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Culture and the Evolution of the Human Social Instincts

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Human societies are extraordinarily cooperative compared to those of most other animals. In the vast majority of species, individuals live solitary lives, meeting only to mate and, sometimes, raise their young. In social species, cooperation is limited to relatives and (maybe) small groups of reciprocators. After a brief period of maternal support, individuals acquire virtually all of the food that they eat. There is little division of labor, no trade, and no large scale conflict. Communication is limited to a small repertoire of self-verifying signals. No one cares for the sick, or feeds the hungry or disabled. The strong take from the weak without fear of sanctions by third parties. Amend Hobbes to account for nepotism, and his picture of the state of nature is not so far off for most other animals. In contrast, people in even the simplest human societies regularly cooperate with many unrelated individuals. Human language allows low-cost honest communication of virtually unlimited complexity. The sick are cared for, and sharing leads to substantial flows of food from the middle aged to the young and old. Division of labor and trade are prominent features of every historically known human society, and archaeology indicates that they have a long history. Violent conflict among sizable groups is common. In every human society, social life is regulated by commonly held moral systems that specify the rights and duties of individuals enforced, albeit imperfectly, by third party sanctions.

Thus, we have an evolutionary puzzle. Doubtless, the societies of our Plio-Pleistocene hominin ancestors were much like those of other primates, small, without much division of labor or cooperation. Sometime over the last five million years ago, important changes occurred in human psychology that gave rise to larger more cooperative societies. Given the magnitude and complexity of the changes, they were probably the product of natural selection. However, the standard theory of the evolution of social behavior is consistent with Hobbes, not observed human behavior. Apes fit the bill, not humans.

Something makes our species different, and in this essay we argue that something is cultural adaptation. Over the last million years or so, humans evolved the ability to learn from other humans, creating the possibility of cumulative, non-genetic evolution. These capacities were strongly beneficial in the chaotic climates of the Pleistocene, allowing humans to culturally evolve highly refined adaptations to rapidly varying environments. However, cultural adaptation also vastly increased heritable variation among groups, and this gave rise to the evolution of group beneficial cultural norms and values. Then, in such culturally evolved cooperative social environments, genetic evolution new, more pro-social motives.

We begin by reviewing the evolutionary theory of social behavior, explaining why natural selection does not normally favor large-scale cooperation. Then, we argue that cumulative cultural adaptation generates between group variation which potentiates the evolution of cooperation. Next, we suggest that such changes would lead to the evolution genetically transmitted social instincts favoring tribal scale cooperation, and summarize some of the evidence consistent with this hypothesis. Finally, we briefly discuss how these ideas relate to the theme of this volume, the nature of everyday human interactions.

<A> Cooperation is defined as costly, group-beneficial behavior

In this essay we use the word cooperation to mean costly behavior performed by one individual that increases the payoff of others. This usage is typical in game theory, and common, but by no means universal in evolutionary biology. It contrasts with ordinary usage in which cooperation refers to any coordinated, mutually beneficial behavior. It is important to

distinguish between cooperation in narrow, technical sense used here and other forms of cooperation because they have very different evolutionary properties.

To see why, consider a game called the “stag hunt,” so named because it is thought to capture the state of nature as described Rousseau in his Discourse on Inequality. Assume there is a population in which pairs of individuals have two options: They can hunt for “a stag” or for “hare.” Hunting hare is a solitary activity and an individual who chooses to hunt hare gets a small payoff, h , no matter what the other individual does. Stag hunting, however, requires coordinated action. If both players hunt for the stag, they usually succeed and each gets a large payoff, s . However, a single individual hunting stag always fails and gets a payoff of 0 (Table 1).

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The best thing for the population is if everybody hunts stags, and thus stag hunting is “cooperative” in sense of a mutually beneficial activity. However, it is not cooperative in the technical sense because individuals do not experience a cost to provide a benefit. When most of the population hunts stag, switching to hunting hare lowers an individual’s payoff, and therefore once it is common, stag hunting is not costly; it is individually beneficial. Assuming that strategies with higher payoff spread (due to natural selection if they are genetically transmitted, or because successful behaviors are imitated if they are culturally transmitted), then it follows that both behaviors are evolutionarily stable, meaning that once common they can resist rare invaders. In the jargon of game theory, the stag hunt is a game of coordination because players do better if they coordinate their behavior with the behavior of others.

Now contrast the stag hunt with its more famous cousin, the Prisoner’s dilemma. Once again consider a population of players who interact in pairs. Each individual has an opportunity to help his partner. If he does, the partner’s payoff is increased an amount b but

the helper's payoff is decreased an amount c —cooperation is clearly cooperative in the narrow sense. As long as helping provides more benefit than it costs ($b > c$), everybody is better off if everybody helps. However, unlike the stag hunt, the group beneficial behavior is not evolutionarily stable. As shown in fig. 2, non-helpers (conventionally labeled “defectors”) have a higher payoff no matter what the frequency of helpers (conventionally called cooperators). This means that defectors always increase, and, even though everyone is better off if everyone cooperates, cooperation cannot evolve.

