

Gene–Culture Coevolution and the Evolution of Social Institutions

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Abstract

Social institutions are the laws, informal rules, and conventions that give durable structure to social interactions within a population. Such institutions are typically not designed consciously, are heritable at the population level, are frequently but not always group beneficial, and are often symbolically marked. Conceptualizing social institutions as one of multiple possible stable cultural equilibrium allows a straightforward explanation of their properties. The evolution of institutions is partly driven by both the deliberate and intuitive decisions of individuals and collectivities. The innate components of human psychology coevolved in response to a culturally evolved, institutional environment and reflect a prosocial tendency of choices we make about institutional forms.

Introduction

The idea of social institutions has a long history in the social sciences and, accordingly, has been widely used in ways that only partially overlap. Sometimes the term refers to ideal types, such as religion or the family. Other times, scholars use it to refer to particular organizations: General Motors or the University of California. Still other times it is used to denote informal norms like Nuer bride price rules or the ways that Genovese and Mahgrebi traders financed long-distance trade in the Mediterranean.

Our intention here is not to make a proper scholarly review of the concept. Instead, we adopt the definition offered by Samuel Bowles in his recent book, *Microeconomics, Behavior, Institutions, and Evolution* (2004). According to

Bowles (2004, p. 47), “Institutions are the laws, informal rules, and conventions that give durable structure to social interactions in a population.”

Human societies vary on a vast range of culturally transmitted attributes that affect how people behave. People in different populations may have diverse beliefs about the state of the world. Most Americans believe that disease is caused by tiny, invisible organisms, whereas people in some other cultures believe that disease is caused by the actions of malevolent neighbors. People’s knowledge of technology can also vary between different populations. Californian agriculture of the 1980s was different from that in the 1880s because mechanical traction and more rapid transportation changed the economics of various crops. Peoples can also differ in their understanding of symbols, their norms about action, and many other concepts. From this long list, Bowles’s definition of social institutions focuses on cultural variants that specify how people behave when they interact with others. This includes formal law, but also informal norms and conventions.

Institutions play a key role in shaping human behavior in all human societies. It is obvious that social institutions have played a fundamental role in regulating people’s behavior in urbanized, state-level societies over the last few thousand years of human history. Explicit laws, systems of governance, and nongovernmental institutions (e.g., churches, firms, and universities) were central to their organization. However, social institutions also play a crucial role in even the simplest human society. Land tenure, marriage, food sharing, and governance are regulated by culturally transmitted rules. Some institutions in small-scale societies rival those of state-level societies in complexity. For example, among hunter gatherers living in northern and western Australia, marriage and identity were regulated by “eight section” systems so complex that they have baffled generations of anthropology students.

In this chapter, we sketch a theory of the evolution of social institutions. We begin by proposing several stylized facts about institutions which such a theory should explain. We then argue that a theory in which social institutions are conceptualized as alternative, stable equilibria of a cultural evolutionary process can account for these facts. Finally, we contend that the cultural evolution of social institutions over the last half a million years created novel social environments that led to the genetic evolution of new social adaptations in our species.

Institutions illustrate how the processes of cultural evolution economize on information and decision-making costs. In essence, cultural evolution leverages individual decision making by allowing individuals to acquire complex codes for behavior, mainly by the relatively cheap process of imitation. Of course, if everyone always imitated, cultural traditions could be made adaptive only by the painful process of natural selection. Culture is adaptive in certain kinds of variable environments because it can enlist human decision-making capacities as evolutionary forces that shape institutions and other traditions. Some human decisions are made using fast, low-cost, relatively automatic, and

often unconscious heuristics. If past genetic or cultural evolution has shaped this sort of decision making to be adaptive on average, even weak, error-prone heuristics can act as forces that cumulatively build cultural adaptations when they are integrated over many individuals and appreciable spans of time.

Cultural evolution can also amortize slow, costly deliberate, conscious decisions over many individuals. In law, for example, legislators, lawyers, and judges expend much effort crafting legislation and interpreting it. To the extent that they are successful, the entire society benefits. Most of us do not need to participate in the costly process of legal decision making; we merely need to know something of the laws that apply to us. Indeed, to the extent that everyday mores and the formal law coevolve, individuals can acquire useful behaviors economically by quite unconsciously imitating the behavior they see around them. In this way, culture is analogous to habit formation in individuals. Variants that were invented by deliberate reasoning and carried to dominance by formal collective decision making may be acquired by subsequent generations through unreflective imitation.

