

to a particular environment can favor cooperators over cheaters. In *Pseudomonas* bacteria and yeast, for example, mutations improve the intracellular uptake of cooperatively acquired nutrients (Figure 3G). In *P. aeruginosa*, this can be achieved by the inactivation of a repressor of an amino-acid and peptide-transport system. Non-social adaptation works best if cooperators are initially more abundant than cheaters, because a larger population is more likely to sample beneficial mutations.

Conclusion and outlook

Fast growth, ease of handling, and excellent genetics make many microbes ideal experimental models for studying the evolution and maintenance of cooperation via public goods. Social interactions within genetically defined populations and communities can be studied under controlled conditions in the laboratory. These studies have revealed the many forms of public goods in microbes, the dynamics of cooperation and cheating, and a range of mechanisms that help optimize and stabilize cooperative behavior.

A current challenge is to capture the existence and scale of these interactions in more complex, natural ecosystems. Another intriguing area of study is the emergent heterogeneity of public-good expression in clonal microbial populations. The underlying mechanisms and potential benefits of heterogenous expression — such as division of labor — are beginning to be understood. There is also the potential for intriguing applications in the treatment of infections, including the administration of cheater strains that may weaken pathogens, or the development of ‘evolution-proof’ drugs that specifically inhibit the production of public virulence factors.

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Primer

The evolution of human cooperation

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Darwin viewed cooperation as a perplexing challenge to his theory of natural selection. Natural selection generally favors the evolution of behaviors that enhance the fitness of individuals. Cooperative behavior, which increases the fitness of a recipient at the expense of the donor, contradicts this logic. William D. Hamilton helped to solve the puzzle when he showed that cooperation can evolve if cooperators direct benefits selectively to other cooperators (i.e. assortment). Kinship, group selection and the previous behavior of social partners all provide mechanisms for assortment (Figure 1), and kin selection and reciprocal altruism are the foundation of the kinds of cooperative behavior observed in many animals. Humans also bias cooperation in favor of kin and reciprocating partners, but the scope, scale, and variability of human cooperation greatly exceed that of other animals. Here, we introduce derived features of human cooperation in the context in which they originally evolved, and discuss the processes that may have shaped the evolution of our remarkable capacity for cooperation. We argue that culturally-evolved norms that specify how people should behave provide an evolutionarily novel mechanism for assortment, and play an important role in sustaining derived properties of cooperation in human groups.

A case for cooperation

Our species, *Homo sapiens*, first appeared about 200,000 years ago in Africa, and rapidly spread and diversified across the globe — a success, that has, in part, been attributed to our capacity for cooperation. Until the advent of agriculture about 10,000 years ago, all humans made a living by hunting game and gathering wild plant foods. Today, there is a rich array of human populations with diverse modes of subsistence, languages, religions and forms of cooperation. Because much of this diversity originated very recently in



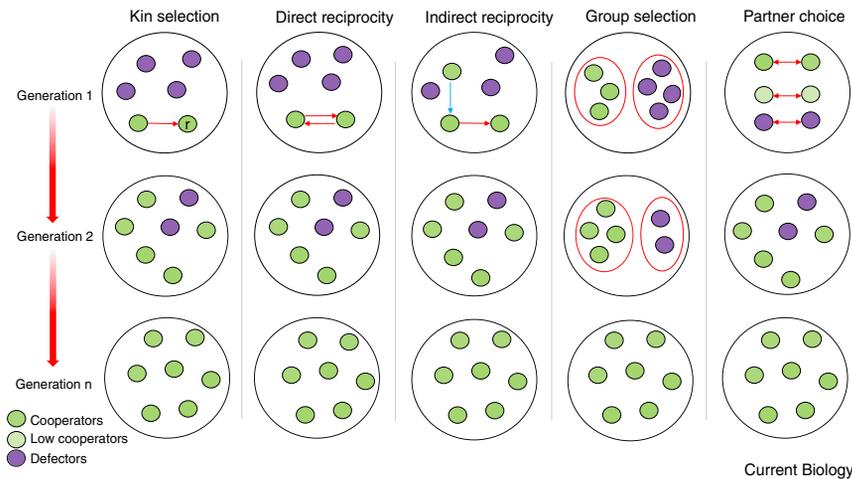


Figure 1. All mechanisms for the evolution of cooperation rely on the same basic assumption of assortment.