<TABLE 2 ABOUT HERE>

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<A> The potential for cooperation is everywhere in nature

Opportunities for cooperation are omnipresent in social life. Exchange and division of labor increase the efficiency of productive processes for all the reasons given by Adam Smith in The Wealth of Nations. However, participating in exchange typically requires cooperation. In all but the simplest transactions, individuals to experience a cost now in return for a benefit later and thus are vulnerable to defectors who take the benefit but don't produce the return. Exchange and division of labor also typically are characterized by imperfect monitoring or effort and quality that give rise to opportunities for free riding. The potential for conflict over land, food, and other resources is everywhere. In such conflicts larger more cooperative groups defeat smaller less cooperative groups. However, each warrior's sacrifice benefits everyone in the group whether or not they too went to war and thus defector who repeat the fruits of victory without risking their skins. Honest, low-cost communication provides many benefits – coordination is greatly facilitated, resources can be used more efficiently, hazards avoided; the list is long. However, once individuals come to rely on the signals of others, the door is open for liars, flim-flam artists, and all the rest. Of course, widely held stable moral systems enforced by stern sanctions can solve most of these problems; cheats, cowards,

and liars can be punished. The problem is that punishment is typically costly, and defectors can reap the benefits of the moral order without paying the costs of punishment.

However, aside from humans, only a few other taxa, most notably social insects, cooperate very much. Interestingly, those that have are, like humans, spectacular evolutionary successes. It has been estimated, for example, that termites account for half of the animal biomass in the tropics. So, if cooperation produces such spectacular benefits, why is it so rare?

<A> The genetic evolution of cooperation requires assortment

The answer is simple: cooperation benefits groups, (sometimes large, sometimes small) and as we have seen, group benefits are (usually) irrelevant to course of organic evolution. Selection usually favors traits that increase the reproductive success of individuals, or sometimes individual genes, and when there is a conflict between what is good for the individual and what is good for the group, selection usually leads to the evolution of the trait that benefits the individual.

Selection favors costly group beneficial behavior only if the benefits flow disproportionately to individuals who are genetically similar to the actor who performs the behavior. To see why, suppose that groups are formed at random. Then each prosocial act has the same average effect on the fitness of helpers and egoists. This means that prosocial behavior has no effect on the relative fitness of helpers and selfish types, so there will be no change in the frequency of these two types in the population. The group benefits of the trait are irrelevant to its evolution. At the same time, it's important to see that the costs of performing prosocial behavior solely fall on helpers, and thus decrease their fitness relative to egoists. Thus, the group beneficial behaviors do not evolve. Now suppose instead that groups are made up of close relatives. Selection can favor the genes that give rise to prosocial behavior because the benefits of prosocial acts are non-randomly directed toward others who carry the same genes. Thus, the benefits of the act raise the average fitness of

the genes leading to the prosocial behavior, and if this effect is big enough to compensate for the cost, selection will lead to the evolution of the behavior.

This simple example illustrates a fundamental evolutionary principle: costly group beneficial behavior cannot evolve unless the benefits of group beneficial behavior flow non-randomly to individuals who carry the genes that give rise to the behavior. Altruism toward kin can be favored by selection because kin are similar genetically. W.D. Hamilton worked out the basic calculus of kin selection in 1964¹ and deduced many of its most important effects on social evolution. Full siblings can count on sharing half of their genes through common descent, and can therefore afford to help a sibling reproduce so long as the fitness payoffs are twice the costs. More distant relatives require a higher benefit cost ratio.² This principle, often called Hamilton's rule, successfully explains a vast range of behavior and morphology in a very wide range of organisms.³

<A> Selection can favor cooperation among small groups of reciprocators

When animals interact repeatedly, past behavior also provides a cue that allows non-random social interaction. To see why, suppose that animals live in social groups and the same pair of individuals interacts repeatedly. During each interaction one member of the pair has the opportunity to help the other, at some cost to itself. Suppose that there are two types: defectors who do not help, and reciprocators who use the strategy: Help on the first interaction. After that, help your partner as long as she keeps helping you, but if she doesn't help, don't help her any more. Initially, partners are chosen at random so that during the first interaction reciprocators are no more likely to be helped than defectors. However, after the first interaction, only reciprocators receive any help, and if interactions continue long enough, the high fitness of reciprocators in such pairings will be enough to cause the average fitness of reciprocators to exceed that of defectors.

Beyond this basic story, there is little agreement among scientists about how reciprocity works. The contrast with kin selection theory is instructive. The simple principle embodied by Hamilton's rule allows biologists to explain a wide range of phenomena.

Despite much work, evolutionary theorists have not managed to derive any widely applicable general principles describing the evolution of reciprocity. Worse, there is little evidence that reciprocity is important in nature. There are only a handful of studies that provide any evidence for reciprocity, and none of them are definitive.⁴

 Reciprocity in large groups is unlikely to evolve

Despite its many problems, theoretical work does make one fairly clear prediction that is relevant here: reciprocity can support cooperation in small groups, but not in larger ones.⁵ Instead of assuming that individuals interact in pairs, suppose that individuals live in groups, and each helping act benefits all group members. For example, the helping behavior could be an alarm cry that warns group members of an approaching predator, but makes the callers conspicuous and thereby increases their risk of being eaten. Suppose there is a defector in the group who never calls. If reciprocators use the rule, only cooperate if all others cooperate, this defector induces other reciprocators to stop cooperating. These defections induce still more defections. Innocent cooperators suffer as much as guilty defectors when the only recourse to defection is to stop cooperating. On the other hand, if reciprocators tolerate defectors, then defectors can benefit in the long run.

