

Cultural Evolution of Human Cooperation

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ABSTRACT

Evolutionary theory relevant to the question of human cooperation is reviewed and compared to other theoretical perspectives. A compound explanation is distilled as a plausible account of human cooperation and selfishness. This account leans heavily on group selection on cultural variation but also includes lower-level forces driven by both micro-scale cooperation and purely selfish motives. It is proposed that innate aspects of human social psychology coevolved with group-selected cultural institutions to produce just the kinds of social and moral faculties originally proposed by Darwin. This is termed the “tribal social instincts” hypothesis. The account is systemic in the sense that human social systems are functionally differentiated, conflicted, and diverse. A successful explanation of human cooperation has to account for these complexities. For example, a tribal-scale cultural group selection process alone cannot account for human patterns of cooperation because, on one hand, much conflict exists within tribes and, on the other, people have proven able to organize cooperation on a much larger scale than tribes. Multilevel selection and gene-culture coevolution effects are included to account for some of these complexities and empirical tests of the resulting hypotheses are discussed. In particular, it is argued that strong support for the tribal social instincts hypothesis comes from the structure of modern social institutions. These institutions have conspicuous “work-arounds” that shed light on the underlying instincts.

INTRODUCTION

Cooperation¹ is a problem that has long interested evolutionists. In both the *Origin* and *Descent of Man*, Darwin worried about how his theory might handle cases such as the social insects in which individuals sacrificed their chances to reproduce by aiding others. Darwin could see that such sacrifices would not

ordinarily be favored by natural selection. He argued that honeybees and humans were similar. Among honeybees, a sterile worker who sacrificed her own reproduction for the good of the hive would enjoy a vicarious reproductive success through her siblings. Humans, Darwin (1874, pp. 178–179) thought, competed tribe against tribe as well as individually, and that the “social and moral faculties” evolved under the influence of group competition:

It must not be forgotten that although a high standard of morality gives but slight or no advantage to each individual man and his children over other men of the 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.

More than a century has passed since Darwin wrote, but the debate among evolutionary social scientists and biologists is still framed in similar terms—the conflict between individual and prosocial behavior guided by selection on individuals versus selection on groups. In the meantime social scientists have developed various theories of human social behavior and cooperation—rational choice theory takes an individualistic approach while functionalism analyzes the group advantageous aspects of institutions and behavior. However, unlike more traditional approaches in the social sciences, evolutionary theories seek to explain both contemporary behavioral patterns and the origins of the impulses, institutions, and preferences that drive behavior.

THEORIES OF COOPERATION

We draw evidence about cooperation from many sources. Ethnographic and historical sources include diverse religious doctrines, norms and customs, and folk psychology. Anthropologists and historians document an immense diversity of human social organizations, and most of these are accompanied by moral justifications, if often contested ones. Johnson and Earle (2000) provide a good introduction to the vast body of data collected by socio-cultural anthropologists. Some important empirical topics are the focus of sophisticated work. For

¹ “Cooperation” has a broad and a narrow definition. The broad definition includes all forms of joint action by two or more individuals. The narrow definition is restricted to situations in which joint action poses a dilemma for at least one individual such that, at least in the short run, that individual would be better off not cooperating. We employ the narrow definition in this chapter. The “cooperate” vs. “defect” strategies in the prisoner’s dilemma and commons games anchor our concept of cooperation, making it more or less equivalent to the term “altruism” in evolutionary biology. Thus, we distinguish “coordination” (joint interactions that are “self-policing” because payoffs are highest if everyone does the same thing) and division of labor (joint action in which payoffs are highest if individuals do different things) from cooperation.

example, the cross-cultural study of commons management is already a well-advanced field (Baland and Platteau 1996), drawing upon the disciplines of anthropology, political science, and economics.