Assortment solves the free-rider problem by allowing cooperation to preferentially flow between cooperators. When there is assortment, cooperators (in green), will have higher payoffs than defectors (in purple). As a result, natural selection will favor cooperators and, accordingly, they will become more abundant in future generations. Kin selection leads to assortment when cooperators preferentially help those who share the same (cooperative) genes with them and those genes get passed on to the next generation. With direct reciprocity, assortment is achieved by directing help to those who have helped you. Indirect reciprocity leads to assortment when help is directed towards those who have helped others. In gene-culture co-evolutionary models, cultural learning and norm-psychology lead to assortment on cooperation in groups. Here, groups with more cooperative norms will be more successful and displace less cooperative groups. In models of partner choice, assortment is achieved when individuals compete for the most cooperative partners and the most cooperative choose each other.

evolutionary terms, the puzzle of human cooperation is best understood within the context of the lifestyle of hunter-gatherers (also referred to as ‘foragers’) and the adaptive problems that it solves. Unique aspects of human diet, life-history and reproduction made cooperation a necessary element of human life.

There are detailed ethnographic data for present-day and some past hunter-gatherer societies. Such information can be useful for inferring how our ancestors may have behaved. The vast majority of hunter-gatherers live in small, mobile, residential bands comprising several nuclear families. Food is brought back to a central location and shared widely with other band members, many of whom are genetically unrelated. In most societies, there is also a sexual division of labor in which women tend to focus on gathering plant foods with relatively predictable returns and men tend to focus on hunting and collecting honey.

Both the sexual division of labor and food sharing enable hunter-gatherers to offset the fact that hunting yields very variable returns. A successful hunt may provide enough meat to feed many people, but even the most skilled

hunter will often return from a hunt empty-handed. Without some means to offset this risk, hunting would not be a sustainable subsistence strategy. And because meat often comes in big, energy-dense packages that provide more than enough food for the hunter and his immediate family and cannot be stored, the cost-benefit ratio of sharing is highly favorable. In fact, when sufficiently large, meat packages may even be shared between resident groups.

Compared to other apes, including chimpanzees, foragers also rely more on extracted foods, such as tubers, honey and shelled fruits and nuts, as well as foods that require complex foraging technology. For example, many of the foods that hunter-gatherers eat must be processed to deactivate toxins or cooked to enhance digestibility, and much of this labor is shared. Chimpanzees do eat some extractive foods and hunt small mammals, but there is no sexual division of labor and food transfers do not comprise a substantial amount of their diet.

Derived features of human reproduction and life history include high

fertility, shortened intervals between births and extended childhoods with longer juvenile dependency. This unique pattern of reproduction and growth poses the problem for women of how to raise multiple, overlapping, energetically expensive children. A solution to this problem is to spread child-rearing responsibilities to other caregivers, a practice commonly referred to as ‘cooperative breeding’. Unlike female chimpanzees, which rear their offspring with little to no help from others and whose offspring become nutritionally independent at weaning, women need considerable help. Studies of hunter-gatherers suggest that for most of their reproductive lives, women produce fewer calories than they and their dependent children consume. Children in hunter-gatherer societies participate in foraging and offset the costs of their care, but in most societies, they do not begin to produce as many calories as they consume until their mid to late teens. This is partly because the foraging skills that hunters and gatherers rely on require years of learning and practice, as well as strength. Thus, across a range of forager groups, women and children are subsidized by the foraging efforts of other group members, particularly adult men and post-menopausal women.

Given the high demands of reproduction and the unique nature of the human diet, high levels of cooperation would have afforded many advantages to our ancestors. But recognizing the benefits of cooperation still does not solve the problem of how cooperation evolved in the face of potential exploitation by free-riders. To help answer this question, anthropologists have studied patterns of food sharing and cooperative care in hunter-gatherers and, more recently, deployed the use of behavioral economic games (Box 1).

Scope of cooperation

Humans direct cooperation to a wide range of other humans, including relatives, reciprocating partners and even strangers. While forager food distributions are often biased towards kin, a substantial fraction of the food that a household produces each day is redistributed to other unrelated households. And, the relationships between households are often contingency-based such that those who

Box 1. Experimental studies of social preferences.

