

## A Cooperative Species: Précis

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I will advance two propositions. First, people cooperate not only for self-interested reasons but because they are genuinely concerned about the well being of others, try to uphold social norms, and value behaving ethically for its own sake. People punish those who exploit the cooperative behavior of others for the same reasons. Contributing to the success of a joint project for the benefit of one's group, even at a personal cost, evokes feelings of satisfaction, pride, even elation. Failing to do so is often a source of shame or guilt. Second, we came to have these moral sentiments (to use a phrase of Adam Smith) because our ancestors lived in environments, both natural and socially constructed, in which groups of individuals who are predisposed to cooperate and uphold ethical norms tended to survive and expand relative to other groups, thereby proliferating these pro-social motivations.

Cooperation is common in many species. But cooperation in *Homo sapiens* is exceptional in that human cooperation extends beyond close genealogical kin to include even total strangers, and occurs on a much larger scale than other species except for the social insects.

Cooperative behavior may confer benefits net of costs on the individual cooperator, and thus may be motivated entirely by self-interest. In this case, cooperation is a form of *mutualism*, namely an activity that confers net benefits both on the actor and on others. But, cooperation may also impose net costs upon the individual. In this case cooperative behavior constitutes a form of *altruism*. By contrast to mutualistic cooperation, altruistic cooperation would not be undertaken by an individual whose motives were entirely self-regarding and thus did not take account of the effects of one's actions on others.

The evolution of cooperation that is mutualistic or involving only close family relatives is easily explained. Cooperation among close family members could have evolved by natural selection because the benefits of cooperative actions are conferred on the close genetic relatives of the cooperator, thereby helping to pro-

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liferate genes associated with the cooperative behavior. Cooperation could also have evolved because one individual's costly contribution to the welfare of another individual is reliably reciprocated at a future date, thereby making cooperation mutualistic. Models of altruism towards close family members and reciprocal altruism, which really should be called "enlightened self-interest," are popular among biologists and economists alike and explain many forms of human cooperation, particularly those occurring among close kin or in dyadic (two-person) or other very small group interactions.

But these models fail to explain two facts about human cooperation: that it takes place in groups far larger than the immediate family, and that both in real life and in laboratory experiments, it occurs in interactions that are unlikely to be repeated, and where it is impossible to obtain reputational gains from behaving prosocially.

The most parsimonious proximal explanation of cooperation, supported by extensive experimental and other evidence, is that people enjoy cooperating, or feel morally obligated to cooperate, with like-minded people. People also enjoy punishing those who exploit the cooperation of others, or feel morally obligated to do so. Free-riders frequently feel guilt, and if they are sanctioned by others, they may feel ashamed. These feelings are termed *social preferences*. Social preferences include a concern for the well being of others (positive or negative) and a desire to uphold ethical norms.

In many human groups, these motives are sufficiently common to sustain socially valuable norms that support contributions to projects of common benefit, even when cooperators bear costs in order to benefit others. The forms of cooperation and the behaviors that elicit punishment by peers differ from society to society, but the critical role of social preferences in sustaining altruistic cooperation is ubiquitous.

Why are the social preferences that sustain altruistic cooperation are so common? Why do so many people care about fairness and reciprocity and value the well-being of fellow members of their groups, often favoring them over outsiders? Proximate answers to this question are to be found in the way that our brains process information and induce cooperative behavioral responses. But how did we come to have brains that function in this manner? Early human environments are part of the answer.

Early modern humans inhabited the large, mammal-rich African savannah and other environments in which cooperation in acquiring and sharing food yielded substantial benefits at relatively low cost. The slow human life-history with prolonged periods of dependency of the young also made the cooperation of non-kin in child rearing beneficial. As a result, members of groups that sustained cooperative strategies for provisioning, child-rearing, sanctioning non-cooperators, defending

against hostile neighbors, and sharing truthfully transmitted information had significant advantages over members of non-cooperative groups.

In the course of our subsequent history we created novel social and physical environments exhibiting similar, or even greater, benefits of cooperation, among them the division of labor coordinated by generalized exchange and respect of rights of property, systems of production characterized by increasing returns to scale (irrigated agriculture, modern industry, information systems with network externalities), and warfare. The impressive scope of these modern forms of cooperation was facilitated by the emergence in the last seven millennia of governments capable of enforcing property rights and providing incentives for the self-interested to contribute to common projects.

Both prior to the emergence of governments and since, however, cooperation has been sustained also by motives that led some people to bear costs on behalf of others, contributing to common projects, punishing transgressors, and excluding outsiders. These altruistic social preferences supporting cooperation out-competed unmitigated self-interest and proliferated for three reasons.

First, human groups have devised ways to protect their altruistic members from exploitation by the self-interested. Prominent among these is the public spirited shunning, ostracism, and even execution of free-riders and others who violate cooperative norms. Other group activities protecting altruists from exploitation are levelling practices that limit hierarchy and inequality, including the sharing of food and information.

Second, humans adopted prolonged and elaborate systems of *socialization* that lead individuals to internalize the norms that induce cooperation, so that contributing to common projects and punishing defectors became objectives in their own right rather than constraints on behavior. Together the internalization of norms and the protection of the altruists from exploitation were sometimes sufficient to halt entirely or even reverse within-group selection pressures operating against those who were motivated to bear personal costs to benefit others.