Six Stylized Facts about Social Institutions

The social world is both complex and diverse. Any real social system is immensely complicated. Moreover, systems differ widely from place to place as well as throughout time. This means that the answer to any interesting question inevitably depends on a host of historical and contextual details. Our ability to make formal models of complex, diverse systems is extremely limited, and, as a result, many scholars from diverse disciplines often eschew formal models in favor of rich, contextualized accounts. Practitioners in economics and evolutionary biology, however, take a different approach: they build very simple formal models with the goal of explaining the general features of some phenomenon of interest, and leave the details of particular situations to less formal methods. Economists call the usually-but-not-always-true things that they seek to explain “stylized facts.” Here are six stylized facts about human social institutions that we seek to explain:

1. *Social institutions are usually heritable at the population level*; that is, cultural information that causes particular institutions to have the form they do is transmitted through time within populations in such a way that the form of institutions is largely preserved through time. Institutions are not simply a product of the environment and technologies that characterize a particular group. Rather, their form is transmitted from one generation to the next.

Two types of evidence support this claim. First, what we call “common garden experiments” occur when people from different cultural backgrounds move into the same environment. When these different

people maintain their institutions, this provides evidence that the institutions are heritable at the population level. The movement of peoples over the last several hundred years provides numerous examples. For example, Sonya Salamon (1980) compared the farming institutions among Swedish and Yankee settlers of Illinois. The Swedes came to the United States in the middle of the 19th century with institutions governing the transfer of farms from one generation to the next within a family—a practice that differed markedly from that practiced by the Yankees. For example, among the Swedes, parents were expected to vacate the main house and move to a small cottage on the farm when the son took over working the farm, while Yankee parents remained in the house until their death. When Salamon studied the descendants of these people in the 1980s, these differences still existed.

The second kind of evidence is the existence of phylogenetic patterns. Cultural groups that are linguistically similar often have more similar institutions than groups that are more distantly related (Guglielmino et al. 1995; Jorgenson 1980; Mace and Holden 1999), even when one controls for economic or ecological variables. This data indicates that the form of institutions is transmitted in populations from one generation to the next in parallel to lexical and phonological variants that form the basis of genetic linguistic classification. Thus people are plausibly relying on the relatively cheap uptake of traditional institutions by imitation and teaching rather than engaging in the costly rehashing of their form every generation.

2. *Most social institutions are not consciously designed.* In modern societies, institutions like the systems of governance of firms are at least partially designed, or more often result from the competing design aims of multiple interests. However, many institutions, in fact probably most, are not consciously designed, but rather evolve as the result of a variety of evolutionary processes. The mental rules that structure the morpho-syntax of spoken language provide a good example. Grammatical devices begin as lexical items used, often metaphorically, to make some important distinction (e.g., when an action occurred). Then, unconscious choices cause these lexical items to become grammaticized, leading, for example, to a system of verb conjugation that expresses tense (Deutscher 2005). The same applies to many institutions. Even if people wished to operate and change institutions wholly on the basis of deliberate processes, the complexity of institutions would defeat them. Ellickson (1991) gives an interesting example of how informal institutions that apparently evolved in this piecemeal way coexist with the formal law in a modern society. Moreover, in most societies throughout human history, the size of the cultural group that shared an institutional form was much larger than the size of any political decision-making body that could design institutions.

3. *Many social institutions are complicated structures with multiple interacting attributes.* Lately, game theorists have taken an interest in social institutions (e.g., Young 1998), modeling them as equilibria of games in which more than one equilibrium is possible. There is much to recommend this approach. However, we wish to point out a possible confusion that needs to be avoided: arguments are often exemplified using very simple binary coordination games, such as the so-called Stag Hunt (e.g., Bowles 2004). Although such simple games may be adequate for didactic purposes, real social institutions, even in simple societies, are complicated structures with many interacting dimensions. A theory of social institutions should be able to explain how such complex institutions arise, how they are maintained, and why they have the properties that they do.
4. *Social institutions often benefit social groups.* Property rights create incentives and reduce transaction costs; legal institutions prevent predatory behavior, help resolve disputes, and maintain contractual relationships. Corporate institutions, like clans and firms, allow the maintenance of productive capital over generations. Marriage rules regulate reproduction, and inheritance systems reduce conflict over intergenerational transfers. The list is long, so long in fact, that sometimes the group functional nature of institutions has been taken as one of their essential features.
5. *Social institutions do not always benefit social groups.* It is easy to think of institutions that seem unlikely to be group beneficial. Take, for example, the Gebusi: a group living in the Fly River region of Papua New Guinea. The Gebusi practice witchcraft and believe that most deaths are due to malevolent magic. Accordingly, deaths are typically followed by an inquest to determine who performed the magic, and when divination methods point to a perpetrator, he is executed by the group. Ethnographer Bruce Knauft (1985) reports that this process was leading to the extinction of the Gebusi. The legalistic formality of the deliberative process by which this maladaptive institution was operated is impressive. On the other hand, the Gebusi seem entirely unaware that the best statistical predictor of witchcraft accusations is unmet obligations to provide marriage partners to other lineages. Although this is a particularly spectacular example, there are many others.
6. *Many social institutions are symbolically marked.* Corporate social institutions, such as clans and nations, are typically associated with symbolic traits that mark both the group and its members. Such markers are arbitrary symbols. The clan's totem, the land crab, could just as well have been a sea turtle, and the tricolor could have been yellow, red, and black. However, the symbols are as much parts of the institution as the more functional rules that regulate behavior. They are endowed with meaning and emotional salience. Such attributes stabilize groups through time but also tend to induce deliberate thinking about them.

