kin.

Acknowledgments

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