

Gene-Culture Coevolution and the Nature of Human Sociality

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1 Gene-culture Coevolution

Because of the importance of culture and complex social organization to the evolutionary success of *Homo sapiens*, individual fitness in humans depends on the structure of social life. Because culture is constrained and promoted by the human genome, human cognitive, affective, and moral capacities are the product of an evolutionary dynamic involving the interaction of genes and culture. We call this dynamic *gene-culture coevolution* (Cavalli-Sforza and Feldman 1982, Boyd and Richerson 1985, Dunbar 1993, Richerson and Boyd 2004). This coevolutionary process has endowed us with preferences that go beyond the self-regarding concerns emphasized in traditional economic and biological theory, and with a social epistemology that facilitates the sharing of intentionality across minds. Gene-culture coevolution is responsible for the salience of such other-regarding values as a taste for cooperation, fairness, and retribution, the capacity to empathize, and the ability to value such character virtues as honesty, hard work, piety, and loyalty.

Gene-culture coevolution is the application of *sociobiology*, the general theory of the social organization of biological species, to species that transmit culture without informational loss across generations. An intermediate category is *niche construction*, which applies to species that transform their natural environment to facilitate social interaction and collective behavior (Odling-Smee et al. 2003).

The genome encodes information that is used both to construct a new organism and to endow it with instructions for transforming sensory inputs into decision outputs. Because learning is costly and error-prone, efficient information transmission will ensure that the genome encode all aspects of the organism's environment that

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are constant, or that change only slowly through time and space. By contrast, environmental conditions that vary rapidly can be dealt with by providing the organism with the capacity to *learn*.

There is an intermediate case, however, that is efficiently handled neither by genetic encoding nor learning. When environmental conditions are positively but imperfectly correlated across generations, each generation acquires valuable information through learning that it cannot transmit genetically to the succeeding generation, because such information is not encoded in the germ line. In the context of such environments, there is a fitness benefit to the transmission of *epigenetic* information concerning the current state of the environment. Such epigenetic information is quite common (Jablonka and Lamb 1995), but achieves its highest and most flexible form in *cultural transmission* in humans and to a considerably lesser extent in other primates (Bonner 1984, Richerson and Boyd 1998). Cultural transmission takes the form of vertical (parents to children) horizontal (peer to peer), and oblique (elder to younger), as in Cavalli-Sforza and Feldman (1981), prestige (higher influencing lower status), as in Henrich and Gil-White (2001), popularity-related as in Newman et al. (2006), and even random population-dynamic transmission, as in Shennan (1997) and Skibo and Bentley (2003).

The parallel between cultural and biological evolution goes back to Huxley (1955), Popper (1979), and James (1880)—see Mesoudi et al. (2006) for details. The idea of treating culture as a form of epigenetic transmission was pioneered by Richard Dawkins, who coined the term “meme” in *The Selfish Gene* (1976) to represent an integral unit of information that could be transmitted phenotypically. There quickly followed several major contributions to a biological approach to culture, all based on the notion that culture, like genes, could evolve through replication (intergenerational transmission), mutation, and selection.

Cultural elements reproduce themselves from brain to brain and across time, mutate, and are subject to selection according to their effects on the fitness of their carriers (Parsons 1964, Cavalli-Sforza and Feldman 1982). Moreover, there are strong interactions between genetic and epigenetic elements in human evolution, ranging from basic physiology (e.g., the transformation of the organs of speech with the evolution of language) to sophisticated social emotions, including empathy, shame, guilt, and revenge-seeking (Zajonc 1980, 1984).

Because of their common informational and evolutionary character, there are strong parallels between models of genetic and cultural evolution (Mesoudi et al. 2006). Like biological transmission, culture is transmitted from parents to offspring, and like cultural transmission, which is transmitted horizontally to unrelated individuals, so in microbes and many plant species, genes are regularly transferred across lineage boundaries (Jablonka and Lamb 1995, Rivera and Lake 2004, Abbott et al. 2003). Moreover, anthropologists reconstruct the history of

social groups by analyzing homologous and analogous cultural traits, much as biologists reconstruct the evolution of species by the analysis of shared characters and homologous DNA (Mace and Pagel 1994). Indeed, the same computer programs developed by biological systematists are used by cultural anthropologists (Holden 2002, Holden and Mace 2003). In addition, archeologists who study cultural evolution have a similar *modus operandi* as paleobiologists who study genetic evolution (Mesoudi et al. 2006). Both attempt to reconstruct lineages of artifacts and their carriers. Like paleobiology, archaeology assumes that when analogy can be ruled out, similarity implies causal connection by inheritance (O'Brian and Lyman 2000). Like biogeography's study of the spatial distribution of organisms (Brown and Lomolino 1998), behavioral ecology studies the interaction of ecological, historical, and geographical factors that determine distribution of cultural forms across space and time (Smith and Winterhalder 1992).