The Evolution of Social Institutions

We have argued at length (Richerson and Boyd 2005) that population thinking provides the most natural way of modeling human cultural change and its consequences for cultural variation. Much evidence indicates that the differences between human groups are at least partly due to culturally transmitted beliefs and values. People acquire beliefs about the world, about right and wrong, and what things mean by teaching and imitation from the people with whom they interact. To explain why a group of people have the culturally transmitted beliefs that they do, we need to understand how everyday events cause some beliefs to spread and others to diminish. Some of these processes are psychological: beliefs that are more readily learned or remembered will tend to spread at the expense of those that are less readily learned or remembered. Others have to do with what happens to people with different beliefs: beliefs that lead to long life or high social status are likely to spread at the expense of beliefs that lead to early death or low social status.

The resulting theory, which is sometimes called the theory of gene–culture coevolution, resembles evolutionary game theory. Both theories keep track of the dynamics of the frequencies of different transmitted variants, and evolutionarily stable equilibria of the dynamic system are candidate long-term outcomes of the evolutionary process. The primary difference is that evolutionary game theory assumes that evolutionary dynamics are driven solely by some kind of payoff: fitness when applied to genetic evolution, and utility when applied to social evolution. If the main directional forces in cultural evolution are due to relatively domain-general psychological mechanisms, then gene–culture coevolution will be very similar. However, there is also evidence that cultural change is sometimes affected strongly by narrow, domain-specific psychological mechanisms. For example, Pascal Boyer (2006) has argued that certain kinds of ritual behavior are attractive and memorable because they activate those psychological mechanisms that evolved to protect people against serious risks (e.g., disease and predation).

Institutions Are Social Arrangements with Multiple Stable Equilibria

The six stylized facts about social institutions are consistent with the view that beliefs and values which give rise to a particular social institution constitute one of perhaps many possible evolutionarily stable equilibrium. We illustrate this idea with a very simple “toy” example. Suppose in a particular population there are two cultural variants governing beliefs about inheritance: equal partition among brothers and primogenitor, only the oldest brother inherits. To keep things simple, let us suppose that all families have exactly two sons and that the payoffs associated with each combination of beliefs within a family are:

		Younger son	
		Partition	Primogenitor
Older son	Partition	2, 2	0, 0
	Primogenitor	0, 0	5, 1

When brothers agree, they receive a higher payoff than when they disagree, because disputes are costly. This means that once either system becomes common, people with the more common belief achieve a higher payoff on average, and if the cultural evolution is driven by payoffs (e.g., because people imitate the successful), then both inheritance institutions will be evolutionarily stable.

This conceptualization explains immediately how commonly held social institutions can arise without any group deliberation. Individuals respond myopically to the incentives they experience and, as a result, institutions evolve. It also explains why institutions are heritable at the group level. For traits to be heritable at the group level, two things must be true: (a) there must be stable variation among groups and (b) when groups split, daughter groups must be more similar to each other and the parent. If institutions are multiple stable equilibria, variation among groups will be maintained as long as the rate at which people evolve locally is faster than the effect of mixing of ideas or people among groups. Similarly, cultural variants that are common in the parental group will remain common in the daughter groups.

This simple example leaves out much. First, as evolutionary psychologists have emphasized, humans are not domain-general payoff maximizers. We find it easier to learn and adopt some beliefs rather than others so that payoffs alone are not sufficient to predict outcomes. For example, there is much evidence that people have evolved psychological mechanisms that, under most circumstances, make them averse to mating with close relatives. It might be that brother–sister marriage would be a highly desirable mechanism for preserving property, but that this would not evolve because our evolved psychology makes such marriages unstable. Multiple equilibria might still exist in payoff terms, but the choice-based forces may make some equilibria difficult to achieve or maintain independent of the payoff structure of the game. Second, real institutions are complex structures involving many beliefs. The institution of primogenitor includes rules to apply if there are no sons or if there are illegitimate or adopted sons, to resolve disputes and distribute different kinds of property, to define the rights of the widow, to assess penalties, and so on. The complexity of real social institutions means that they cannot be understood as simple conventions. They evolve cumulatively. Thus, to explain real-world complex institutions, a vast range of different institutions must be evolutionarily stable. Fortunately, this is not much of a problem.