Some authors have emphasized that punishment takes other forms – non-cooperators are punished by reduced status, fewer friends, and fewer mating opportunities.⁶ Following Trivers⁷ we will call this “moralistic punishment.” While moralistic punishment and reciprocity are often lumped together, they have very different evolutionary properties. Moralistic punishment is more effective in supporting large-scale cooperation than reciprocity for two reasons. First, punishment can be targeted so that only defectors are affected. This means that defectors can be penalized without generating the cascade of defection that follows when reciprocators refuse to cooperate with defectors. Second, with reciprocity, the severity of the sanction is limited by the effect of a single individual’s cooperation on each other group member, an effect that becomes small as group size increases. Moralistic sanctions can be much more costly to defectors, making it possible for cooperators to induce

others to cooperate in large groups even when they are rare. Cowards, deserters, and cheaters may be attacked by their erstwhile compatriots and shunned by their society, made the targets of gossip, or denied access to territories or mates. Thus, moralistic punishment provides a much more plausible mechanism for the maintenance of large-scale cooperation than reciprocity.

There are two problems with moralistic punishment that remain to be explained:⁸ First, why should individuals punish? If punishing is costly and the benefits of cooperation flow to the group as a whole, administering punishment is a costly group beneficial act, and therefore, selfish individuals will cooperate but not punish. Second, moralistic punishment can stabilize any arbitrary behavior – wearing a tie, being kind to animals, or eating the brains of dead relatives. It does not matter whether or not the behavior produces group benefits. All that matters is that, when moralistic punishers are common, being punished is more costly than performing the sanctioned behavior, whatever it might be. When any behavior can persist at a stable equilibrium, then the fact that cooperation is a stable equilibrium does not tell us whether it is a likely outcome or not.

While much of the debate about moralistic punishment has focused on the first problem, we think the second presents a much bigger obstacle to the evolution of cooperation in large groups. Explaining the persistence of moralistic punishment is much easier than explaining why moralistic punishment would be used to maintain cooperation rather than some other form of behavior. If moralistic punishment is common, and punishments sufficiently severe, then cooperating will pay. As a result, most people may go through life without having to punish very much. This in turn means that on average having a predisposition to punish may be cheap compared to a disposition to cooperate (in the absence of punishment). This means that relatively weak evolutionary forces can maintain a moralistic predisposition, and then punishment can maintain group beneficial behavior. However, getting around the second problem is more difficult. If evolutionary change is driven only by individual costs and benefits, then moralistic punishment can stabilize cooperation, but it can stabilize anything else too. Since cooperative behaviors are a tiny

subset of all possible behaviors, punishment does not explain why large-scale cooperation is so widely observed. In other words, moralistic punishment may be necessary to sustain large-scale cooperation, but it is not sufficient to explain why large scale cooperation evolves in the first place.

 Selection among large, partially isolated groups is not effective

Group selection may be the number one hot button topic among evolutionary biologists, and as with many heated controversies it is more about how to use words than about what the world is like. The controversy began in the early 1960's when V. C. Wynne-Edwards, a British bird biologist, published a book that explained a number interesting bird behaviors in terms of the benefit to the group.⁹ While this kind of explanation not unusual in those days, Wynne-Edwards was much clearer than his contemporaries about the process that gave rise to such group level adaptations. Groups that had the display survived and prospered, while those that didn't over exploited their food supply and perished. The book generated a storm of controversy, with biological luminaries such as David Lack, George Williams, and John Maynard Smith¹⁰ penning critiques explaining why this mechanism, then called group selection, could not work. At the same time Hamilton's newly minted theory of kin selection provided an alternative explanation for cooperation. The result was the beginning of an ongoing, and highly successful revolution in our understanding of the evolution of animal behavior, a revolution that is rooted in carefully thinking about the individual and nepotistic function of behaviors.

In the early 1970's, a retired engineer named George Price published two papers¹¹ that presented a new way to think about evolution. Up until that time, most evolutionary theory kept track of the average fitness of alternative genes (just as we did above in explaining kin selection and reciprocity). Price argued that it was also fruitful to think about selection going on in a series of nested levels: among genes within an individual, among individuals within groups, and among groups, and he discovered a very powerful mathematical formalism for describing these processes. Using Price's method kin selection

is conceptualized as occurring at two levels: selection within family groups favors defectors because defectors always do better than other individuals within their own group. Selection among family groups favors groups with more helpers because each helper increases the average fitness of the group. The outcome depends on the relative amount of variation within and between groups. If group members are closely related, most of the variation will occur between groups. Price's multi-level selection approach, and the older gene centered approaches are mathematically equivalent, and if you do your sums properly, you will come up with the same answer either way.¹²

The multilevel selection approach has led to a renaissance in group selection in recent years, and this has led to new wrangling between those who thought that they had killed group selection, and those who, thinking in multi-level terms, see nothing wrong with it.¹³ This argument is mainly about what kinds of evolutionary processes should be called "group selection." Some people use group selection to mean the process that Wynne-Edwards envisioned – selection between large groups made up of mostly genetically unrelated individuals, while others use group selection to refer to selection involving any kind of group in a multilevel selection analysis, including groups made up of close kin.

