FOCUS ARTICLES

The Evolution of Human Cooperation

By Herbert Gintis | No Comments

Contemporary research on human cooperation yields several insights. First, interdisciplinary research currently yields results that obeyed traditional disciplinary research goals. While the twentieth century was an era of increased disciplinary specialization, the twenty-first may well turn out to be an era of trans-disciplinary synthesis. Its motto might be: when different disciplines focus on the same object of knowledge, their models must be consistent where they overlap. Second, by combining economic theory (game theory in particular) with the experimental techniques of social psychologists, economists, and other behavioral scientists, we can empirically test sophisticated models of human behavior in novel ways. The data derived from this unification allows us to deduce explicit principles of human behavior that cannot be unambiguously derived using more traditional sources of empirical data.

The power of the experimental approach is obvious: it allows theories convinced a generation of researchers that, except for sacrifice on behalf of kin, what appears to be altruism—personal sacrifice on behalf of others—is really just long-run material self-regard. Ironically, human biology has settled in the same place as economic theory, though from a quite different starting point, and using a quite contrasting logic.

The experimental evidence supporting the ubiquity of non-self-regarding motives, however, casts doubt on both the economist's and the biologist's model of the self-regarding human actor. Many of these experiments have in common a nexus of behaviors that we term strong reciprocity. Strong reciprocity is a predisposition to cooperate with others, and to punish those who violate the norms of cooperation, at personal cost, even when it is implausible to expect that these costs will be recovered at a later date.

Strong reciprocity contributes not only to the analytical modeling of human behavior, but also to the larger task of creating a cogent political philosophy for the twenty-first century. While the writings of the great political philosophers of the past were usually both penetrating and both natural and socially constructed, in which groups of individuals who were predisposed to cooperate and uphold ethical norms tended to survive and expand relative to other groups, thereby allowing these prosocial motivations to proliferate. The first proposition concerns proximate motivations for prosocial behavior, the second addresses the distant evolutionary origins and ongoing perpetuation of these cooperative dispositions.

The Roots of Human Cooperation

Our Late Pleistocene ancestors 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 and provisioning beneficial. As a result, members of groups that sustained cooperative strategies for provisioning, child-rearing, sanctioning non-cooperators, defending against hostile neighbors, and truthfully sharing information had significant advantages over members of non-cooperative groups.

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 leveling practices that limit hierarchy and inequality, including sharing food and information.

Second, humans adopted prolonged and elaborate systems of socialization that led 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 served to offset, at least partially, the competitive handicaps born by those who were motivated to bear personal costs to benefit others.

Third, between-group competition for resources and survival was and remains a decisive

Why did humans, rather than chimps, lions, or meerkats, develop such exceptional forms of cooperation? The answer lies in the human cognitive, linguistic and what 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 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 language, 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

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 Gachter 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 were found to be fair-minded, generous toward those similarly inclined, and nasty toward those who violate these prosocial 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.

Social Preferences and Social Dilemmas

Social preferences are a concern for the well-being of others and a desire to uphold ethical norms. By contrast with self-regarding preferences, which are based on states concerning dilemmas modeled by game theorists are the prisoner's dilemma, the public goods game, sometimes termed an n-person prisoner's dilemma, the so-called war of attrition and other so-called arms race interactions, the tragedy of the commons and the common pool resource game in which contributing to the common project takes the form of forgoing the overexploitation of a jointly utilized resource such as a fishery, water supply, or forest. We say a person free rides if he benefits from the contributions of other group members while himself contributing less or nothing at all.

Another-regarding player cares about not only his own payoff, but that of his partner as well. Such a player might reason as follows. "I feel sufficiently positive toward a partner who cooperates that I would rather cooperate even if by doing so I forgo the larger payoff ($15) I could have had by defecting. If my partner defects, I of course prefer to defect as well, both to increase my earnings, and to decrease the earnings of a person who has behaved uncharitably toward me." If Bob and Alice reason in this manner, and if each believes the other is sufficiently likely to cooperate, both will cooperate. Thus, both mutual cooperate and

and others have provided compelling instances of these cultural effects on genetic evolution.

Recognizing the intimate interactions between genes and culture in humans, Edward Wilson, Charles Lumsden, Robert Boyd, Peter Richerson, Luigi Luca Cavalli-Sforza and Marcus Feldman began working in the 1970's on the parallels between genetic and cultural evolution and their interactions, their work initiating the modeling of gene-culture coevolution, the second concept underpinning a plausible explanation of the origins and nature of distinctive cooperation among humans. According to gene-culture coevolution, human preferences and beliefs are the product of a dynamic whereby genes affect cultural evolution and culture affects genetic evolution, the two being tightly intertwined in the evolution of our species.