Repeated Interactions Allow a Vast Range of Stable Social Equilibrium

Moralistic punishment can stabilize a very wide range of behaviors. To understand this, consider the following simple example. Imagine a population subdivided into a number of groups. Cultural practices spread between groups because people migrate or ideas are adopted from neighboring groups. Two alternative culturally transmitted moral norms (norm x and norm y) exist in the population, norms that are enforced through moralistic punishment. These could be “must wear a business suit at work” and “must wear a dashiki to work,” or “a person owes primary loyalty to their kin” and “a person owes primary loyalty to their group.” In groups where one of the two norms is common, people who violate the norm are punished. Suppose that people’s innate psychology causes them to be biased in favor of norm y , and therefore y will tend to spread, all other things being equal. Nonetheless, when norm x is sufficiently common, the effects of punishment overcome this bias and people tend to adopt norm x . In such groups, new immigrants whose beliefs differ from the majority (or people who have adopted “foreign” ideas) learn rapidly that their beliefs get them into trouble and thus adopt the prevailing norm. When more norm y believers arrive, they find themselves to be in the minority and learn the local norms rapidly, maintaining norm x despite the fact that it is not the norm that fits best with their evolved psychology.

This kind of mechanism works only when the adaptation occurs rapidly; it is not likely to be an important force in genetic evolution. Normally evolutionary biologists think of selection as being weak and, although there are many exceptions to this rule, it is a useful generalization. For example, if one genotype had a 5% selection advantage over the alternative genotype, this would be thought to be strong selection. Now suppose that a novel group-beneficial genotype has arisen and that it has become common in one local group, where it has a 5% advantage over the genotype that predominates in the population as a whole. For group selection to be important, the novel genotype must remain common long enough to spread by group selection, and this is only possible if the migration rate per generation is substantially less than 5%. Otherwise, the effects of migration will swamp the effects of natural selection. This, however, is not very much migration. The migration rate between neighboring primate groups is on the order of 25% per generation. Although migration rates are notoriously difficult to measure, migration rates are typically high among small local groups that suffer frequent extinction. Migration rates between larger groups are much lower, but so too will be the extinction rate.

Conformist Social Learning Can Also Stabilize Many Equilibria

A conformist bias can also maintain variation among groups. We argue that natural selection can favor a psychological propensity to imitate the common type (Richerson and Boyd 2005, chapter 4). This propensity is an evolutionary

force that causes common variants to become more common and rare variants to become rarer. If this effect is strong compared to migration, then variation among groups can be maintained.

As before, think of a number of groups linked by migration. Now, however, assume that two memes affect religious beliefs: “believers” are convinced that moral people are rewarded after death and the wicked suffer horrible punishment for eternity, while “nonbelievers” do not believe in any afterlife. Because they fear the consequences, believers behave better than nonbelievers: more honestly, charitably, and selflessly. As a result, groups in which believers are common are more successful than groups in which nonbelievers are common. People’s decision to adopt one cultural variant over the other is only weakly affected by content bias. People do seek comfort, pleasure, and leisure, and this tends to cause them to behave wickedly. However, a desire for comfort also causes thoughtful people to worry about spending an eternity buried in a burning tomb. Since people are uncertain about the existence of an afterlife, they are not strongly biased in favor of one cultural variant or the other. As a result, they are strongly influenced by the cultural variant that is common in their society. People who grow up surrounded by believers, choose to believe, whereas those who grow up among worldly atheists do not.

The difference between moralistic punishment and conformist learning is illustrated by the different answers to the question: Given that people have grown up in a devout Christian society, why do they believe in the tenets of the Christian faith? If cultural variation is maintained primarily through moralistic punishment, those who do not adopt Christian beliefs in a devout Christian society are punished by believers, and people who do not punish such heretics (e.g., by continuing to associate with them) are themselves punished. People adopt the prevalent belief because it yields the highest payoff in readily measurable currencies. If cultural variation is maintained largely by conformist transmission and similar cultural mechanisms, then young people adopt the tenets of Christianity as accurate descriptions of the world because such beliefs are widely held, fit with certain content-based biases, and are difficult for individuals to prove or disprove. (Of course, any mixture of the two effects is also possible; the answer is quantitative not qualitative.)

