

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,

Author contributions: K.S. wrote the paper.

The author declares no conflict of interest.

See companion article on page 8597.

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or blue, or yellow beards as rallying signals for cooperators (9, 10).

The underlying principle is that of a shibboleth, or secret handshake. But such a specially-contrived trait, evolved for the purpose of signaling cooperation, is not always necessary.

Tag-based cooperation can also rely on self-similarity. All that is needed is some general means to recognize what is like yourself and what is not, i.e., to distinguish “us” from “them.”

With familiars, you need no badge, or password. This has been called the “armpit effect” (by Dawkins see ref. 3). Although an obvious variation of the green-beard principle could mediate, in principle, symbiosis between 2 different species, the armpit effect is self-referential. You need not sprout a special recognition device but simply check whether the other looks, smells, or sounds like you.

Mechanisms based on self-similarity are commonly used among cells of an organism or among members of a species. Kin recognition seems widespread: it is useful, not only for promoting nepotism, but also for avoiding incest (11). Bats or birds recognize their offspring on crowded cave roofs and cliff faces through vocalizations; hamsters and wasps pick up the odor of their nest or colony, etc. Interestingly, these faculties seem always acquired through imprinting, rather than genetically encoded. Thus, they indicate in-group rather than kin. This use of associative learning is well supported by theory (12).

An armpit effect has been recently found in hamsters (13). Self-similarity appears to work in humans, too: we like our like. Neat economic experiments show that players preferentially trust similar-looking copleys (14) (Fig. 1). (The players are provided with pictures of their ostensible partners, and these photos are manipulated to look to a

greater or lesser degree like themselves). Clearly, such cues for self-similarity can be enhanced by cultural means. Many groups provide their members with characteristic uniforms, badges, tattoos, ties, haircuts, hangouts, accents, musical tastes, or slang idioms.

In most tag-based models, the tags are discrete; you either look like me or you do not. In general, defectors can be

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overcome only for a restricted range of recombination between tag and behavior (cf. refs. 15–17). However, similarity is likely to be a question of degree; you can look more or less like me. In the case of continuous gradation, it is likely that cooperative behavior is addressed toward all those who are tolerably similar.

Such models show intriguing patterns: cliques of similar cooperators grow, are beset and undermined by defectors, and regroup around other phenotypes (18, 19). Extending tolerance to a larger range of tag values enlarges the basis of collaboration, whereas restricting tolerance shields from exploiters: this leads to endlessly fluctuating “tides of tolerance” (20).

In the model of Antal et al. (1), members of a well-mixed population of constant size N are distinguished by a tag that can take infinitely many values and is coded by integers.

Defectors help nobody, and cooperators provide help exclusively to members of their own tag group. From time to time, individuals produce offspring in numbers proportional to their fitness. Some N of these offspring are randomly chosen to form the next generation. Offspring inherit from their parent both their behavior (cooperator or defector) and their tag, up to mutation. Each configuration of the population is specified by the number of defectors and cooperators for each tag. The expected payoff values for defectors and cooperators can easily be computed in terms of conditional probabilities (e.g., for defectors to interact with cooperators, etc.). This specifies the configurations for which cooperators are sufficiently assorted with other cooperators to earn more than defectors do. But the configurations move and cluster in a very fluid manner through the range of possible tags. It needs considerable mathematical dexterity to average the payoffs over all configurations in the stationary state. This yields, under the limiting assumption of weak selection, a condition for cooperators to be more frequent than defectors in the long term, requiring that the benefit-to-cost ratio exceeds a specific threshold. Under the most favorable conditions, i.e., when mutations between tags are frequent and mutations in the behavior rare, that threshold is slightly larger than 2. In contrast to previous models (9, 15, 16), no additional requirements on spatial population distribution are used. The analysis of several limiting cases shows that the results depend significantly on mutation structure, about which empirical data are lacking at present. The elusive nature of the game of hide and seek between cooperators and defectors, an age-long spur for biological and cultural evolution, continues to challenge experimentalists and theoreticians alike.

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