Behavioral economic experiments provide a tool for studying social preferences that shape behavioral decisions. In these experiments, or ‘games’, subjects are presented with options that have different material pay-offs for themselves and others. The pay-off distributions are structured so that subjects must make tradeoffs between competing social preferences, i.e. rewards for themselves vs. rewards for others. To reduce the possibility that reputational concerns might affect subjects’ choices, subjects are paired with anonymous partners who they never meet or interact with. In addition, many games last only one round, so subjects’ decisions are not influenced by explicit expectations of reciprocity or retribution. Subjects earn material rewards (usually money), and are fully informed about the consequences of their choices. Four common economic games are described briefly below.

Dictator game: One subject (P) is allocated an endowment; P can keep all of the money for themselves or send some amount to another individual (R). Ps who only value their own welfare will keep the full endowment, while those that place some value on the welfare of others will allocate some amount to R.

Ultimatum game: This game adds a second step to the dictator game, as R can accept or reject P’s offer. If the offer is accepted P and R receive the amounts that P has proposed. If the offer is rejected, P and R receive nothing. Rejections constitute a form of altruistic punishment, because R incurs a material cost to punish P.

Third-party punishment game: P and R play a dictator game. A third party (T) is given an endowment and informed about the allocation. T can spend one unit of their endowment to reduce P’s payoff by three units. T’s expenditures constitute a form of altruistic punishment because T incurs a cost to punish P.

Public goods game: This is a multiplayer game where all subjects are allocated an endowment and each have to decide how much of their endowment they would like to contribute to a public good or keep for themselves. The total contributions are then multiplied by some number (N) and split evenly amongst the players.

share less, receive less from others. Thus, as in chimpanzees, kinship and reciprocity influence the patterns of food sharing in foragers. Still, there are sometimes long-term imbalances between households in the amount of food exchanged, which is not predicted by reciprocity models. In addition, egalitarian values are pervasive in forager societies, and need influences sharing decisions. Food is distributed to those who are too old to forage for themselves, ill or injured, or have many dependent offspring to care for.

The nature of human generosity is also revealed by behavior in incentivized economic games. For example, people in many societies reject low offers in the ultimatum game (Box 1), which implies that they have some expectation of receiving fair offers, and these expectations are reflected in the offers that are made. People also incur costs to punish unfair offers in the third-party punishment game and show aversions to inequity even when they are at an advantage. Finally, people in various societies around the world, including foragers, make charitable donations to anonymous strangers in one-shot situations. That is, humans give to others, who are not related to them, and with no expectation for repayment. In contrast, experimental studies of captive chimpanzees

using similar forms of incentivized economic games demonstrate that their choices are based on their own personal gain with little consideration for the needs of others. Chimpanzees do not consistently take advantage of opportunities to deliver rewards to others, reject unfair offers or perform third-party punishment.

The observed patterns of human cooperation are not easily reconciled with theories of kin selection and reciprocity. That said, some supporters have rationalized these findings by evoking ‘mismatch’ explanations. Such mismatch explanations suggest that human psychology is calibrated to ancestral conditions of hunter-gatherer life, which consisted of small, stable groups of closely related individuals in which cooperative behaviors are continually surveilled. Because humans are now interacting in larger, more anonymous group settings — a change that occurred very recently in evolutionary terms — natural selection has not had time to modify our psychology; hence the mismatch: we treat all our encounters as though they are either kin or long-term reciprocating partners. The problem with this explanation is that recent studies of current hunter-gatherers show that relatedness within hunter-gatherer bands is low and, because residence is remarkably fluid,

bands are continually reconstituted with new members. For instance, in Hadza hunter-gatherers, individuals continue to live with, on average, only one in five of their bandmates from the prior year. This suggests that much of the cooperative behavior observed in some hunter-gatherers involves short-term, genetically unrelated partners. Therefore, ethnographic data from contemporary people living in small-scale societies show that cooperation extends beyond close kin and reciprocating partners. And often, norms of sharing based on egalitarian values dictate cooperative behavior.

Scales of cooperation

Human cooperation occurs on a much larger scale than is observed in other species. Like other animals, handfuls of people can come together to cooperate but human cooperation scales up to include hundreds, thousands and even millions of individuals. Even in hunter-gatherer societies, cooperation can occur in large groups. Foragers are able to coordinate labor for large-scale public works, such as the construction of drive lines. Hunters and gatherers are also able to mobilize large parties to wage war.