The real scientific question is what kinds of population structure can produce enough variation between groups so that selection at that level can have an important effect? The answer to this question is fairly straightforward. Selection between large groups of unrelated individuals is not usually an important force in organic evolution. Even very small amounts of migration are sufficient to reduce the genetic variation between groups to such a low level that group selection is not important.¹⁴ However, as we will see below, the same conclusion does not hold for cultural variation.

 Among primates, cooperation is limited to small groups

The punch line is that evolutionary theory predicts that cooperation in primates and other species that have small families will be limited to small groups. Kin selection results in large-scale social systems only when there are large numbers of closely related individuals. The

social insects, where a few females produce a mass of sterile workers, and multicellular invertebrates are examples of such exceptions. Primate societies are nepotistic, but cooperation is mainly restricted to relatively small kin groups. Theory suggests that reciprocity can be effective in small groups, but not in larger ones. Reciprocity may play some role in nature (though many experts are unconvinced), but there is no evidence that reciprocity has played a role in the evolution of large-scale sociality. All would be well if humans did not exist, because human societies, even those of hunter-gatherers, are based on groups of people linked together into much larger highly cooperative social systems.

 Rapid cultural adaptation potentiates group selection

So why aren't human societies very small in scale, like those of other primates? We believe that the most likely explanation is that rapid cultural adaptation led to a huge increase in the amount of behavioral variation among groups. In other primate species, there is little heritable variation among groups because natural selection is weak compared to migration. This is why group selection at the level of whole primate groups is not an important evolutionary force. In contrast, there is a great deal of behavioral variation among human groups. Such variation is the reason why we have culture – to allow different groups to accumulate different adaptations to a wide range of environments.

In the Origin Of Species, Darwin famously argued that three conditions are necessary for adaptation by natural selection: First, there must be a “struggle for existence” so that not all individuals survive and reproduce. Second, there must be variation so that some types are more likely to survive and reproduce than others, and finally, variation must be heritable so that the offspring of survivors resemble their parents. While Darwin usually focused on individuals,¹⁵ the same three postulates apply to any reproducing entity – molecules, genes, and cultural groups.¹⁶ Only the first two conditions are satisfied by most other kinds of animal groups. For example, vervet monkey groups compete with one another, and groups vary in their ability to survive and grow, but, and this is the big but, the causes of group-level variation in competitive ability aren't heritable, so there is no

cumulative adaptation. Once rapid cultural adaptation in human societies gave rise to stable, between-group differences, the stage was set for a variety of selective processes to generate adaptations at the group level.

The simplest mechanism is intergroup competition. The spread of the Nuer at the expense of the Dinka in the 19th century Sudan provides a good example. During the 19th century each consisted of a number of politically independent groups. Cultural differences in norms between the two groups meant that the Nuer were able to cooperate in larger groups than the Dinka. The Nuer, who were driven by the desire for more grazing land, attacked and defeated their Dinka neighbors, occupied their territories, and assimilated tens of thousands of Dinka into their communities. This example illustrates the requirements for cultural group selection by intergroup competition. Contrary to some recent critics,¹⁷ there is no need for groups to be strongly bounded, individual-like entities. The only requirement is that there are persistent cultural differences between groups, and these differences must affect the group's competitive ability. Losing groups must be replaced by the winning groups. Interestingly, the losers do not have to be killed. The members of losing groups just have to disperse or to be assimilated into the victorious group. Losers will be socialized by conformity or punishment, so even very high rates of physical migration need not result in the erosion of cultural differences. This kind of group selection can be a potent force even if groups are usually very large.

Group competition is common in small scale societies. The best data come from New Guinea, which provides the only large sample of simple societies studied by professional anthropologists before they experienced major changes due to contact with Europeans. Joseph Soltis assembled data from the reports of early ethnographers in New Guinea.¹⁸ Many studies report appreciable intergroup conflict and about half mention cases of social extinction of local groups. Five studies contained enough information to estimate the rates of extinction of neighboring groups (Table 3). The typical pattern is for groups to be weakened over a period of time by conflict with neighbors and finally to suffer a sharp defeat. When enough members become convinced of the group's vulnerability to further attack, members

take shelter with friends and relatives in other groups, and the group becomes social extinct. At these rates of group extinction, it would take between 20 and 40 generations, or 500 to 1000 years, for an innovation to spread from one group to most of the other local groups by cultural group selection.

<TABLE 3 ABOUT HERE>

These results imply that cultural group selection is a relatively slow process. But then, so are the actual rates of increase in political and social sophistication we observe in the historical and archaeological records. New Guinea societies were no doubt actively evolving systems,¹⁹ yet the net increase in their social complexity over those of their Pleistocene ancestors was modest. Change in the cultural traditions that eventually led to large-scale social systems like the ones that we live in proceeded at a modest rate. The relatively slow rate of evolution cultural group selection may explain the 5000 year lag between the beginnings of agriculture and the first primitive city-states, and the five millennia that transpired between the origins of simple states and modern complex societies.

A propensity to imitate the successful can also lead to the spread of group beneficial variants. People often know about the norms that regulate behavior in neighboring groups. They know that we can marry our cousins here, but over there they cannot; or anyone is free to pick fruit here, while individuals own fruit trees there. Suppose different norms are common in neighboring groups, and that one set of norms causes people to be more successful. Both theory and empirical evidence suggest that people have a strong tendency to imitate the successful.²⁰ Consequently, behaviors can spread from groups at high payoff equilibria to neighboring groups at lower payoff equilibria because people imitate their more successful neighbors. A mathematical model suggests that this process will spread of group beneficial beliefs over in a wide range of conditions.²¹ The model also suggests that such spread can be rapid. Roughly speaking, it takes about twice as long for a group beneficial

trait to spread from one group to another as it does for an individually beneficial trait to spread within a group.