Conformist transmission can potentiate group selection only if it is strong compared to the opposing content biases, and this can occur only if individuals have difficulty deliberately evaluating the costs and benefits of alternative memes. In some cases this is not very difficult: should you cheat on your taxes or fake illness to avoid military service? The threat of punitive action may be sufficient to keep taxpayers and conscripts honest. However, there are also many beliefs whose effects are hard to judge. Will children turn out better if they are sternly disciplined or lovingly indulged? Is smoking marijuana harmful to one’s health? Is academia a promising career option? These are difficult questions to answer, even with all of the information available to us today. For most people at most times and in most places, even more basic questions

may be very difficult to answer: Does drinking dirty water cause disease? Can people affect the weather by appealing to the supernatural? The consequences of such difficult choices often have a profound effect on people's behavior and their welfare.

Heritable Variation between Groups + Intergroup Conflict = Group Selection

With this background, we can now explain why social institutions are sometimes group beneficial. In the *Origin of Species*, Darwin famously argued that three conditions are necessary for adaptation by natural selection:

1. There must be a "struggle for existence" so that not all individuals survive and reproduce.
2. There must be variation so that some types are more likely to survive and reproduce than others.
3. The variation must be heritable so that the offspring of survivors resemble their parents.

Darwin usually focused on individuals, but the multilevel selection approach tells us that the same three postulates apply to *any* reproducing entity: molecules, genes, or cultural groups. 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. However, the causes of group-level variation in competitive ability are not heritable, so there is no cumulative adaptation.

Richard Sosis's (2000) study of the survival of religious communes in the U.S. shows how selection among institutions can give rise to the evolution of group beneficial ones. Sosis collected a sample of 200 communes formed during the 19th and 20th centuries. Of these, 88 were religious; the rest were based on secular ideologies (e.g., Fourierism or Owenism). Sosis excluded 20 Hutterite communities from his analysis. As is shown in Figure 14.1, communes based on religious ideology had a much higher survival rate than communes based on secular ideologies, which means that selection among communities acts to increase the frequency of religiously based institutions. At the onset, about half of the communes were religious; after 40 years, almost all of the communes still in existence are religious. Sosis's work suggests that religious communes survive because they have fewer conflicts and more commitment to group goals.

Group Beneficial Cultural Variants Can Spread Because People Imitate Successful Neighbors

Competition between institutions is not the only mechanism that can lead to the spread of institutions based on group beneficial ideologies; the propensity

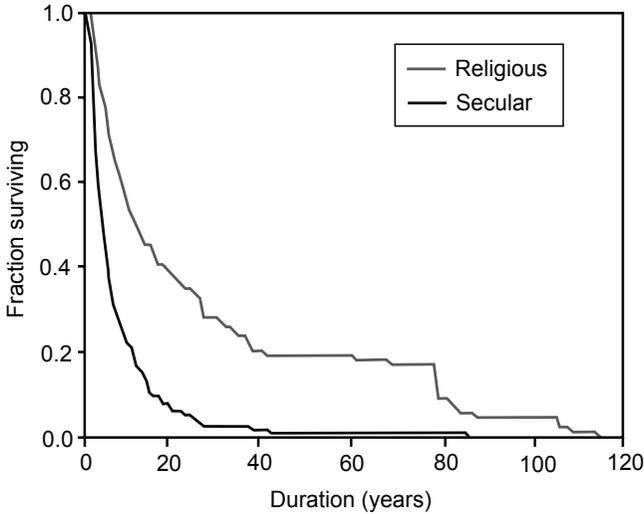


Figure 14.1 Proportion of communes surviving as a function of time since the founding of the commune. The black line traces the development of 112 secular communes and the gray line indicates 88 religious ones (from Sosis 2000).

to imitate the successful can also induce the spread of group beneficial variants. Up to this point, we have focused mainly on what people know about the behavior of members in their own group. Often, people also know something about the norms that regulate behavior in neighboring groups. For example, they know that in a particular firm, employees are discouraged from jumping the chain of command, but that among competitors, the hierarchy is much flatter. Now, suppose different norms are common in neighboring groups and that one set of norms causes people to be more successful. Both theoretical and empirical evidence (Henrich and Gil-White 2001) suggest that people have a strong tendency to imitate the successful. Consequently, behaviors can spread from groups at high payoff equilibria to neighboring groups at lower payoff equilibria because people imitate their more successful neighbors.

One might wonder if this mechanism can really work. It requires enough diffusion between groups so that group beneficial ideas can spread and, at the same time, there cannot be too much diffusion or the necessary variation between groups will not be maintained. Is this combination possible? To answer this question, we constructed a mathematical model of the process, and our results suggest that the process can lead to the spread of group beneficial beliefs over a wide range of conditions (Boyd and Richerson 2002). 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. This process is faster than intergroup competition because it depends on the rate at

which individuals imitate new strategies, rather than the rate at which groups become extinct.

