

Sympathy and similarity: The evolutionary dynamics of cooperation

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The advantage of mutual help is threatened by defectors, who exploit the benefits provided by others without providing benefits in return. Cooperation can only be sustained if it is preferentially channeled toward cooperators and away from defectors. But how? A deceptively simple idea is to distinguish cooperators from defectors by tagging them. It clearly is in the interest of cooperators to use some distinctive cue to assort with their like. Such an assortment, however, conflicts with the interests of the cheaters, who have every incentive to also acquire that tag. This makes for an inherently unstable situation. The history of evolutionary thinking on this issue is long. An article in this issue of PNAS by Antal et al. (1) opens new ground by providing an in-depth analysis of a selection-mutation model.

The first to investigate a tag for altruism was W. D. Hamilton (2). He conceived what he called a supergene, able to produce (i) a distinctive phenotypic trait, (ii) the faculty to recognize the trait in others, and (iii) the propensity to direct benefits toward bearers of that trait, even though this entails a fitness cost. Soon afterward, Richard Dawkins described Hamilton's thought experiment by using as phenotypic trait the fanciful example of a green beard. The supergene was now termed "green beard gene," in part to acknowledge its inherent unlikelihood. "Too good to be true," were Dawkins' words (3): for the gene would have to be able to program for 3 effects, namely the feature, its recognition, and the altruistic propensity.

The green-beard concept relates to both major approaches to cooperation in evolutionary biology, namely kin selection (2) and reciprocal altruism (4). It helps in promoting assortment between cooperators; as a result, cooperators can get more than they give, so that altruism becomes a thriving business. Because wearers of green beards both confer and receive benefits, the tag works as a kind of promise that the altruistic action will be returned, not necessarily by the recipient, but by another member of the green-bearded guild. In this sense, the green beard mediates an indirect form of reciprocation, through third parties. In the usual models of indirect reciproc-



Fig. 1. Face transitions. Players in a game theoretic experiment are provided with pictures of their partners who, through digital sorcery, are made to look like themselves, to a greater or lesser extent. Here, the face in the middle is the result of a 60:40 mix of the other 2 faces. Players preferentially trust coplayers who look more like themselves. Thus, familiarity enhances trust. With permission from Lisa DeBruine, see ref. 14.

ity, "good guys" are recognized by their reputation, which is based on their past deeds (5). Here, however, recognition is ensured by a phenotypic trait, which is a less sophisticated (and possibly less reliable) signal.

Mostly, the green beard is studied in the context of kin selection. If you carry a green beard, your relatives are likely to carry one, too. Directing benefits at green-bearded individuals confers the benefits preferentially to your kin and raises your indirect fitness (because your kin shares your genes with a higher-than-average probability). In many cases, kin are living close by. But the viscosity of the population (to use another term by Hamilton) is not enough to guarantee a local increase in cooperation, because it is counterbalanced by a local increase in competition. Limited dispersal alone is therefore not enough. A gene for kin recognition can help to direct positive rather than negative effects toward relatives. But it is important to realize that the green beard can promote altruism beyond the realm of the family.

Some 10 years ago, it was found that green beards are not as implausible as their name suggests. In particular, Haig (6) remarked that genes for homophilic cell adhesion could perform all 3 tasks required from a green-beard gene (trait, recognition, and action) by coding for a surface protein that allows them to stick to copies of themselves on other cells. A

few years later, it was found that *csA* genes in *Dictyostelium discoideum* fit the bill (7). In hard times, these amoeba literally stick together to form stalks for dispersing their spores. A similar gene has also been discovered in flocculating yeast cells (8). Other candidates for more sophisticated green-beard effects have been found in ants and lizards.

An obvious way to cheat is to grow a green beard but skip the altruism. For homophilic cell adhesion, this seems barely feasible. In other examples, cheating may be prevented by genetic constraints. But in principle, one would expect that a tight link between a gene for altruistic behavior and a gene for tag recognition will ultimately be broken, and cooperation be destroyed. Surprisingly, it turned out that if the link is not too tight (but not too loose either), a dynamic regime of cooperation can emerge, based on tag diversity. Whenever some tag becomes too frequent, it can be faked by defectors, but cooperative behavior subsists nevertheless, by allying itself with another tag. This phenomenon has been termed "beard chromodynamics," to suggest that green beards can over time be replaced by red,

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