The rapid spread of Christianity in the Roman Empire may provide an example of this process. Between the death of Christ and the rule of Constantine, a period of about 260 years, the number of Christians increased from a only a handful to somewhere between 6 and 30 million people (depending on whose estimate you accept). This sounds like a huge increase, but it turns out that it is equivalent to a 3-4% annual rate of increase, about growth rate of the Mormon Church over the last century. According to the sociologist Rodney Stark²² many Romans converted to Christianity because they were attracted to what they saw as a better quality of life in the early Christian community. Pagan society had weak traditions of mutual aid, and the poor and sick often went without any help at all. In contrast, in the Christian community norms of charity and mutual aid created “a miniature welfare state in an empire which for the most part lacked social services.”²³ Such mutual aid was particularly important during the several severe epidemics that struck the Roman Empire during the late Imperial period. Unafflicted pagan Romans refused to help the sick or bury the dead. As a result, some cities devolved into anarchy. In Christian communities, strong norms of mutual aid produced solicitous care of the sick, and reduced mortality. Both Christian and pagan commentators attribute many conversions to the appeal of such aid. For example, the emperor Julian (who detested Christians) wrote in a letter to one of his priests that pagans need to emulate the virtuous example of the Christians if they wanted to compete for their souls, citing “their moral character even if pretended” and “their benevolence toward strangers.”²⁴ Middle class women were particularly likely to convert to Christianity, probably because they had higher status and greater marital security within the Christian community. Roman norms allowed polygyny, and married men had great freedom to have extramarital affairs. In contrast, Christian norms required faithful monogamy. Pagan widows were required to remarry, and when they did they lost control of all of their property. Christian widows could retain property, or, if poor, would be sustained by the church community. Demographic factors were also important in the growth of Christianity. Mutual aid led to

substantially lower mortality rates during epidemics, and a norm against infanticide led to substantially higher fertility among Christians.

 The credulity required for the cultural evolution of novel forms of cooperation is consistent with an evolved, genetically adaptive psychology

The claim that cultural evolution can give rise to forms of novel cooperation is vulnerable to two related objections: First, there is what might be called the “bootstrap problem:” Cultural evolution can lead to the spread of cooperation in large, weakly related groups only if computational and motivational systems existed in the human brain that allowed people to acquire and perform the requisite behaviors. Given that such behaviors were not favored by natural selection, why should these systems exist? Second, even they were accidentally present at the outset, why didn’t natural selection modify our psychology so that we did not acquire such deleterious behaviors? Why don’t we have a “cultural immune system” that protects us from bad ideas abroad in our environment?

Like living primates, our ancestors were large brained mammals capable of flexibly responding to a range of biotic and social environments. Natural cannot equip such organisms with fixed action patterns; instead it endows them with a complex psychology that causes them to modify their behavior adaptively in response to environmental variation.²⁵ Cultural evolution can generate novel behaviors by generating the cues that activate these modules in novel combinations. For example, cooperation among relatives requires (among other things) a means of assessing costs and benefits, and of identifying relatives and assessing their degree of relatedness. Such systems can be manipulated by culturally transmitted input. Individuals have to learn the costs and benefits of different behaviors in their particular environment. Thus people who learn that sinners suffer an eternity of punishment may be more likely to behave morally than those who only fear the reprisals of their victims. Individuals have to learn who their relatives are in different environments. So the individual who learns that members of his patriclan are brothers may behave quite differently than one who learns that he owes loyalty to the band of brothers in his platoon.

Once activated, such computational systems provide input to existing motivational systems which in turn generate behavior.

This account raises an obvious question: If cultural inputs regularly lead to what is, from the genes point of view, maladaptive behavior, why hasn't selection modified our psychology so that it is immune to such maladaptive inputs. This is a crucial question, and we have dealt with it at length elsewhere.²⁶ In brief, we believe that cumulative cultural evolution creates a novel evolutionary tradeoff. Social learning allows human *populations* to accumulate adaptive information over many generations, leading to the cultural evolution of highly adaptive behaviors and technology. Because this process is much faster than genetic evolution, human populations can evolve cultural adaptations to local environments, an especially valuable adaptation to the chaotic, rapidly changing world of the Pleistocene. However, the same psychological mechanisms that create this benefit necessarily come with a built in cost. To get the benefits of social learning, humans have to be credulous,²⁷ for the most part accepting the ways that they observe in their society as sensible and proper, and such credulity opens up human minds to the spread of maladaptive beliefs. This cost can be shaved by tinkering with human psychology, but it cannot be eliminated without also losing the adaptive benefits of cumulative cultural evolution.