Perhaps the most common critique of the analogy between genetic and cultural evolution is that the gene is a well-defined, discrete, independently reproducing and mutating entity, whereas the boundaries of the unit of culture are ill-defined and overlapping. In fact, however, this view of the gene is simply outdated. Overlapping, nested, and movable genes discovered in the past 35 years, have some of the fluidity of cultural units, whereas quite often the boundaries of a cultural unit (a belief, icon, word, technique, stylistic convention) are quite delimited and specific. Similarly, alternative splicing, nuclear and messenger RNA editing, cellular protein modification and genomic imprinting, which are quite common quite undermine the standard view of the insular gene producing a single protein, and support the notion of genes having variable boundaries and having strongly context-dependent effects.

Dawkins added a second fundamental mechanism of epigenetic information transmission in *The Extended Phenotype* (1982), noting that organisms can directly transmit environmental artifacts to the next generation, in the form of such constructs as beaver dams, bee hives, and even social structures (e.g., mating and hunting practices). The phenomenon of a species creating an important aspect of its environment and stably transmitting this environment across generations, known as *niche construction*, is a widespread form of epigenetic transmission (Odling-Smee et al. 2003). Niche construction shades into gene-environment coevolution, because a genetically-induced environmental regularity becomes the basis for genetic selection, and gene mutations that give rise to novel niche elements will survive if they are fitness-enhancing for their constructors.

An excellent example of gene-environment coevolution is the honey bee, in which the origin of its eusociality likely lay in the high degree of relatedness fostered by haplodiploidy, but which persists in modern species despite the fact that relatedness in the hive is generally quite low, due to multiple queen matings, mul-

multiple queens, queen deaths, and the like (Gadagkar 1991, Seeley 1997, Wilson and Holldobler 2005). The social structure of the hive is transmitted epigenetically across generations, and the honey bee genome is an adaptation to the social structure laid down in the distant past.

Gene-culture coevolution in humans is a special case of gene-environment coevolution in which the environment is culturally constituted and transmitted (Feldman and Zhivotovsky 1992). The key to the success of our species in the framework of the hunter-gatherer social structure in which we evolved is the capacity of unrelated, or only loosely related, individuals to cooperate in relatively large egalitarian groups in hunting and territorial acquisition and defense (Boehm 2000, Richerson and Boyd 2004). While some contemporary biological and economic theorists have attempted to show that such cooperation can be effected by self-regarding rational agents (Trivers 1971, Alexander 1987, Fudenberg et al. 1994), the conditions under which their models work are implausible even for small groups (Boyd and Richerson 1988, Gintis 2009). Rather, the social environment of early humans was conducive to the development of prosocial traits, such as empathy, shame, pride, embarrassment, and reciprocity, without which social cooperation would be impossible.

Neuroscientific studies exhibit clearly the genetic basis for moral behavior. Brain regions involved in moral judgments and behavior include the prefrontal cortex, the orbitalfrontal cortex, and the superior temporal sulcus (Moll et al. 2005). These brain structures are virtually unique to, or most highly developed in humans and are doubtless evolutionary adaptations (Schulkin 2000). The evolution of the human prefrontal cortex is closely tied to the emergence of human morality (Allman et al. 2002). Patients with focal damage to one or more of these areas exhibit a variety of antisocial behaviors, including the absence of embarrassment, pride and regret (Beer et al. 2003, Camille 2004), and sociopathic behavior (Miller et al. 1997). There is a likely genetic predisposition underlying sociopathy, and sociopaths comprise 3% to 4% of the male population, but they account for between 33% and 80% of the population of chronic criminal offenders in the United States (Mednick et al. 1977).

It is clear from this body of empirical information that culture is directly encoded into the human brain, which of course is the central claim of gene-culture coevolutionary theory.

2 Culture is not a Byproduct of Genetic Evolution

It might be thought that the complex and intimate interaction of genes and culture outlined above is overdrawn, and that human genetic evolution is the effect of

genetic inclusive fitness maximization, culture begin an effect of genes that can be factored out in the long run. For instance, Tooby and Cosmides (1997) explicitly deny a causal role of culture in constituting the human behavioral repertoire:

A defining characteristic of [evolutionary psychology] is the explicit rejection of the usual nature/nurture dichotomies. . . What effect the environment will have on an organism depends critically on the details of its evolved cognitive architecture. . . the real scientific issues concern the design, nature, and number of these evolved mechanisms, not “biology versus culture” or other malformed oppositions.