Human Cooperation Is Extensive and Diverse

Human patterns of cooperation are characterized by a number of features:

- *Humans are prone to cooperate, even with strangers.* Many people cooperate in anonymous one-shot prisoner's dilemma games (Marwell and Ames 1981) and often vote altruistically (Sears and Funk 1990). People begin contributing substantially to public goods sectors in economic experiments (Ostrom 1998; Falk et al. 2002). The experimental results accord with common experience. Most of us have travelled in foreign cities, even poor foreign cities filled with strange people for whom our possessions and spending money are worth a small fortune, and found risk of robbery and commercial chicanery to be small. These observations apply across a wide spectrum societies, from small-scale foragers to modern cities in nation states (Henrich, in press).
- *Cooperation is contingent on many things.* Not everyone cooperates. Aid to distressed victims increases substantially if a potential altruist's empathy is engaged (Batson 1991). Being able to discuss a game beforehand and to make promises to cooperate affects success (Dawes et al. 1990). The size of the resource, technology for exclusion and exploitation of the resource, and similar gritty details affect whether cooperation in commons management arises (Ostrom 1990, pp. 202-204). Scientific findings correspond well to personal experience. Sometimes people cooperate enthusiastically, sometimes reluctantly, and sometimes not at all. People vary considerably in their willingness to cooperate even under the same environmental conditions.
- *Institutions matter.* People from different societies behave differently because their beliefs, skills, mental models, values, preferences, and habits have been inculcated by long participation in societies with different institutions. In repeated play common property experiments, initial defections induce further defections until the contribution to the public good sector approaches zero. However, if players are allowed to exercise strategies they might use in the real world (e.g., to punish those who defect) participation in the commons stabilizes (Fehr and Gächter 2002), even in one-shot (nonrepeated) contexts. Strategies for successfully managing commons are generally institutionalized in sets of rules that have legitimacy in the eyes of the participants (Ostrom 1990:Chapter 2). Families, local communities, employers, nations, and governments all tap our loyalties with rewards and punishments and greatly influence our behavior.
- *Institutions are the product of cultural evolution.*² Richard Nisbett's group have shown how people's affective and cognitive styles become intimately entwined with their social institutions (Cohen and Vandello 2001; Nisbett and

Cohen 1996; Nisbett et al. 2001). Because such complex traditions are so deeply ingrained, they are slow both to emerge and decay. Many commons management institutions have considerable time depths (Ostrom 1990, Chapter 3). Throughout most of human history, institutional change was so slow as to be almost imperceptible by individuals. Today, change is rapid enough to be perceptible. The slow rate means that different populations experiencing the same environment and using the same technology often have quite different institutions (Kelly 1985; Salamon 1992).

- *Variation in institutions is huge.* Already with its very short list of societies and games, the experimental ethnography approach has uncovered striking differences (Henrich et al. 2001; Nisbett et al. 2001). Plausibly, design complexity, coordination equilibria, and other phenomena generate multiple evolutionary equilibria and much historical contingency in the evolution of particular institutions (Boyd and Richerson 1992); consider how different communities, different universities, and different countries solve the same problems differently.

Evolutionary Models Can Explain the Nature of Preferences and Institutions

These facts constrain the theories we can entertain regarding the causes of human cooperation. For example, high levels of cooperation are difficult to reconcile with the usual rational choice theorist's assumption of self-regarding preferences, and the diversity of institutional solutions to the same environmental problems challenges any theory in which institutions arise directly from universal human nature. The "second generation" bounded rational choice theory, championed by Ostrom (1998), has begun to address these challenges from within the rational choice framework. These approaches add a psychological basis and institutional constraints to the standard rational choice theory. Experimental studies verify that people do indeed behave quite differently from rational selfish expectations (Fehr and Gächter 2002; Batson 1991). Although psychological and social structures are invoked to explain individual behavior and its variation, an explanation for the origins and variation in psychology and social structure is not part of the theory of bounded rationality.

Evolutionary theory permits us to address the origin of preferences. A number of economists have noted the neat fit between evolutionary theory and economic theory (Hirshleifer 1977; Becker 1976). Evolution explains what organisms want, and economics explains how they should go about getting what they want. Without evolution, preferences are exogenous, to be estimated empirically, but not explained. The trouble with orthodox evolutionary theory is that its predictions are similar to predictions from selfish rationality, as we will

² By cultural evolution we mean changes in the pool of cultural variants carried by a population of individuals as a function of time.

see below. At the same time, unvarnished evolutionary theory does do a good job of explaining most other examples of animal cooperation. To do a satisfactory job of explaining why *humans* have the unusual forms of social behavior depicted in our list of stylized facts, we need to appeal to the special properties of *cultural* evolution, and more broadly to theories of culture-gene coevolution (Henrich and Boyd 2001; Richerson and Boyd 1998, 1999; Henrich, in press).