 Natural selection in culturally evolved social environments may have favored new, genetically transmitted prosocial social instincts

We hypothesize that this new social world, created by rapid cultural adaptation, drove the genetic evolution of new, derived social instincts in our lineage. Cultural evolution created cooperative groups. Such environments favored the evolution of a suite of new social instincts suited to life in such groups including a psychology which “expects” life to be structured by moral norms, and that is designed to learn and internalize such norms. New emotions evolved, like shame and guilt, which increase the chance the norms are followed. Individuals lacking the new social instincts more often violated prevailing norms and experienced adverse selection. They might have suffered ostracism, been denied the

benefits of public goods, or lost points in the mating game. Cooperation and group identification in inter-group conflict set up an arms race that drove social evolution to ever-greater extremes of in-group cooperation. Eventually, human populations came to resemble the hunter-gathering societies of the ethnographic record. We think that the evidence suggests that after about 100,000 years ago most people lived in tribal scale societies.²⁸ These societies are based upon in-group cooperation where in-groups of a few hundred to a few thousand people are symbolically marked by language, ritual practices, dress, and the like. These societies are egalitarian, and political power is diffuse. People are quite ready to punish others for transgressions of social norms, even when personal interests are not directly at stake.

These new tribal social instincts were superimposed onto human psychology without eliminating ancient ones favoring self, kin, and friends. The tribal instincts that support identification and cooperation in large groups, are often at odds with selfishness, nepotism, and face-to-face reciprocity. People feel deep loyalty to their kin and friends, but they are also moved by larger loyalties to clan, tribe, class, caste, and nation. Inevitably, conflicts arise. Families are torn apart by civil war. Parents send their children to war (or not) with painfully mixed emotions. Criminal cabals arise to prey upon the public goods produced by larger scale institutions. Elites take advantage of key locations in the fabric of society to extract disproportionate private rewards for their work. The list is endless.

Some of our friends in evolutionary psychology have complained to us that this story is too complicated. Wouldn't it be simpler to assume that culture is shaped by a psychology adapted to small groups of relatives? Well, maybe. But the same people almost universally believe an equally complex co-evolutionary story about the evolution of an innate language acquisition device.²⁹ Such innate language instincts must have coevolved with culturally transmitted languages in much the same way that we hypothesize that the social instincts coevolved with culturally transmitted social norms. Initially, languages must have been acquired using mechanisms not specifically adapted for language learning. This combination created a new and useful form of communication. Those individuals innately prepared to

learn a little more proto-language, or learn it a little faster, would have a richer and more useful communication system than others not so well endowed. Then selection could favor still more specialized language instincts, which allowed still richer and more useful communication, and so on. We think that human social instincts constrain and bias the kind of societies that we construct, but the details are filled in by the local cultural input.³⁰ When cultural parameters are set, the combination of instincts and culture produces operational social institutions.

 Experiments indicate people have prosocial instincts

Lots of circumstantial evidence suggests that people are motivated by altruistic feelings toward others, feelings that motivate them to help unrelated people even in the absence of rewards and punishments.³¹ People give to charity, often anonymously. People risk their own lives to save others people in peril. Suicide bombers give their lives to further their cause. People vote. The list of examples is long.

Long, but not long enough to convince many who are skeptical about human motives. The skeptics think that all examples of altruism are really self-interest in disguise. Charity is never anonymous; the right people know who gave what. Heroes get on Letterman. Resources are lavished on the families of suicide bombers. They even give you those little pins when you vote. Or, in the words of the evolutionary biologist Michael Ghiselin, "Scratch an altruist and watch a hypocrite bleed."³² The possibility of covert selfish motives can never be excluded in these kinds of real world examples.

In recent years, however, experimental work by psychologists and economists has made it a lot tougher to hang on to dark suspicions about the motives behind good deeds. In these, experiments the possibility of selfish reward is carefully excluded. Nonetheless, people still behave altruistically, sometimes risking several months' salary. They also engage in costly punishment of non-altruists, even when there is no possibility of reward or enhanced reputation. Moreover, experiments have been conducted in a number of small scale non-western societies, and while there is much cultural variation, nowhere are people

purely selfish.³³ The news couldn't be much worse for the view that people have purely selfish motives.

 Human interaction may depend on prosocial instincts

Several of the papers in this volume suggest that everyday human interactions depend on cooperative psychological mechanisms. For example, at the most micro level, Schegloff³⁴ shows that even seemingly mundane everyday conversations are actually made possible by rules that regulate who speaks when and for how long. At a broader comparative level, Levinson³⁵ argues that face-to-face human interaction entail complex embedded sequences of speech and gesture that can succeed only if actors are cooperative.

Complex cooperative signaling is rare in nature. Signaling systems in most other animals are limited to a small repertoire of signals, referential signals are rare, and there is scant evidence for anything resembling a two-way conversation. This state of affairs is generally consistent with evolutionary theory which suggests that honest, low cost communication is a form of cooperation, and cooperation should be limited to kin and reciprocating partners. The various forms of communication, such as the famous waggle dance of honeybees, that make social insect colonies going concerns are examples.

Thus, the psychological mechanisms that enable human interaction may depend on the same prosocial instincts that regulate other forms of human cooperation. If so, studying the way that cooperation fails in human interaction may provide insight into the selective forces that shaped these instincts. If, as some have argued, our prosocial instincts evolved in small groups of kin, conversations should fail differently among kin than nonkin. If reciprocity was the key, then failure of conversation among friends should differ from those among strangers. Finally, if the cultural evolution account given here is correct, ethnic and other group boundaries should be crucial.