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 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 this is equivalent to a 3–4% annual rate of increase, about the growth rate of the Mormon Church over the last century. According to the sociologist Rodney Stark (1997), 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. Such mutual aid was particularly important during the several severe epidemics that struck the Roman Empire during the late Imperial period” (Johnson 1976, p. 75, quoted in Stark 1997). 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. Demographic factors were as important as conversion 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 Christianity.

Both mechanisms that lead to the spread of group beneficial beliefs are relatively slow: differential extinction because it depends on the relatively rare group extinctions, and differential diffusion because it depends on the transfer of beliefs among groups. The fact that these selective processes are slow is consistent with the fact that many institutions are not group beneficial. Moreover, social groups are complex and their welfare is affected by many different institutions, so that deleterious institutions may often hitchhike on more successful ones.

Rapid Cultural Adaptation Generates Symbolically Marked Corporate Institutions

Conceptualizing institutions as evolutionary equilibria also explains why corporate institutions are typically symbolically marked. One of the most striking features of human sociality is the symbolic marking of corporate groups. Examples include nations, ethnic groups, clans, guilds, and clubs. Some symbolic markers are seemingly arbitrary traits (e.g., distinctive styles of dress, emblems like flags) whereas others are complex ritual systems accompanied by elaborately rationalized ideologies. It is commonplace that social relations

are regulated by norms embedded in a group's sanctified belief system. Even in simple hunting and gathering societies, symbolically marked groups are large. This phenomenon is diverse and impossible to define except in terms of ideal types. Ethnicity grades into class, nation, religion, firm, team, and all the myriad systems of symbolic marking humans use to make intuitive social decisions.

There is considerable evidence that symbolic marking is not simply a by-product of a similar cultural heritage. Children acquire many traits from the same adults, and if cultural boundaries were impermeable, something like species boundaries, this fact would then explain the association between symbolic markers and other traits. However, much evidence shows that ethnic identities are flexible and ethnic boundaries are porous. This argument applies with even more force to corporate groups, such as firms or churches, where membership is not primordial. The movement of people and ideas between groups exists everywhere and will tend to attenuate group differences. Thus, the persistence of differences between institutions requires that other social processes resist the homogenizing effects of migration and the strategic adoption of ethnic identities.

We think that the processes that maintain symbolically marked boundaries are the consequences of rapid cultural adaptation (Richerson and Boyd 2005). The first step in our line of reasoning is to see that symbolic marking is useful because it allows people to identify in-group members. There are two reasons why this would be useful. First, the ability to identify in-group members allows selective imitation. When there is rapid cultural adaptation, the local population becomes a valuable source of information about what is adaptive in the local environment. It is important to imitate locals and to avoid learning from immigrants who bring ideas from elsewhere. Second, the ability to identify in-group members allows selective social interaction. As we have seen, rapid cultural adaptation can preserve differences in moral norms between groups. It is best to interact with people who share the same beliefs about what is right and wrong, what is fair, and what is valuable. Thus, once reliable symbolic markers exist, selection will favor the psychological propensity to imitate and interact selectively with individuals who share the same symbolic markers.

The second, and less obvious, step is to see that these same propensities will also create and maintain variation in symbolic marker traits (McElreath et al. 2003). To understand why, consider the following simple example. Suppose that there are two groups: call them red and blue. In each group, a different social norm is common: call them the red norm and the blue norm. Interactions among people who share the same norm are more successful than interactions among people with different norms. For example, suppose that the norm concerns disputes involving property, and people with shared norms resolve property disputes more easily than people whose norms differ. There are also two neutral, but easily observable marker traits in these groups. Perhaps they are dialect variants. Call them red-speak and blue-speak. Suppose red-speak is

relatively more common in the red group, and blue-speak in the blue group. Further suppose that people tend to interact with others who share their dialect. Individuals who have the more common combination of traits, red-norm and red-speak in the red group and blue-norm, blue-speak in the blue group, are most likely to interact with individuals like themselves. Since they share the same norms, they will be relatively successful. Conversely, individuals with the rare combinations will do less well. Then, as long as cultural adaptation leads to the increase of successful strategies, the red-marked individuals will become more common in the red group while the blue-marked individuals will become more common in the blue group. The real world is obviously much more complicated than this. Nonetheless the same logic should hold. As long as people are predisposed to interact with others who look or sound like themselves, and if that predisposition leads to more successful social interaction, then markers will tend to become correlated with social groups.