This denial of gene-culture coevolution can be shown to be *prima facie* untenable. To see this, suppose we have a vector \mathbf{g} of genetic variables, a vector \mathbf{c} of cultural variables, and a vector \mathbf{e} of environmental variables, including the prevalence of predators and prey, weather, and the like. In an evolutionary model, the rate of change of variables is a function of the variables, so we have

$$\dot{\mathbf{g}} = F(\mathbf{g}, \mathbf{c}, \mathbf{e}) \quad (1)$$

$$\dot{\mathbf{c}} = G(\mathbf{g}, \mathbf{c}, \mathbf{e}) \quad (2)$$

$$\dot{\mathbf{e}} = H(\mathbf{e}). \quad (3)$$

The contention that culture is an effect of genetic fitness maximization in this framework is the assertion that \mathbf{c} can be eliminated from these equations. Under what conditions can this occur? Taking the derivative of the first equation, and substituting the second and third into the first, we get

$$\ddot{\mathbf{g}} = F_{\mathbf{g}}(\mathbf{g}, \mathbf{c}, \mathbf{e})F(\mathbf{g}, \mathbf{c}, \mathbf{e}) + F_{\mathbf{c}}(\mathbf{g}, \mathbf{c}, \mathbf{e})G(\mathbf{g}, \mathbf{c}, \mathbf{e}) + F_{\mathbf{e}}(\mathbf{g}, \mathbf{c}, \mathbf{e})H(\mathbf{e}). \quad (4)$$

If \mathbf{c} is to be absent from this second order differential equation, the derivative of the right hand side of (4) with respect to \mathbf{c} must be identically zero. Thus, we have

$$0 \equiv F_{\mathbf{g}\mathbf{c}}F + F_{\mathbf{g}}F_{\mathbf{c}} + F_{\mathbf{c}\mathbf{c}}G + F_{\mathbf{c}}G_{\mathbf{c}} + F_{\mathbf{e}\mathbf{c}}H. \quad (5)$$

All five of the above terms must then be identically zero, so $F_{\mathbf{c}} \equiv 0$, implying that \mathbf{c} does not enter on the right hand side of the defining equations (1); i.e., genes are not a function of culture. This is obviously not appropriate for humans, since both genes and culture are functions of culture. We will give two examples, the repositioning of the larynx and other physiological changes facilitating linguistic communication (Deacon 1998), and the role of culture in creating a genetic predisposition for cooperative activity in humans (Gintis 2003a).

3 Gene-Culture Coevolution and the Physiology of Communication

The evolution of the physiology of speech and facial communication is a dramatic example of gene-culture coevolution. The increased social importance of communication in human society rewarded genetic changes that facilitate speech. Regions in the motor cortex expanded in early humans to facilitate speech production. Concurrently, nerves and muscles to the mouth, larynx, and tongue became more numerous to handle the complexities of speech (Jurmain et al. 1997). Parts of the cerebral cortex, Broca's and Wernicke's areas, which do not exist or are relatively small in other primates, are large in humans and permit grammatical speech and comprehension (Binder et al. 1997, Belin et al. 2000).

Adult modern humans have a larynx low in the throat, a position that allows the throat to serve as a resonating chamber capable of a great number of sounds (Relethford 2007). The first hominids that have skeletal structures supporting this laryngeal placement are the *Homo heidelbergensis*, who lived from 800,000 to 100,000 years ago. In addition, the production of consonants requires a short oral cavity, whereas our nearest primate relatives have much too long an oral cavity for this purpose. The position of the hyoid bone, which is a point of attachment for a tongue muscle, developed in *Homo sapiens* in a manner permitting highly precise and flexible tongue movements.

Another indication that the tongue has evolved in hominids to facilitate speech is the size of the hypoglossal canal, an aperture that permits the hypoglossal nerve to reach the tongue muscles. This aperture is much larger in Neanderthals and humans than in early hominids and non-human primates (Dunbar 2005). Human facial nerves and musculature have also evolved to facilitate communication. This musculature is present in all vertebrates, but except in mammals, it serves feeding and respiratory functions alone (Burrows 2008). In mammals, this mimetic musculature attaches to the skin of the face, thus permitting the facial communication of such emotions as fear, surprise, disgust, and anger. In most mammals, however, a few wide sheet-like muscles are involved, rendering fine information differentiation impossible, whereas in primates, this musculature divides into many independent muscles with distinct points of attachment to the epidermis, thus permitting higher bandwidth facial communication. Humans have the most highly developed facial musculature by far of any primate species, with a degree of involvement of lips and eyes that is not present in any other species.

This example is quite a dramatic and concrete illustration of the intimate interaction of genes and culture in the evolution of our species.