In fact, easy communication in simple human societies usually ends at the boundaries of the group that routinely cooperates. Only a few hundred to a few thousand people spoke the same language or at least the same dialect. Modern human groups

cooperate on a large scale and have a common language. Sociolinguists have taught us that linguistic variation arises rapidly to reflect social cleavages within a language.³⁶ Typically, the bonds of patriotism rest upon a speech community. The development of mass literacy, mass communication, and the replacement of local dialects by a national language, are the foundations upon which the modern style of nationalism and nation-state rest.³⁷ Nations are much larger systems than the ancient tribes in which our social instincts evolved yet a nation can contrive to *feel* like a tribe if members share a common language and have access to a common set of ideas and concepts born from reading a common set of newspapers and magazines. In Benedict Anderson's memorable phrase, modern nations are "imagined communities." At the same time, minority languages and class, caste, and regional dialects commonly mark patterns of conflict and cooperation within nations.

 "Nothing in biology makes sense except in the light of evolution"³⁸

Evolutionary biologists are a tiny minority in their discipline, vastly outnumbered by molecular biologists, physiologists, developmental biologists, ecologists, and all the rest. Nonetheless, evolution plays a central role in biology because it provides answers to why questions. Why do humans have big brains? Why do female spotted hyenas dominate males? Why do horses walk on the tips of their toes? The answers to these questions draw on all parts of biology. To explain why horses walk on their toes we need to connect the ecology of Miocene grasslands, the developmental biology of the vertebrate limb, the genetics of quantitative characters, the molecular biology and biophysics of keratin, and much more. Because evolution provides the ultimate explanation for why organisms are the way they are, it serves to all the other areas of biology into a single, satisfying explanatory framework. As Dobzhansky put it, without the light of evolution, biology "...becomes a pile of sundry facts some of them interesting or curious but making no meaningful picture as a whole."

We think that evolution can play the same role in the explanation of human culture. The ultimate explanation for cultural phenomena lies in understanding genetic and cultural evolutionary processes that generate cultural phenomena. Genetic evolution is important

because culture is deeply intertwined with other parts of human biology. The ways we think, the ways we learn, and the ways we feel shape culture, affecting which cultural variants are learned, remembered, and taught, and thus which variants persist and spread. Parents love their own children more than those of siblings or friends, and this must be part of the explanation for why some marriage systems persist. But why do people value their own children more than others? Obviously an important part of the answer is that such feelings were favored by natural selection in our evolutionary past. Cultural evolution is also important. Because culture is transmitted, it is subject to natural selection. Some cultural variants persist and spread because they cause their bearers to be more likely to survive and be imitated. The answer to why mothers and fathers send their sons off to war may be that social groups with such norms that encourage such behavior out compete groups which do not have such norms. Finally, genetic and cultural evolution interact in complex ways. Social psychologists and experimental economists, working from very different research traditions, have produced compelling evidence that people have prosocial predispositions. But why do we have such predispositions in the first place? Evolutionary theory and the lack of large scale cooperation in other primates suggest that selection directly on genes is unlikely to produce such predispositions. So, why did they evolve? We think cultural evolutionary processes constructed a social environment that caused ordinary natural selection acting on genes to favor empathetic altruism, and a tendency to direct that altruism preferentially to fellow members of symbolically marked groups. These social instincts evolved in the late Pleistocene but the radically new social institutions that have evolved in the Holocene were (and continue to be) both enabled and constrained by them. Our specific explanation may be in error; you seldom get it straight on the first try. The important point is that evolving culture, certainly in theory and probably in practice, has a fundamentally important role in making humans what they are.

Endnotes

¹ Hamilton (1964).

² The great population geneticist J. B. S. Haldane gave what is perhaps the pithiest summary of this principle. When asked by a reporter whether the study of evolution had made it more likely that he would give up his life for a brother, Haldane is supposed to have answered, “No, but I would give up my life to save two brothers or eight cousins.”

³ (Silk 2002), Keller and Chapuisat (1999), Queller and Strassmann (1998), Queller (1989).

⁴ Hammerstein 2003.

⁵ See Axelrod and Dion (1988), Nowak and Sigmund (1993, 1998) for reciprocity in small groups. Boyd and Richerson (1988, 1989), and Joshi (1987) for larger groups. Glance and Hubermann (1994) present a model in which reciprocity evolves in large groups, but this result depends on constraints on their choice of a set of possible strategies. Simple unconditional defection invades their cooperative ESS.

⁶ e.g. Binmore (1994).

⁷ Trivers (1971).

⁸ Boyd and Richerson (1992).

⁹ Wynne-Edwards (1962).

¹⁰ Maynard Smith (1964), Williams (1966), Lack (1966).

¹¹ Price (1972, 1970).

¹² The Price approach has been very fruitful, generating a much clearer understanding of many evolutionary problems. For example, Alan Grafen's (1984) work on kin selection and Steven Frank's work on the evolution of the immune system, multicellularity, and related issues (Frank 2002). This approach can also be used to study cultural evolution. See Henrich (2004) and Henrich and Boyd (2002).

¹³ Sober and Wilson (1998).

¹⁴ Eshel (1972), Aoki (1982), Rogers (1990).

¹⁵ Darwin (1874), in the Descent of Man, did invoke group selection to explain human cooperation. “It must not be forgotten that although a high standard of morality gives but a

slight or no advantage to each individual man and his children over other men of the same tribe, yet that an increase in the number of well-endowed men and an advancement in the standard of morality will certainly give an immense advantage to one tribe over another. A tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to aid one another, and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection” (pp. 178-179).