Such evolutionary models have both intellectual and practical payoffs. The intellectual payoff is that evolutionary models link answers to contemporary puzzles to crucial long time-scale processes. The most important economic phenomenon of the past 500 years is the rise of capitalist economies and their tremendous impact on every aspect of human life. Expanding the time scale a bit, the most important phenomena of the last 10 millennia are the evolution of evermore complex social systems and evermore sophisticated technology following the origins of agriculture (Richerson et al. 2001). A real explanation of both current behavior and its variation must be linked to such long-run processes, where the times to reach evolutionary equilibria are measured in millennia or even longer spans of time. More practically, dynamism of the contemporary world creates major stresses on institutions that manage cooperation. Evolutionary theory will often be useful because it will lead to an understanding of how to accelerate institutional evolution to better track rapid technological and economic change. Nesse and Williams (1995 provide an analogy in the context of medical practice.

Evolutionary Models Account for the Processes that Shape Heritable Genetic and Cultural Variation through Time

Evolutionary explanations are *recursive*. Individual behavior results from an interaction of inherited attributes and environmental contingencies. In most species, genes are the main inherited attributes; however, inherited cultural information is also important for humans. Individuals with different inherited attributes may develop different behaviors in the same environment. Every generation, evolutionary processes — natural selection is the prototype — impose environmental effects on individuals as they live their lives. Cumulated over the whole population, these effects change the pool of inherited information, so that the inherited attributes of individuals in the next generation differ, usually subtly, from the attributes in the previous generation. Over evolutionary time, a lineage cycles through the recursive pattern of causal processes once per generation, more or less gradually shaping the gene pool and thus the succession of individuals that draw samples of genes from it. Statistics that describe the pool of inherited attributes (e.g., gene frequencies) are basic state variables of evolutionary analysis. They are what change over time.

Note that in a recursive model, we explain individual behavior and population-level processes in the same model. Individual behavior depends, in any given generation, on the gene pool from which inherited attributes are sampled.

The pool of inherited attributes depends in turn upon what happens to a population of individuals as they express those attributes. Evolutionary biologists have a long list of processes that change the gene frequencies, including natural selection, mutation, and genetic drift. However, no organism experiences natural selection. Organisms either live or die, reproduce or fail to reproduce, for concrete reasons particular to the local environment and the organism's own particular attributes. If, in a particular environment, some *types* of individuals do better than others, and if this variation has a heritable basis, then *we* label as "natural selection" the resulting changes in gene frequencies of populations. We use abstract categories like selection to describe such concrete events because we wish to build up some useful generalizations about evolutionary process. Few would argue that evolutionary biology is the poorer for investing effort in this generalizing project.

Although some of the processes that lead to cultural change are very different than those that lead to genetic change, the logic of the two evolutionary problems is very similar. For example, the cultural generation time is short in the case of ideas that spread rapidly but modeling the evolution of such cultural phenomena (e.g., semiconductor technology) presents no special problems (Boyd and Richerson 1985, pp.68-69). Similarly, human choices include ones which modify inherited attributes directly, rather indirectly, by natural selection. These "Lamarckian" effects are easily added to models and the models remain evolutionary so long as rationality remains bounded (Young 1998). Such models easily handle continuous (nondiscrete) traits, low fidelity transmission, and any number of "inferential transformations" that might occur during transmission (Henrich and Boyd 2002; Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985). The degenerate case of omniscient rationality, of course, needs no recursion because everything happens in the first generation (instantly in a typical rational choice model). Viewed from the perspective of bounded rational choice, evolutionary models are a natural extension of the concept to study how the bounds genetically and culturally inherited elements impose on choice arise (Boyd and Richerson 1993).