4 Socialization and the Internalization of Norms

Human society is held together by *moral values* that are transmitted from generation to generation by the process of *socialization*. These values are instantiated through the *internalization of norms* (Parsons 1967, Grusec and Kuczynski 1997, Nisbett and Cohen 1996, Rozin et al. 1999), a process in which the initiated instill values into the uninitiated (usually the younger generation) through an extended series of personal interactions, relying on a complex interplay of affect and authority. Through the internalization of norms, initiates are supplied with moral values that induce them to conform to the duties and obligations of the role-positions they expect to occupy. The internalization of norms of course presupposes a genetic predisposition to moral cognition that can be explained only by gene-culture co-evolution.

The human openness to socialization is perhaps the most powerful form of epigenetic transmission found in nature. This epigenetic flexibility in considerable part accounts for the stunning success of the species *Homo sapiens*, because when individuals internalize a norm, the frequency of the desired behavior will be higher than if people follow the norm only instrumentally—i.e., when they perceive it to be in their to do so on other grounds. The increased incidence of prosocial behaviors are precisely what permits humans to cooperate effectively in groups (Gintis et al. 2005).

There are, of course, limits to socialization (Tooby and Cosmides 1992, Pinker 2002), and it is imperative to understand the dynamics of emergence and abandonment of particular values, which in fact depend on their contribution to fitness and well-being, as economic and biological theory would suggest (Gintis 2003a,b). Moreover, there are often swift society-wide value changes that cannot be accounted for by socialization theory (Wrong 1961, Gintis 1975). However, socialization theory has an important place in the general theory of culture, strategic learning, and moral development.

The susceptibility to socialization is controlled by neuronal structures and hence the product of genetic evolution. The socialized individual is highly sensitized to the particular rewards offered for prosocial and penalties imposed for antisocial behavior. But this sensitivity is characteristic of all creatures who live in social settings. The distinguishing characteristic of the internalization of norms is that individuals behave prosocially even when there is no possibility of being rewarded for prosocial or penalized for antisocial behavior. Such altruistic behavior has been confirmed in scores of laboratory and field studies across a wide variety of societies (Camerer 2003, Gintis et al. 2003, Gintis 2009).

Gintis (2003a) provides a plausible evolutionary scenario in which the genetic predisposition to internalize norms may have developed. The prerequisite is a cul-

tural system sufficiently complex that the learning process for youth in acquiring facility with this system extend throughout childhood, and hence take the form of an authoritarian imposition carried out by elders. Because the skills acquired in this manner (e.g., hunting, recognizing and preparing nutritious foodstuffs) do not have immediate intrinsic payoffs for the learner, those who respond to the rewards and sanctions of teachers will reproduce at the expense of those who do not. Internalizing the norms associated with instrumental skills will then be directly fitness-enhancing, and hence the neural structures that support internalization will be privileged in human evolution. Once these neural structures are in place, they can be deployed for more general purposes, including internalizing moral values and deriving pleasure from helping others and punishing those who act contrary to social norms.

5 Altruism is an Emergent Property of Human Gene-Culture Evolution

Those who deny the causal importance of culture in human evolution generally argue that the altruistic behavior exhibited in modern societies is simply a maladaptation to current environmental conditions. Thus, altruistic cooperation and punishment, they argue stem from mental confusion due to the absence of anonymity in our evolutionary past. Throughout most of the history of our species, they argue, hunter-gatherer societies offered room for anonymous interaction (Haley and Fessler 2005, Trivers 2007). However, our understanding of contemporary hunter-gatherer societies indicates the lack of credibility of this argument, as do analyses of trade and migration patterns in Pleistocene (Fehr and Henrich 2004, Bowles and Gintis 2009).

If the altruism-as-maladaptation view were correct, we should expect similar behavior from our closest primate relatives. Many nonhuman primates live in hunter-gather type groups and there constant migration among groups for reasons of exogamous mating. Primates are also to distinguish kin from nonkin, and engage in repeated interactions, much as humans. Nevertheless, there is no evidence of behaviors akin to altruistic cooperation and punishment in any primate group (Silk et al. 2005, Silk 2006) Even in such “unnatural” situations as living in large groups in zoos and protective environments, such primates do not exhibit the “confusions” that the mistake hypothesis attributes to humans.

The maladaptation explanation of altruistic cooperation suggests that humans find it difficult to distinguish between one-shot and repeated interactions because humans experienced only repeated interaction prior to the appearance of settled communities some 10,000 before the present. However, humans are perfectly capa-

ble of distinguishing short- from long-term interactions, and they cooperate much more in the latter case than in the former (Keser and van Winden 2000, Fehr and Gächter 2000, Gächter and Falk 2002).