¹⁶ Price’s (1970, 1972) formula show that this argument is rigorously true.

¹⁷ Palmer, Fredrickson, and Tilley (1997).

¹⁸ Soltis, Boyd, and Richerson 1995.

¹⁹ Wiessner and Tumu (1998).

²⁰ Richerson and Boyd 2004.

²¹ Henrich and Gil-White (2001), Richerson and Boyd (2004).

²² Stark (1997).

²³ Johnson (1976:75), quoted in Stark (1997).

²⁴ Stark (1997:83-84).

²⁵ Tooby and Cosmides (1992).

²⁶ Richerson and Boyd (2004:ch. 5).

²⁷ Simon (1990) made the same argument, apparently independently. He used the term “docility” because he believed that we are especially prone to accept group beneficial beliefs. We think his account is unsatisfactory because it does not explain why such beliefs spread.

²⁸ Kelly (1995), Richerson and Boyd (1998, 2001).

²⁹ Pinker (1994:111-112).

³⁰ Steward (1955: chs. 6-8), Kelly (1995).

³¹ Mansbridge’s (1990) edited volume gives an excellent sampler.

³² Ghiselin (1974: 247).

³³ Camerer (2003).

³⁴ Schegloff (Forthcoming).

³⁵ Levinson (forthcoming).

³⁶ Labov (2001), Lodge (1993).

³⁷ Anderson (1991).

³⁸ Dobzhansky (1973).

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Table 1: The Stag Hunt. In Rosseau's parable hunters can either hunt stag or hare. Hunting together does not affect the success of hare hunters; they always get an small payoff, h . If they hunt stag together the are likely to succeed and achieve a high payoff s , but a single stag hunter fails receives a payoff of zero.

		<i>Right</i>	
		Stag	Hare
<i>Left</i>	Stag	s, s	$0, h$
	Hare	$h, 0$	h, h

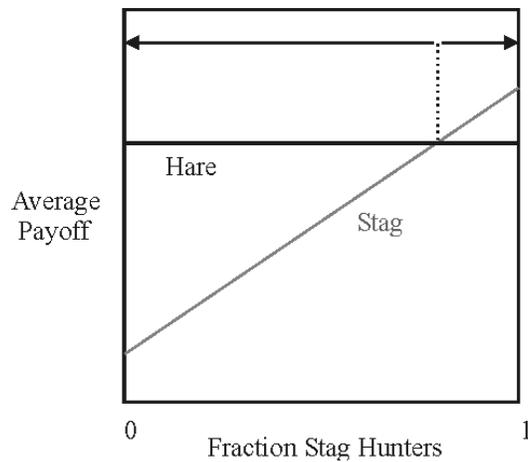


Figure 1: Now suppose that there were a population of people who are paired at random and play the stag hunt. The average payoff of each strategy as a function of the fraction of players who choose to hunt stag. Assuming that strategies with higher payoffs increase in frequency, there are two stable equilibria: everybody chooses stag or everybody chooses hare. Now however the average payoff of the whole population is maximized only at the all stag equilibrium. However, unless stag hunting has a much larger payoff than hunting hares ($2h < s$), the basin of attraction of the stag equilibrium is smaller than that of the lower payoff hare equilibrium.

Table 2: The Prisoner's Dilemma. Each individual has the opportunity to cooperate by helping the other individual. Helping increased the payoff of the receiver 2 units and costs the helper 1 unit.

		<i>Right</i>	
		Cooperate	Defect
<i>Left</i>	Cooperate	$b - c, b - c$	$-c, b$
	Defect	$b, -c$	$0, 0$

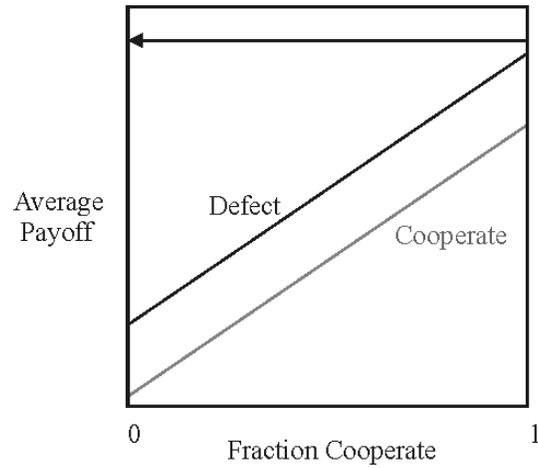


Figure 2: Finally suppose that there were a population of people who are paired at random and play the prisoner's dilemma. The average payoff of each strategy as a function of the fraction of players who choose to cooperate. Now there is only one stable equilibria, everybody defects at which the average payoff of the whole population is minimized. The payoff maximizing equilibrium, everybody cooperates, is unstable because defectors have a higher payoff than cooperators.

Table 3. Extinction rates for cultural groups from five regions in New Guinea. From Soltis et al 1995.

Region	Number of groups	Number of social extinctions	Number of years	% groups extinct every 25 years	Source
Mae Enga	14	5	50	17.9%	Meggitt 1977
Maring	13	1	25	7.7%	Vayda 1971
Mendi	9	3	50	16.6%	Ryan 1959
Fore/Usurufa	8–24	1	10	31.2%–10.4%	Berndt 1962
Tor	26	4	40	9.6%	Oosterwal 1961