By contrast, cooperation in chimpanzees is limited to group members, particularly kin and reciprocating partners. Relationships

with other groups are uniformly hostile. Bonobos are more tolerant of neighbors, and can sometimes interact peacefully with them. However, chimpanzees and bonobos do not participate in cooperative activities with members of other social groups. In contrast, humans have extensive social networks built on strong, often lifelong, cooperative bonds that include relatives and friends. This is, in part, due to the fact that humans recognize bilateral kin (maternal and paternal) as well as affines (relatives through marriage). Thus, despite considerable residential mobility, relationships are often maintained with relatives and friends over long distances and stretches of time. Perhaps unsurprisingly, extensive cooperative networks between individuals of different residence groups have been observed in foragers. These extended social networks and shared identity are what allow foragers to come together to construct public works and wage war against members of other ethnolinguistic groups. In fact, it is possible that the high rates of mobility and residential change in foragers are a means of cultivating and maintaining larger cooperative networks. Almost everywhere, humans live in cooperative groups of varying size and type — from families to nations, from religious sects to sporting clubs. Shared norms, conventions and values provide powerful markers of group identity and a means by which to selectively channel cooperation to one's own group members. These markers are especially important when there are multiple groups within a larger ethnolinguistic group or when multiple ethnolinguistic identities exist within the same group. In both of these situations, ethnolinguistic markers, such as shared language, become less useful in identifying group members and shared norms and customs become more useful. More than this, however, social norms lead to phenotypic assortment, making interactors more similar to one other. In the context of cooperation, social norms, then, provide a path for scaling up cooperation to ever larger groups. And indeed, there is much evidence to suggest that human psychology is adapted to norm-based group living. This includes a psychology well-suited for the cultural transmission of information, such as teaching and

high-fidelity imitation, and the proclivity to adopt norms and to punish violators.

Variation in cooperation

Cross-cultural studies using behavioral economic games (Box 1) have demonstrated substantial heterogeneity in levels of giving in the dictator, ultimatum and public goods games across societies and differences in levels of punishment and responder rejection rates in the ultimatum game. Even studies sampling from single populations have demonstrated group-level differences in cooperation. For instance, in the Hadza, within-group variation in levels of cooperation is uniformly low while between-group variation is high. This set of findings highlights the flexible nature of human cooperation and also suggests that the standard models for the evolution of cooperation, based on assortment, are plausible.

Numerous lines of evidence suggest that variation in cooperation is, at least partly, explained by differences in culture and local norms. Variation in levels of cooperation has been linked to adherence to world religions and belief in punitive, all-knowing gods who also care about how individuals treat one another. Markets, which are built on norms of fairness, cooperation and trust, are also thought to generate higher levels of cooperation. Support for this comes from cross-cultural studies demonstrating that societies with increased market integration exhibit higher levels of cooperation and data from single populations, where distance from markets predicts more cooperative behavior in individuals. Laboratory studies with Western participants suggest that social norms, and not just payoff distributions, drive cooperative play in a number of behavioral economic games. And across societies, children seem to become sensitive to local cultural norms in middle childhood, and eventually converge on the cooperative behavior of adults in their group. Finally, longitudinal data tracking both residence and cooperative behavior in Hadza individuals over a six-year period reveals no temporal consistency in levels of cooperation between individuals. Instead, individuals shift their levels of cooperation to match their new group members year after year, a finding consistent with social norms.

Summary

Cooperative foraging and breeding provide the evolutionary backdrop for understanding the evolution of cooperation in humans, as the returns from cooperating in these activities would have been high in our hunter-gatherer ancestors. Still, explaining how our ancestors effectively dealt with the problem of free-riders within this context remains a challenge. Derived features of human cooperation, however, give us some indication of the mechanisms that could lead to assortativity. These derived features include: first, the scope of cooperation — cooperation is observed between unrelated and often short-term interactors; second, the scale of cooperation — cooperation extends beyond pairs to include circumscribed groups that vary in size and identity; and third, variation in cooperation — human cooperation varies in both time and space in accordance with cultural and social norms. We argue that this pattern of findings is best explained by cultural evolutionary processes that generate phenotypic assortment on cooperation via a psychology adapted for cultural learning, norm sensitivity and group-mindedness.

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