Moreover, if altruism results from confusion, we would not expect individuals to adjust their level of altruistic contribution rationally according to the costs and benefits. The evidence is that they do. Preferences for altruistic acts entail transitive preferences as required by the notion of rationality in decision theory (Andreoni and Miller 2002). In the Dictator Game, the experimenter gives a subject, called the Dictator, a certain amount of money and instructs him to give any portion of it he desires to a second, anonymous, subject, called the Receiver. The Dictator keeps whatever he does not choose to give to the Receiver. Obviously, a self-regarding Dictator will give nothing to the Receiver. Suppose the experimenter gives the Dictator m points (exchangeable at the end of the session for real money) and tells him that the price of giving some of these points to the Receiver is p , meaning that each point the Receiver gets costs the giver p points. For instance, if $p = 4$, then it costs the Dictator 4 points for each point that he transfers to the Receiver. The Dictator's choices must then satisfy the budget constraint $\pi_s + p\pi_o = m$, where π_s is the amount the Dictator keeps and π_o is the amount the Receiver gets. The question, then, is simply, is there a preference function $u(\pi_s, \pi_o)$ that the Dictator maximizes subject to the budget constraint $\pi_s + p\pi_o = m$? If so, then it is just as rational, from a behavioral standpoint, to care about giving to the Receiver as to care about consuming marketed commodities.

Varian (1982) developed a generalized axiom of revealed preference (GARP) that ensures that individuals are rational as in the sense of traditional consumer demand theory. Andreoni and Miller (2002) worked with 176 students in an elementary economics class and had them play the Dictator Game multiple times each, with the price p taking on the values $p = 0.25, 0.33, 0.5, 1, 2, 3$, and 4, with amounts of tokens equaling $m = 40, 60, 75, 80$, and 100. They found that only 18 of the 176 subjects violated GARP at least once and that of these violations, only four were at all significant. By contrast, if choices were randomly generated, we would expect that between 78% and 95% of subjects would have violated GARP.

As to the degree of altruistic giving in this experiment, Andreoni and Miller found that 22.7% of subjects were perfectly selfish, 14.2% were perfectly egalitarian at all prices, and 6.2% always allocated all the money so as to maximize the total amount won (i.e., when $p > 1$, they kept all the money, and when $p < 1$, they gave all the money to the Receiver).

Fischbacher et al. (2009) also found that subjects adjust their altruistic behavior strategically when strategic parameters change. They staged an Ultimatum Game with one Proposer and several Responders, who had to respond simultaneously to

the proposal.¹ If no Responder accepts the offer, both Responders and the Proposer receive zero payoff. If more than one Responder accepted the offer, one of the accepting Responders was chosen randomly to receive the proposed amount, and the Proposer received the remainder, rejecting Responders receiving zero. If rejecting a positive offer is simply muddle-headed or blindly emotional, this new setting should not change Responder behavior. If Responders reject offers with the goal of punishing Proposers, then the frequency of rejection should be very low in the new situation, because no single Responder could ensure that punishment would take place. If, however, there are adaptive reasons altruistic punishment, then we would expect the punishing behavior to occur only when it can be instrumentally effective, which it cannot in the multiple-Recipient version of the Ultimatum Game. The experimenters found that with multiple Responders, the rejection rate fell significantly in the two-Responder case, and even more in the five-Responder case. For instance, whereas in the traditional single-Responder case, offers of 20% of the pie are rejected with 80% probability, such offers are rejected with 15% probability when there are five Responders. Moreover, the average share of the pie accruing to the Responders falls from about 40% with one Responder to 20% with two responders, and to about 15% with five Responders.

Many additional examples can be given suggesting that other-regarding and moral behavior in humans is part of our adaptive repertoire, rather than being the results of misdirected attempts at maximizing long-term self-interest.

6 Behavioral Ethics

Behavioral ethics develops models of human morality based upon the fact that morality is an emergent property of the gene-culture evolutionary dynamic that gave rise to our species. Propositions concerning moral behavior are framed and tested using the methods of game theory, using subjects from a variety of social backgrounds and cultures. This section will outline some major themes in behavioral ethics.

In behavioral ethics, we recognize that people consider moral statements to have truth values, but we consider these values as being valid only for the specific social group involved, rather than having universal scope. We thus treat ethics in a manner similar to linguistics, where grammaticality and correct usage are important and analytically tractable, yet highly specific to a particular society of speakers. As it turns out, there are a host of human values that are universal in that they

¹ In the standard Ultimatum Game, the Proposer is given some money (the “pie”), and is instructed to offer any fraction he desires to an anonymous second player, the Responder. If the Responder accepts, they divide the money accordingly. If the Responder rejects the offer, neither player receives anything.

are present in virtually every known society (Brown 1991). We account for this universality in terms of the general requirements for social living of our species.