Evolution Is Multilevel

Evolutionary theory is always *multilevel*; at a minimum, it keeps track of properties of individuals, like their genotypes, and of the population, such as the frequency of a particular gene. Other levels also may be important. Individual's phenotypes are derived from many genes interacting with each other and the environment. Populations may be structured (e.g., divided into social groups with limited exchanges of members). Thus, evolutionary theories are systemic, integrating every part of biology. In principle, everything that goes into causing change through time plays its proper part in the theory.

This in-principle completeness led Ernst Mayr (1982) to speak of "proximate" and "ultimate" causes in biology. Proximate causes are those that

physiologists and biochemists generally treat by asking *how* an organism functions. These are the causes produced by individuals with attributes interacting with environments and producing effects upon them. Do humans use innate cooperative propensities to solve commons problems or do they have only self-interested innate motives? Or are the causes more complex than either proposal? Ultimate causes are evolutionary. The ultimate cause of an organism's behavior is the history of evolution that shaped the gene pool from which our samples of innate attributes are drawn. Evolutionary analyses answer *why* questions. Why do human communities typically solve at least some of the commons dilemmas and other cooperation problems on a scale unknown in other apes and monkeys? Human-reared chimpanzees are capable of many human behaviors, but they nevertheless retain many chimpanzee behaviors and cannot act as full members of a human community (Savage-Rumbaugh and Lewin 1994; Gardner et al. 1989). Thus we know that humans have different innate influences on their behavior than chimpanzees, and these must have arisen in the course of the two species' divergence from our common ancestor.

In Darwinian evolutionary theories, the ultimate source of cooperative behavior are classically categorized into three evolutionary processes operating at different levels of organization (for a framework unifying these classical divisions, see Henrich, in press,):

- *Individual-level selection.* Individuals and the variants they carry are obviously a locus of selection. Selection at this level favors selfish individuals who are evolved to maximize their own survival and reproductive success. Pairs of self-interested actors can cooperate when they interact repeatedly (Axelrod and Hamilton 1981; Trivers 1971). Alexander (1987) argued that such reciprocal cooperation can also explain complex human social systems, but most formal modeling studies make this proposal doubtful (Leimar and Hammerstein 2001; Boyd and Richerson 1989). Still, some version of Alexander's *indirect reciprocity* is perhaps the most plausible alternative to the cultural group selection hypothesis we champion here. Most such proposals beg the question of how humans and not other animals can take massive advantage of indirect reciprocity (e.g., Nowak and Sigmund 1998). Smith (this volume) proposes to make language the key.³
- *Kin selection.* Hamilton's (1964) papers showing that kin should cooperate to the extent that they share genes identical by common descent are one of the theoretical foundations of sociobiology. Kin selection can lead to cooperative

³ It is not obvious that language potentiates indirect reciprocity. Whereas superficially language may seem to promote the exchange of high-quality information required for indirect reciprocity to favor cooperation, this addition merely changes the question slightly to one of why individuals would cooperate in information sharing; language merely re-creates the same public goods dilemma. Lies about hunting success, for example, are difficult to check, and often ambiguous. Among the Gunwinggu (Australian foragers), members of one band often lied to members of other bands about their success to avoid having to share meat (Altman and Peterson 1988).

social systems of a remarkable scale, as illustrated the colonies of termites, ants, and some bees and wasps. However, most animal societies are small because individuals have few close relatives. It is the fecundity of insects, and in one case rodents, that permits a single queen to produce huge numbers of sterile workers and hence large, complex societies composed of close relatives (Campbell 1983).

