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A cue of kinship promotes cooperation for the public good

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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.

Keywords: Kinship; Cooperation; Public goods; Tragedy of the commons

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.

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[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.

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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. Moreover, 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 "familiarity" 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); magnanimity 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.