Moral behavior is often held to be incompatible with rational choice. This is incorrect. The rational actor model of economic theory presupposes that people have consistent preferences, but does not require that preferences be self-regarding or materialistic. We can just as easily chart how people value honesty or loyalty in the same way that we can chart how they value fried chicken or cashmere sweaters.

Because the use of the word “rational” in the rational actor model is so circumscribed compared with the general usage of the word, we often call the rational actor model the *beliefs, preferences, and constraints* model (BPC), because this captures the notion of consistent preference, the centrality of beliefs, and the notion making tradeoffs subject to informational and material constraints.

In the BPC model, choices give rise to probability distributions over outcomes, the expected values of which are the payoffs to the choice from which they arose. Game theory extends this analysis to cases where there are multiple decision makers. In the language of game theory, players are endowed with strategies, and have certain information, and for each array of choices by the players, the game specifies a distribution of payoffs to the players. Game theory predicts the behavior of the players by assuming each is rational; in other words, each maximizes a preference function subject to beliefs as well as informational and material constraints.

7 Experimental Findings on the Rationality of Altruistic Behavior

The experiments described below are all based on using game theory to set up the choices available to subjects, the knowledge they have on which their choices are based, and the payoffs to each subject as a function of their joint strategy choices. We assume the subjects are rational (i.e., consistent) decision-makers, so that their choices reflect their subjective trade-offs among heterogeneous payoffs—some material and some moral and/or other-regarding.

7.1 Conditional Altruistic Cooperation

A *social dilemma* is a situation in which a number of people can gain by cooperating, but cooperating is costly, so each individual does better personally by not cooperating, no matter what the others do. For instance, suppose if a member of a group of size $n \geq 2$ pays the cost $c > 0$, he benefits each of the others by an amount $b > 0$. If $b(n - 1) > c$, we have a social dilemma: at cost c , an individual can help the group by the amount $(n - 1)b > c$, but a selfish individual will not do so. If all cooperate, each will earn $b - c > 0$, but in a group of self-regarding

individuals, each will earn zero.

Conditional altruistic cooperation is a predisposition to cooperate in a social dilemma as long as the other players also cooperate. Consider the above social dilemma, with $n = 2$, called the Prisoner's Dilemma. In this game, let CC stand for "both players cooperate," let DD stand for "both players defect," let CD stand for "Player 1 cooperates but his partner defects," and let DC stand for "Player 1 defects and his partner cooperates." A self-regarding Player 1 will prefer DC to CC , will prefer CC to DD , and will prefer DD to CD , while an altruistic cooperator will prefer CC to DC , will prefer DC to DD , and will prefer DD to CD ; i.e. the self-regarding individual prefers to defect no matter what his partner does, whereas the conditional altruistic cooperator prefers to cooperate so long as his partner cooperates.

Kiyonari et al. (2000) ran an experiment based on this game with real monetary payoffs using 149 Japanese university students. The experimenters ran three distinct treatments, with about equal numbers of subjects in each treatment. The first treatment was a standard "simultaneous" Prisoner's Dilemma, the second was a "second-player" situation in which the subject was told that the first player in the Prisoner's Dilemma had already chosen to cooperate, and the third was a "first-player" treatment in which the subject was told that his decision to cooperate or defect would be made known to the second player before the latter made his own choice. The experimenters found that 38% of the subjects cooperated in the simultaneous treatment, 62% cooperated in the second player treatment, and 59% cooperated in the first-player treatment. The decision to cooperate in each treatment cost the subject about \$5 (600 yen). This shows unambiguously that a majority of subjects were conditional altruistic cooperators (62%). Almost as many were not only cooperators, but were also willing to bet that their partners would be (59%), provided the latter were assured of not being defected upon, although under standard conditions, without this assurance, only 38% would in fact cooperate.

7.2 Altruism and Cooperation in Groups

The *Public Goods Game*, an n -person social dilemma, captures many areas of altruistic cooperation in social life, including voluntary contribution to team and community goals. Researchers (Ledyard 1995, Yamagishi 1986, Ostrom et al. 1992, Gächter and Fehr 1999) uniformly find that groups exhibit a much higher rate of cooperation than can be expected assuming the standard model of the self-regarding actor.

A typical Public Goods Game consists of a number of rounds, say 10. In each round, each subject is grouped with several other subjects—say 3 others. Each

subject is then given a certain number of points, say 20, redeemable at the end of the experimental session for real money. Each subject then places some fraction of his points in a “common account” and the remainder in the subject’s “private account.” The experimenter then tells the subjects how many points were contributed to the common account and adds to the private account of *each* subject some fraction, say 40%, of the total amount in the common account. So if a subject contributes his whole 20 points to the common account, each of the 4 group members will receive 8 points at the end of the round. In effect, by putting the whole endowment into the common account, a player loses 12 points but the other 3 group members gain in total 24 (8 times 3) points. The players keep whatever is in their private accounts at the end of the round.