- *Group selection.* Selection can act on any pattern of heritable variation that exists (Price 1972). Darwin's model of the evolution of cooperation by intertribal competition is perfectly plausible, as far as it goes. The problem is that genetic variation between groups other than kin groups is hard to maintain unless the migration between groups is very small or unless some very powerful force generates between-group variation (e.g., Aoki 1982; Boorman et al. 1980; Slatkin and Wade 1978; Wilson 1983). In the case of altruistic traits, selection will tend to favor selfish individuals in all groups, tending to aid migration in reducing variation between groups. Success of kin selection in accounting for the most conspicuous and highly organized animal societies (except humans) has convinced many, but not all, evolutionary biologists that group selection is of modest importance in nature (see Sober and Wilson 1998 for a group selectionist's eye view of the controversy). It is also important to note that the problem of maintenance of between-group variation applies *only* to altruistic/cooperative traits, not to social behavior in general. Nearly all evolutionary biologists would agree that group selection is likely to be important for any social interaction with multiple stable equilibria, such as those "coordination" situations mentioned by Smith (this volume).

If one added higher and lower levels as well as cross-cutting forms of structure, this picture could be made more complex; many examples from human societies will occur to the reader, such as gender. Indeed, Rice (1996) has elegantly demonstrated that selection on genes expressed in the different sexes sets up a profound conflict of interest between these genes. If female *Drosophila* are prevented from evolving defenses, male genes will evolve that seriously degrade female fitness. The genome is full of such conflicts, usually muted by the fact that an individual's genes are forced by the evolved biology of complex organisms to all have an equal shot at being represented in one's offspring. Our own bodies are a group-selected community of genes organized by elaborate "institutions" to ensure fairness in genetic transmission, such as the lottery of meiosis that gives each chromosome of a pair a fair chance at entering the functional gamete (Szathmari and Smith 1995; also chapters 14–18, this volume).

Culture Evolves

In theorizing about human evolution, we must include processes affecting *culture* in our list of evolutionary processes along side those that affect genes. Culture is a system of inheritance. We acquire behavior by imitating other

individuals much as we get our genes from our parents. A fancy capacity for high-fidelity imitation is one of the most important derived characters distinguishing us from our primate relatives (Tomasello 1999). We are also an unusually docile animal (Simon 1990) and unusually sensitive to expressions of approval and disapproval by parents and others (Baum 1994). Thus parents, teachers, and peers can rapidly, easily, and accurately shape our behavior compared to training other animals using more expensive material rewards and punishments. Finally, once children acquire language, parents and others can communicate new ideas quite economically. Our own contribution to the study of human behavior is a series of mathematical models in the Darwinian style of what we take to be the fundamental processes of cultural evolution (e.g., Boyd and Richerson 1985). Application of Darwinian methods to the study of cultural evolution was forcefully advocated by (Campbell 1965, 1975). Cavalli-Sforza and Feldman (1981) constructed the first mathematical models to analyze cultural recursions. The list of processes that shape cultural change includes:

- *Biases.* Humans do not passively imitate whatever they observe. Rather, cultural transmission is biased by decision rules that individuals apply to the variants they observe or try out. The rules behind such selective imitation may be innate or the result of earlier imitation or a mixture of both. Many types of rules might be used to bias imitation. Individuals may try out a behavior and let reinforcement guide acceptance or rejection, or they may use various rules of thumb to reduce the need for costly trials and punishing errors. Rules like “copy successful,” “copy the prestigious” (Henrich and Gil-White 2001; Boyd and Richerson 1985, Chapter 8) or “copy the majority” (Boyd and Richerson 1985, Chapter 7; Henrich and Boyd 1998) allows individuals to acquire rapidly and efficiently adaptive behavior across a wide range of circumstances, and play an important role in our hypothesis about the origins of cooperative tendencies in human behavior (Henrich and Boyd 2001).
- *Nonrandom variation.* Genetic innovations (mutations, recombinations) are random with respect to what is adaptive. Human individual innovation is guided by many of the same rules that are applied to biasing ready-made cultural alternatives. Bias and learning rules have the effect of increasing the rate of evolution relative to what can be accomplished by random mutation, recombination and natural selection. We believe that culture originated in the human lineage as an adaptation to the Plio-Pleistocene ice-age climate deterioration which includes much rapid, high-amplitude variation of just the sort that would favor adaptation by nonrandom innovation and biased imitation (Richerson and Boyd 2000).
- *Natural selection.* Since selection operates on any form of heritable variation and imitation and teaching are forms of inheritance, natural selection will influence cultural as well as genetic evolution. However, selection on culture is liable to favor different behaviors than selection on genes. Because we often imitate peers, culture is liable to selection at the sub-individual level, poten-

tially favoring pathogenic cultural variants — selfish memes (Blackmore 1999). On the other hand, rules like conformist imitation have the opposite effect. By tending to suppress cultural variation within groups, such rules protect variation between them, potentially exposing our cultural variation to much stronger group selection effects than our genetic variation (Soltis, Boyd, and Richerson 1995; Henrich and Boyd 1998). Human patterns of cooperation may owe much to cultural group selection.