Third, between-group competition for resources and survival was a decisive force in human evolutionary dynamics. Groups with many cooperative members tended to survive these challenges and to occupy the territory of the less cooperative groups, thereby both gaining reproductive advantages and proliferating cooperative behaviors through cultural transmission. From *warfare* and environmental catastrophe among hunter-gatherers to the rise and fall of modern nation states, group extinction, costly group dispersal, and ostracism from groups have been powerful mechanisms supporting the evolution of human cooperation. The extraordinarily high evolutionary stakes of intergroup competition and the contribution of altruistic cooperators to success in these contests meant that sacrifice on behalf of others, extending beyond the immediate family and even to virtual strangers, could proliferate.

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This is part of the reason why humans became extraordinarily group-minded, favoring cooperation with insiders and expressing hostility towards outsiders. Boundary-maintenance sustained within-group cooperation and exchange by limiting group size and within-group linguistic, normative and other forms of heterogeneity while at the same time sustaining the between-group conflicts and differences in behavior that make group competition a powerful evolutionary force.

In short, humans became a cooperative species because cooperation was highly beneficial to the members of groups that practiced it, and we were able to construct social institutions, to enforce norms, to share food, to socialize new members, to distinguish insiders from outsiders, to make war, all of which minimized the within-group selective pressures operating against those with social preferences, while heightening the group-level advantages associated with the high levels of cooperation that these social preferences allowed. Adherence to these institutions across generations was secured through the cultural transmission of the values and beliefs that favored conformity to existing norms. These institutions proliferated because cooperation enhanced the chances that a group would survive as a biological and cultural entity in the face of environmental, military and other challenges.

Early humans were not alone in occupying territory and a feeding niche that made cooperation among group members highly advantageous. Indeed our ancestors competed with lions, hyenas, wild dogs and other possibly hominid cooperative hunters for the very same ungulates and other large mammals. Nor were our ancestors exceptional in the kinds of group competition for territory and other valued resources that made cooperation so essential to survival. Chimpanzees, too, engage in lethal contests between troops where winners gain territory and reproductive advantages. The same is true of species as diverse as meerkats and fire ants. Nor are humans exceptional in constructing their own physical and social environments. Beavers build dams, birds build nests, and burrowing animals build underground catacombs. Why then did humans, rather than chimps, lions, or meerkats, develop such exceptional forms of cooperation?

Central to our reply are the human cognitive, linguistic and physical capacities that made us especially good at all of the above, and more. These capacities allow us to formulate general norms of social conduct, to erect social institutions regulating this conduct, to communicate these rules and what they entail in particular situations, to alert others to their violation and to organize coalitions to punish the violators. No less important is the psychological capacity to internalize norms, to experience such *social emotions* as *shame* and moral outrage, and to base group membership on such non-kin characteristics as ethnicity and linguistic differences, which in turn facilitates costly conflicts among groups. Equally essential was the developmental plasticity of humans and our long period of maturation, the latter

initially a result of the particular feeding niche that early humans occupied. Also important is the unique human capacity to use projectile weapons, a consequence of which is to lower the cost of coordinated punishment of norm violators within a group, to reduce the costs of hunting large animals with concomitant benefits accruing to groups with widely endorsed sharing norms, to render intergroup conflicts more lethal, and hence to elevate group-level competition to a more powerful evolutionary force.

These exceptional aspects of human livelihoods and social interactions have favored the evolution of an individual predisposition to cooperate with others and to punish those who exploit the cooperation of others. But more than individual-level motivation is involved. The regulation of social interactions by group-level norms and institutions plays no less a role than altruistic individual motives in understanding how this cooperative species came to be. Institutions affect the rewards and penalties associated with particular behaviors, often favoring the adoption of cooperative actions over others, so that even the self-regarding are often induced to act in the interest of the group. Of course it will not do to posit these rules and institutions *a priori*. Rather, these co-evolved with other human traits in the relevant ancestral ecologies and social environments.

Cooperation is not an end, but rather is a means. In some settings, competition, the antithesis of cooperation, is the more effective means to a given end. Similarly, the individual motives and group-level institutions that account for cooperation among humans include not only the most elevated, a concern for others, fair-mindedness, and democratic accountability of leaders, for example, but also the most wicked: vengeance, racism, religious bigotry, and hostility towards outsiders.

Price-fixing by cartels and other baleful economic effects of collusion motivated Adam Smith to advocate a competitive economic system under which such forms of anti-social collusion would unravel. In its stead he advocated “an invisible hand” that would guide the efforts of countless self-interested producers to coordinate a modern division of labor in the interest of all.

The tension between the relentless logic of self-interest and the ubiquity of collective action in real world settings was eventually resolved by a series of experiments by psychologists and economists, most notably by Ernst Fehr and his colleagues (Fehr and Gächter 2000, Herrmann et al. 2008). The experiments confirmed that self-interest is indeed a powerful motive, but also that other motives are no less important. Even when substantial sums of money are at stake, many, perhaps most, experimental subjects are fair-minded, generous towards those similarly inclined, and nasty towards those who violate these pro-social precepts. In light of these results, the evidence that the tragedy of the commons is sometimes averted and that collective action is a motor of human history is considerably less

puzzling. The puzzle, instead, is how humans came to be like this.

Evolution can not only foster self-interest but also promote the generous and ethical behaviors that help us escape Hobbes' war of all against all, avert the tragedy of the commons, and permit us to sustain the hope for a society committed to freedom and justice for all. This is true not despite, but in important measure because, evolutionary processes are "red in tooth and claw," in Alfred, Lord Tennyson's famous words.

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