A self-regarding player contributes nothing to the common account. However, most of the subjects do not in fact conform to the self-regarding model. Subjects begin by contributing on average about half of their endowments to the public account. The level of contributions decays over the course of the 10 rounds until in the final rounds most players are behaving in a self-regarding manner. This is, of course, exactly what is predicted by the strong reciprocity model. Because they are altruistic contributors, strong reciprocators start out by contributing to the common pool, but in response to the norm violation of the self-regarding types, they begin to refrain from contributing themselves.

How do we know that the decay of cooperation in the Public Goods Game is due to cooperators punishing free riders by refusing to contribute themselves? Subjects often report this behavior retrospectively. More compelling, however, is the fact that when subjects are given a more constructive way of punishing defectors, they use it in a way that helps sustain cooperation (Orbell, Dawes, and Van de Kragt 1986, Sato 1987, Yamagishi 1988a, 1988b, 1992)

Fehr and Gächter (2000), for instance, used 6- and 10-round Public Goods Games with groups of size 4, and with costly punishment allowed at the end of each round, employing three different methods of assigning members to groups. There were sufficient subjects to run between 10 and 18 groups simultaneously. Under the Partner treatment, the four subjects remained in the same group for all 10 periods. Under the Stranger treatment, the subjects were randomly reassigned after each round. Finally, under the Perfect Stranger treatment, the subjects were randomly reassigned but assured that they would never meet the same subject more than once.

Fehr and Gächter (2000) performed their experiment for 10 rounds with punishment and 10 rounds without. Their results are illustrated in figure 1. We see that when costly punishment is permitted, cooperation does not deteriorate, and in the Partner game, despite strict anonymity, cooperation increases almost to full cooperation even in the final round. When punishment is not permitted, however, the

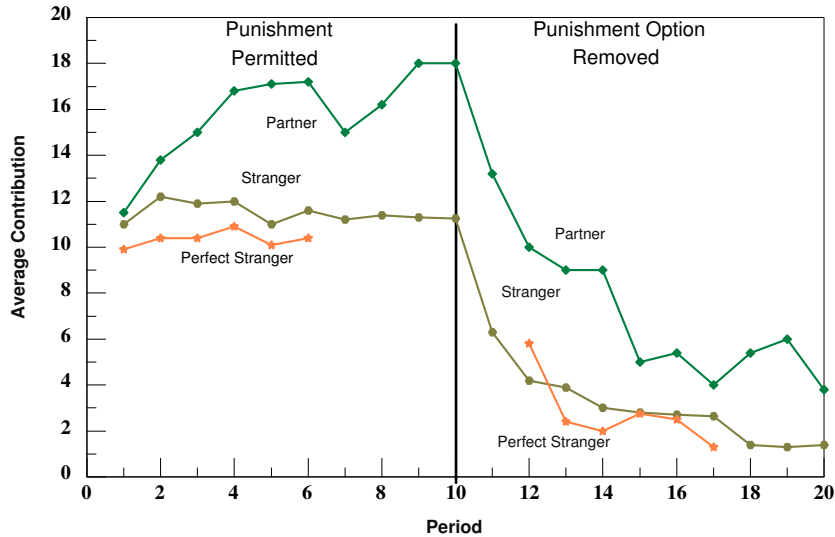


Figure 1: Average contributions over time in the Partner, Stranger, and Perfect Stranger Treatments when the punishment condition is played first (Fehr and Gächter 2000).

same subjects experienced the deterioration of cooperation found in previous Public Goods Games. The contrast in cooperation rates between the Partner treatment and the two Stranger treatments is worth noting because the strength of punishment is roughly the same across all treatments. This suggests that the credibility of the punishment threat is greater in the Partner treatment because in this treatment the punished subjects are certain that, once they have been punished in previous rounds, the punishing subjects are in their group. The prosociality impact of strong reciprocity on cooperation is thus more strongly manifested, the more coherent and permanent the group in question.

7.3 Character Virtues

Character virtues are ethically desirable behavioral regularities that individuals value for their own sake, while having the property of facilitating cooperation and enhancing social efficiency. Character virtues include *honesty*, *loyalty*, *trustworthiness*, *promise keeping*, and *fairness*. Unlike such other-regarding preferences as

strong reciprocity and empathy, these character virtues operate without concern for the individuals with whom one interacts. An individual is honest in his transactions because this is a desired state of being, not because he has any particular regard for those with whom he transacts. Of course, the sociopath *Homo economicus* is honest only when it serves his material interests to be so, whereas the rest of us are at times honest even when it is costly to be so and even when no one but us could possibly detect a breach.