Evolutionary Models Are Consistent with a Wide Variety of Theories

Evolutionary theory prescribes a method, not an answer, and a wide range of particular hypotheses can be cast in an evolutionary framework. If population-level processes are important, we can set up a system for keeping track of heritable variation and the processes that change it through time. Darwinism as a method is not at all committed to any particular picture of how evolution works or what it produces. Any sentence that starts with “evolutionary theory predicts” should be regarded with caution.

Evolutionary social science is a diverse field (Borgerhoff-Mulder 1997; Laland and Brown 2002). Our own work, which emphasizes an ultimate role for culture and for group selection on cultural variation, is controversial. Many evolutionary social scientists assume that culture is a strictly proximate phenomenon, akin to individual learning (e.g., Alexander 1979), or is so strongly constrained by evolved psychology as to be virtually proximate (Wilson 1998). As Alexander (1979, p.80) states, “Cultural novelties do not replicate or spread themselves, even indirectly. They are replicated as a consequence of the behavior of vehicles of gene replication.” We think both theory and evidence suggest that this perspective is dead wrong. Theoretical models show that the processes of cultural evolution can behave differently in critical respects from those only including genes, and much evidence is consistent with these models.

Most evolutionary biologists believe that individually costly group-beneficial behavior can only arise as a side effect of individual fitness maximization. Above, we noted the problems with maintaining variation between groups in theory and the seeming success of alternative explanations. Many, but by no means all, students of evolution and human behavior have followed the argument against group selection forcefully articulated by Williams (1966).⁴

⁴ Several prominent modern Darwinians, W.D. Hamilton (1975), E.O. Wilson (1975, pp. 561-562), R.D. Alexander (1987, p. 169), and I. Eibl-Eibesfeld (1982), have given serious consideration to group selection as a force *in the special case* of human ultra-sociality. They are impressed, as we are, by the organization of human populations into units which engage in sustained, lethal combat with other groups, not to mention other forms of cooperation. The trouble with a straightforward group selection hypothesis is our mating system. We do not build up concentrations of intra-demic relatedness like social insects, and few demic boundaries are without considerable intermarriage. Moreover, the details of human combat are more lethal to the hypothesis of genetic group selection than to the human participants. For some of

However, *cultural* variation is more plausibly susceptible to group selection than is genetic variation. For example, if people use a somewhat conformist bias in acquiring important social behaviors, variation between groups needed for group selection to operate is protected from the variance-reducing force of migration between groups (Boyd and Richerson in press; Henrich and Boyd 2001; Boyd and Richerson 1985, Chapter 7).

EVOLUTION OF COOPERATIVE INSTITUTIONS

Here we summarize our theory of institutional evolution, developed elsewhere in more detail (Richerson and Boyd 1998, 1999), which is rooted in a mathematical analysis of the processes of cultural evolution and is consistent with much empirical data. We make limited claims for this particular hypothesis, although we think that the thrust of the empirical data as summarized by the stylized facts above are much harder on current alternatives. We make a much stronger claim that a dual gene-culture theory of some kind will be necessary to account for the evolution of human cooperative institutions.