The same basic logic works for markers that allow people to imitate selectively. People who imitate others with the locally more common marker have a higher probability of acquiring locally advantageous variants. If people imitate both the marker and the behavior of the marked individuals, then individuals with the locally common marker will, on average, be more successful than people with other markers. This will increase the frequency of locally common markers, which in turn means that they become even *better* predictors of who to imitate. If a sharp environmental gradient or a sharp difference in local norms exists, differences in marker traits will continue to get more extreme until the degree of cultural isolation is sufficient to allow the population to optimize the mean behavior.

Tribal Social Instincts Evolved in Social Environments with Culturally Evolved Institutions

We hypothesize that this new social world, created by rapid cultural adaptation, drove the evolution of new, derived social instincts in our lineage. By “social instincts” we mean simply the genetically transmitted components of our social psychology. Cultural evolution created cooperative, symbolically marked residential groups and institutions like descent groups. Such environments favored the evolution of a suite of new social instincts suited to life in such groups:

- A psychology that “expects” life to be structured by moral norms and is designed to learn and internalize such norms.
- New emotions, such as shame and guilt, which increase the chance that norms are followed.
- A psychology with a naive ontology that includes the social world being divided into symbolically marked groups.

Individuals lacking the new social instincts violated prevailing norms more often 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 intergroup conflict set up an arms race that drove social evolution to ever-greater extremes of in-group cooperation. Eventually, human populations diverged from societies like those of other living apes and came to resemble the hunter-gatherer societies of the ethnographic record. We think that the evidence suggests that since about 100,000 years ago, most people have lived in tribal-scale societies. These societies are based upon in-group cooperation, where in-groups of a few hundred to a few thousand people are symbolically marked, for example, by language, ritual practices, and dress. 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.

Yet why should selection favor new prosocial emotions and intuitive decision-making strategies? People are smart, so should they not just deliberately calculate the best mix of cooperation and defection, given the risk of punishment? We think the answer is that people are not smart enough for evolution to trust them to do the necessary calculations using deliberate reasoning. For example, there is ample evidence that many creatures, including humans, overweight the present in decision making: Most people given the choice between receiving \$1000 right now versus \$1050 tomorrow, take the immediate offer of \$1000. On the other hand, if offered the choice of receiving \$1000 in 30 days or \$1050 in 31 days, most people choose to wait. However, when 30 days have past, people regret their decision. This bias can cause individuals to make decisions that they later regret because they weigh future costs less in the present than they will weigh the same costs in the future. Now suppose that, as we have hypothesized, cultural evolution leads to a social environment in which non-cooperators are subject to punishment by others. In many circumstances the reward for noncooperation will accrue immediately, while the cost of punishment will accrue later, and thus people who overvalue immediate payoffs may fail to cooperate, even though it is in their own interest to do so. If cooperative behavior is generally favored in most social environments, selection may favor genetically transmitted social instincts that predispose people to cooperate and identify within larger social groupings. For example, selection might favor feelings like guilt, which makes defection intrinsically costly, because this would bring the costs of defection into the present where they can be properly compared to the costs of cooperation.

These new tribal social instincts were superimposed onto human psychology without eliminating ancient ones favoring friends and kin. This resulted in an inherent conflict built into human social life. The tribal instincts that support identification and cooperation in large groups are often at odds with selfishness, nepotism, and face-to-face reciprocity. Some people cheat on their taxes, and not everyone pays back the money that they borrow. Not everyone who

listens to public radio pays their dues. 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. Highly cooperative criminal cabals arise to prey upon the production of public goods of 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. The point is that humans suffer these pangs of conflict; most other animals are spared such distress because they are motivated mainly by selfishness and nepotism.

Some of our evolutionist friends have complained to us that this story is too complicated. Would it not be simpler to assume that culture is shaped by a psychology adapted to small groups of relatives? Well, perhaps. Interestingly, the same friends believe almost universally an equally complex coevolutionary story about the evolution of the language instinct. The Chomskian principles-and-parameters model of grammar hypothesizes that children have special-purpose psychological mechanisms that allow them to learn rapidly and accurately the grammar of the language they hear spoken around them. These mechanisms contain grammatical principles that constrain the range of possible interpretations that children can make of the sentences they hear. However, sufficient free parameters exist to allow children to acquire the whole range of human languages. These 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. Most likely, the language instincts and the tribal social instincts evolved in quite close concert. 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 prepared innately 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 similarly constrain and bias the kind of societies that we construct, but that very important details are left to be filled in by the local cultural input. When cultural parameters are set, the combination of instincts and culture produces operational social institutions. Human societies everywhere have the same basic flavor, if the comparison is with, for example, other apes. At the same time, the diversity of human social systems is quite spectacular. As with language instincts, social instincts have coevolved with such institutions over the last several hundred thousand years.