Common sense, as well as the experiments described below, indicate that honesty, fairness, and promise-keeping are not absolutes. If the cost of virtue is sufficiently high, and the probability of detection of a breach of virtue is sufficiently small, many individuals will behave dishonestly. When one is aware that others are unvirtuous in a particular region of their lives (e.g., marriage, tax paying, obeying traffic rules, accepting bribes), one is more likely to allow one's own virtue to lapse. Finally, the more easily one can delude oneself into inaccurately classifying an unvirtuous act as virtuous, the more likely one is to allow oneself to carry out such an act.

One might be tempted to model honesty and other character virtues as *self-constituted constraints* on one's set of available actions in a game, but a more fruitful approach is to include the state of being virtuous in a certain way as an argument in one's preference function, to be traded off against other valuable objects of desire and personal goals. In this respect, character virtues are in the same category as ethical and religious preferences and are often considered subcategories of the latter.

Numerous experiments indicate that most subjects are willing to sacrifice material rewards to maintain a virtuous character even under conditions of anonymity. Sally (1995) undertook a meta-analysis of 137 experimental treatments, finding that face-to-face communication, in which subjects are capable of making verbal agreements and promises, was the strongest predictor of cooperation. Of course, face-to-face interaction violates anonymity and has other effects besides the ability to make promises. However, both Bochet et al. (2006) and Brosig et al. (2003) report that only the ability to exchange verbal information accounts for the increased cooperation.

A particularly clear example of such behavior is reported by Gneezy (2005), who studied 450 undergraduate participants paired off to play three games of the following form, all payoffs to which were of the form (b, a) , where player 1, Bob, receives b and player 2, Alice, receives a . In all games, Bob was shown two pairs of payoffs, $A:(x, y)$ and $B:(z, w)$ where $x, y, z,$ and w are amounts of money with $x < z$ and $y > w$, so in all cases B is better for Bob and A is better for Alice. Bob could then say to Alice, who could not see the amounts of money, either "Option A will earn you more money than option B ," or "Option B will earn you more

money than option A .” The first game was $A:(5,6)$ vs. $B:(6,5)$ so Bob could gain 1 by lying and being believed while imposing a cost of 1 on Alice. The second game was $A:(5,15)$ vs. $B:(6,5)$, so Bob could gain 1 by lying and being believed, while still imposing a cost of 10 on Alice. The third game was $A:(5,15)$ vs. $B:(15,5)$, so Bob could gain 10 by lying and being believed, while imposing a cost of 10 on Alice.

Before starting play, Gneezy asked the various Bobs whether they expected their advice to be followed. He induced honest responses by promising to reward subjects whose guesses were correct. He found that 82% of Bobs expected their advice to be followed (the actual number was 78%). It follows from the Bobs’ expectations that if they were self-regarding, they would always lie and recommend B to Alice.

The experimenters found that, in game 2, where lying was very costly to Alice and the gain from lying was small for Bob, only 17% of Bobs lied. In game 1, where the cost of lying to Alice was only 1 but the gain to Bob was the same as in game 2, 36% of Bobs lied. In other words, Bobs were loathe to lie but considerably more so when it was costly to Alices. In game 3, where the gain from lying was large for Bob and equal to the loss to Alice, fully 52% of Bobs lied. This shows that many subjects are willing to sacrifice material gain to avoid lying in a one-shot anonymous interaction, their willingness to lie increasing with an increased cost to them of truth telling, and decreasing with an increased cost to their partners of being deceived. Similar results were found by Boles et al. (2000) and Charness and Dufwenberg (2004). Gunnthorsdottir et al. (2002) and Burks et al. (2003) have shown that a socio-psychological measure of “Machiavellianism” predicts which subjects are likely to be trustworthy and trusting.

8 Conclusion

Population biology traditionally studies the frequency distribution of species as a function of within-species competition and cross-species strategic interaction. Rarely is the structure of the environment taken into account, even though we know that life-forms affect their own environment and produce the environments that other species inhabit. Niche-construction augments population biology by rendering environmental change itself part of the evolutionary dynamic. Gene-culture co-evolution is the application of niche-construction reasoning to the human species, recognizing that both genes and culture are subject to similar dynamics, and human society is a cultural construction that provides the environment for fitness-enhancing genetic changes in individuals. The resulting social system is a complex dynamic nonlinear system. Such systems have *emergent properties*, some of which

have been analyzed in this paper: social norms, morality, other-regarding preferences, and the internalization of norms.

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