In our gene-culture coevolution model of group-structured populations, the process of differential replication affects the frequency of both individual traits, generosity toward fellow group members, say, and group traits, a system of consensus decision making or property fitness, material reward, social standing or some other metric, influence the evolution of the population shares of various behavioral types, higher payoff behaviors tending to increase their frequency in a population. The resulting so called payoff monotonic dynamic is often implemented using "as if" optimization algorithms, though in doing this we do not attribute conscious optimization to individuals. Nor do we conclude that the resulting outcomes are in any sense optimal. In general they are not. The aggregation of individually optimal choices is universally suboptimal, except under highly unrealistic conditions.

Individuals with higher payoffs may produce more copies of their behaviors in subsequent periods either through the contribution of their greater resources to differential reproductive success or because individuals disproportionately adopt the behaviors of the more successful members of their group. The latter may occur voluntarily, as when youngsters copy stars, or coercively, as when dominant ethnic groups, classes, or nations impose their cultures on subjugated peoples. Of course, cultural transmission may also favor lower payoff behaviors (think of smoking or fast food).

boundaries (through hostility toward "outsiders", for example) and lethal conflict among groups are essential aspects of this process. Within-group non-random pairing of individuals for mating, learning and other activities also plays an important part.

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Gintis (2011) presents an interesting and broad overview of the problem of human cooperation, but some issues need clarification. The most crucial one is the general notion of "human evolution". The question is what is evolving? Abstractly, evolution is a consequence of a birth-death process in a population of replicators with incomplete heredity. In classic, organismic evolution, genes are the replicators, and evolution is the temporal dynamics of gene frequencies. As a consequence, by default the term "human evolution" refers to the dynamics of genetic change in a group of organisms that are called humans in their recent (geological) history.

But I don't think this is what Gintis has in mind when using the term "human evolution". Instead, what is meant is the dynamics of cultural change. It is very likely that most cultural change is not driven by genetic change in humans (as Gintis points out, no genes for culture are known). Some have argued that cultural change may drive genetic change, as e.g. when lactose tolerance evolved, perhaps as a consequence of agricultural changes (Laland et al.

[redacted] technologies and ideologies.

A conceptual problem in thinking about the evolution of cultural content is that such content is always tightly linked to the humans carrying it. As a consequence, cultural evolution is most often modeled in terms of "fitness" of humans carrying different types of cultural content. But this not only leads to potential confusion of human genetic evolution with non-genetic cultural evolution, but it is also problematic from a theoretical point of view, as it is ultimately not the humans, but the cultural content, that is undergoing the birth-death process leading to cultural evolution: some cultural variants thrive, while others vanish.

A useful analogy may be to think of the flora of microbes colonizing humans. Every human carries in and on them more cells of microbes than actual human cells (essentially microbes are present on all interfaces of the human body with the external worlds, such as the gut, etc). These microbes undergo birth-death processes and evolve (according to classical [redacted] the default approach one would take when studying e.g. the evolution of virulence in gut microbes, where it would be misleading to consider survival of the host as the only determinant. Similarly, certain types of culture may evolve despite having a detrimental effect on their human hosts (Boyd and Richerson 1985, Yeaman et al. 2011). With regard to cooperation, it is possible that a culture of cooperation spreads for reasons other than group benefits for the human hosts. For example, cultural variants that are more conducive to cooperation, such as moral religions (Norenzayan and Shariff 2008), may have spread for other reasons, e.g. because they were less reliant on local traditions and hence more transmissible, thereby enabling larger and more cohesive societies. Thus, size and cohesiveness of human groups may be a consequence, rather than the cause of the cultural evolution of cooperation.