Conclusions

If our picture of the evolution of institutions is correct, the reasons why humans exhibit a mixture of more deliberate and more intuitive decision-making strategies are easy to see. If making decisions by formal deliberation (or anything like it) was cheap and accurate, some ur-organism long ago would have evolved something like omniscient rationality, and all subsequent adaptation would have been via phenotypic adjustments of the ur-organism. Photosynthesis optimal in the here and now? Gin up some chloroplasts! Social rules useful? Invent them on the spot!

The rational ur-organism is perhaps barely conceivable, but how would it fare in competition with Darwinian organisms that largely use genes and (in rare instances) culture rather than phenotypic flexibility to adapt to variable environments? Darwinian processes use a distributed blind selection in conjunction with myopic decision making to cause the long-run evolution of very complex adaptations. Although these adaptations can be transmitted genetically or culturally in a relatively inexpensive manner, they are prohibitively expensive to engineer by a single individual using deliberate procedures. The most common “decision” that a Darwinian organism makes is simply to trust the genes and culture it inherits. In the case of genes, decisions play a relatively small role because phenotypic modifications cannot be transmitted (cf. Jablonka and Lamb 2005). While all organisms have mechanisms to adapt as individuals to environmental contingencies, nothing approaching a rational ur-organism has ever evolved.

The problem of the high cost of deliberate decision making is also central to the analysis of cultural evolution. Individuals and groups can invent new cultural variants and choose among existing ones. Both deliberate and unconscious intuitive choices shape cultural evolution. The division of labor between deliberate and intuitive decision making in the cultural evolutionary context is driven by the slower speed and more costly nature of deliberate processes. One of the costs of deliberate processes is errors. Given limited reasoning powers, limited data, and limited time, deliberate reasoning is likely to lead to erroneous choices. Errors are particularly likely when a decision maker tries to improve a complex adaptation. Most changes in such things, even ones that seem reasonable, are liable to degrade the adaptation. Nevertheless, we presumably would not have the capacity for deliberate decision making unless it is sometimes useful. Guthrie (2005, pp. 269–270), following Liebenberg (1990), gives the example of animal tracking by hunters. Successful tracking requires close attention to multiple subtle cues, tapping a store of remembered knowledge of the behavior of the species being tracked, maintaining multiple working hypotheses, and often collaborative discussion with fellow trackers. Guthrie argues that the reasoning that goes into tracking is the same one that we deploy today in science. We suppose that one of the important functions

for unconscious intuition is using heuristic rules for calling upon deliberation when it is most likely to be worth the cost of engaging in deliberation.

The institutions that regulate our social life resemble other domains of culture. Human social psychology, we believe, rests on a coevolved complex of genes and institutions. Most people are innately predisposed to follow the rules of the groups to which they belong, and culturally evolved institutions furnish an elaborate set of social rules even in simple societies. Foreign travel highlights the extent to which institutions are unconscious or nearly so. One's everyday social habits often serve poorly in other lands. One suddenly becomes aware of practices that are not even perceived at home. At the same time, other practices are scrutinized under a deliberate decision-making microscope. Every human social group has politics. Ongoing environmental changes will probably destabilize existing institutional equilibria and make other potential equilibria more attractive. Deliberate, collective decision making is a means to escape failing equilibria and to negotiate a path to a superior new one. In these often controversial domains, we are extremely well aware that there are choices to be made. The arts of reason, empirical science, and rhetoric are deployed to persuade others that some change in an institution is necessary or not.

The visibility of politically driven institutional change might suggest that every institutional feature of a society is subject to strong political influences. History, however, teaches us that institutions have deep roots that guide politics via unexamined attitudes, intuitions, and emotions. The historian David Hackett Fischer (1989) describes how the institutional geography of the U.S. was formed by the four original streams of British migration to North America. The endurance of these influences is reflected in the famed Southern Strategy of the Republican Party. Southern conservatives, disproportionately drawn from the Scots-Irish migrants to the U.S., were deliberately targeted as the civil rights legislation disaffected them from their traditional party, the Democrats. The attitudes of the Scots-Irish that this strategy exploited trace back to the Border Counties of England and Scotland and the turbulent life there before the Union of the Scottish and English Crowns in 1607. Nisbett and Cohen (1996) describe the enduring institutional differences between areas of Scots-Irish settlements in the U.S. and the rest of the country.

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Left to right: Rob Boyd, Stefan Magen, Gerd Gigerenzer, Pete Richerson, Richard McElreath, Jeff Stevens, Andreas Glöckner, Arthur Robson