To disentangle these effects, it seems promising to develop a theory of cultural epidemiology, in which the cultural content itself undergoes a birth-death process based on colonizing

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A powerful framework in the study of social evolution has been game theory. This involves identifying a set of strategies, positing payoffs, assuming a game structure (e.g. tit for tat with repeated interactions in an *n* person setting), and calculating the evolutionary stable strategy, or distribution of strategies that should evolve in a population given certain stability assumptions. Empirical research in social evolution has been closely connected to this theoretical framework. One of two approaches is typically adopted. The experimenter asks of observational data whether there is evidence in nature for tit-for-tat or some other interaction rule. Studies of reciprocity in animal societies that dominated the 1980's and 1990's provide examples (reviewed in Schino and Aureli, 2009). A second, now more common, approach is to recapitulate the game in an experimental setting by asking a set of

This research program has been a powerful source of insight as is reviewed in Gintis's essay. However, there are some intriguing components and ideas missing from this approach. Whereas we now have compelling theories for the evolution of cooperation, we know little about the evolution and development of the social organization in which the cooperation takes place. The importance of social structure has been recognized to some extent. This recognition is reflected in the increasing prevalence of models that include elements of spatial structure and by the concerted development of modeling approaches, like evolutionary set theory (e.g. Tarnita, Antal, Ohtsuki, and Nowak, 2009), that allow for the incorporation of social network structure into cooperation games in interesting, principled ways.

These mathematical advances are clearly steps in the right direction as they give us insight into how social structure influences the evolution of cooperation and other behaviors. Yet, we know little empirically about the diversity of network structures constituting social systems,

[redacted]

strategies but require a more elaborate computation, and when the inputs are not simply individual traits (cooperate, defect, etc.) but network data, then we need to consider explicitly the mapping between behavioral strategies at the individual level and social organization (Flack and Krakauer 2011). How do these strategies get collectively combined by multiple individuals to produce aggregate social properties? Answering these questions requires study of the mesoscopic scale –the causal networks that specify how different combinations of strategies produce different institutions. Once we can describe how an aggregate social property is produced, we can study how the social process producing it might have evolved. The parameters in our game theoretic models will also become more empirically grounded.

The argument put forward in this essay should sound familiar to readers who know the history of the debate in evolutionary theory surrounding the genotype-phenotype map (see Laubichler and Maienschein, 2009). Two long-standing assumptions in population genetics are that the g-p map, as it is called, is simple and that the timescale on which the [redacted]

The role of developmental dynamics has long been debated in the larger evolutionary theory, and so research programs emphasizing developmental mechanisms have been pursued in parallel to population genetics. Hence the current merger of development and evolution was in a way poised to happen as the data to give momentum to the merger have been (partly) collected. In social evolution, on the other hand, there has only been the game theoretic-population genetics trajectory with no sizable quantitative research program on the developmental dynamics of social organization running in parallel.

To catch up we need to collect behavioral time series and social network data at multiple scales from model social systems. Once we have these data, we can extract the strategies and decision-making rules that individuals use during social interactions and we can build the causal networks that specify how these rules when collectively implemented produce aggregate social properties (see DeDeo, Krakauer, and Flack, 2010; Flack and Krakauer, 2011).

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well as plausible models of the evolution of the behaviors we describe in laboratory and field (Bowles and Gintis, 2011, Greif, 2006, Aoki, 2010, Bowles, 2004).

Professor Doebeli's remarks concerning cultural evolution are correct and useful, but he does not fully represent my argument. "The term `human evolution'," he asserts, "refers to the dynamics of genetic change in a group of organisms that are called humans. Instead [what Gintis means] is the dynamics of cultural change." In fact, I argued in favor of a model of human evolution in which genes and culture are *causally interrelated*, genetic evolution in humans being as much a product of cultural evolution as vice-versa. Of course, I am not thinking of cultural evolution over short periods of time, such as years or centuries, but rather over the long period of human evolution as hunter-gatherers in the Pleistocene.

Consider, for instance, the evolution of the physiology of speech and facial communication in humans. The increased social importance of communication in human society rewarded voluntarily, simply because it is the right thing to do (Simon, 1990, Gintis, 2003, Bowles and Gintis, 2011).

Another example is the predisposition to cooperate in social dilemmas, such as the of public goods game described by Ernst Fehr and his colleagues (Fehr and Gächter, 2000, Herrmann et al., 2008). In these and other experiments (described and analyzed in Gintis, Bowles, Boyd and Fehr, 2005 and Gintis, 2009), when subjects are allowed to punish other subjects, many choose to punish, at a cost to themselves, free-riders who have contributed little or nothing to the collective effort, even under conditions where there is no possibility of the punishers being monetarily compensated for their actions. We term this behavior *strong reciprocity*, and we argue that it too is the product of gene-culture coevolution (Gintis, 2000).

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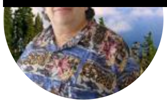

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