Understanding the evolution of contemporary human cooperation requires attention to two different time scales: First, a long period of evolution in the Pleistocene shaped the innate “social instincts” that underpin modern human behavior. During this period, much genetic change occurred as a result of humans living in groups with social institutions *heavily influenced by culture*, including cultural group selection (Richerson and Boyd 2001). On this time scale, genes and culture *coevolve*, and cultural evolution is plausibly a leading rather than lagging partner in this process. We sometimes refer to the process as “culture-gene coevolution.” Then, only about 10,000 years ago, the origins of agricultural subsistence systems laid the economic basis for revolutionary changes in the scale of social systems. Evidence suggests that genetic changes in the social instincts over the last 10,000 years are insignificant. Evolution of complex societies, however, has involved the relatively slow cultural accumulation of institutional “work-arounds” that take advantage of a psychology evolved to cooperate with distantly related and unrelated individuals belonging to the same symbolically marked “tribe” while coping more or less successfully with the fact that these social systems are larger, more anonymous, and more hierarchical than the tribal-scale systems of the late Pleistocene.⁵

the most violent groups among simple societies, wife capture is one of the main motives for raids on neighbors, a process that could hardly be better designed to erase genetic variation between groups, and stifle genetic group selection.

⁵ We are aware that much controversy surrounds the use of microevolutionary models to understand macroevolutionary questions. Our thoughts on the issues are summarized in Boyd and Richerson (1992).

Tribal Social Instincts Hypothesis

Our hypothesis is premised on the idea that selection between groups plays a much more important role in shaping culturally transmitted variation than it does in shaping genetic variation. As a result, humans have lived in social environments characterized by high levels of cooperation for as long as culture has played an important role in human development. To judge from the other living apes, our remote ancestors had only rudimentary culture (Tomasello 1999) and lacked cooperation on a scale larger than groups of close kin (Boehm 1999). The difficulty of constructing theoretical models of group selection on genes favoring cooperation matches neatly with the empirical evidence that cooperation in most social animals is limited to kin groups. In contrast, rapid cultural adaptation can lead to ample variation among groups whenever multiple stable social equilibria arise. We identify two cultural processes that maintain multiple stable equilibria: (a) conformist social learning and (b) moralistic enforcement of norms. Such models of group selection are relatively powerful because they only require the social, not physical, extinction of groups. Formal theoretical models suggest that conformism is an adaptive heuristic for biasing imitation under a wide variety of conditions (Boyd and Richerson 1985, Chapter 7; Henrich and Boyd 1998; Simon 1990), and both field and laboratory work provide empirical support (Henrich 2001). Models of moralistic punishment (Boyd and Richerson 1992; Boyd et al. submitted; Henrich and Boyd 2001) lead to multiple stable social equilibria and to reductions in noncooperative strategies if punishment is prosocial. As a consequence, we believe, a growing reliance on cultural evolution led to larger, more cooperative societies among humans over the last 250,000 years or so.

Ethnographic evidence suggests that small-scale human societies are subject to group selection of the sort needed to favor cooperation at a tribal scale. Soltis et al. (1995) analyzed ethnographic data on the results of violent conflicts among Highland New Guinea clans. These conflicts fairly frequently resulted in the social extinction of clans. Many of the details of this process are consistent with cultural group selection. For example, social extinction does not mean physical elimination of the entire group. Quite the contrary, most people survive defeat but flee as refugees to other groups, into which they are incorporated. This sort of extinction cannot support genetic group selection because so many of the defeated survive and because they would tend to carry their unsuccessful genes into successful groups, rapidly running down variation between groups. However, the effects of conformist cultural transmission combined with moralistic punishment makes between-group cultural variation much less subject to erosion by migration and within-group success of uncooperative strategies than is true in the case of acultural organisms.

The New Guinea cases had little information regarding the cultural variants that might have been favored by cultural group selection. Other examples are more informative in this regard. Kelly (1985) has worked out in detail the way bridewealth customs in the Nuer and Dinka, cattle-keeping people of the Southern Sudan, led to the Nuer maintaining larger tribal systems. These larger tribes, in turn, allowed the Nuer to field larger forces than Dinka in disputes between the two groups. As a result, the Nuer expanded rapidly at the expense of the

Dinka in the 19th and early 20th centuries. Here, as in New Guinea, many Dinka lineages survived these fights and were often assimilated into *Nuer* tribes, a process, again, highly hostile to group selection on genes. The larger ethnographic corpus suggests that the sort of intergroup conflict described by Soltis and Kelly is very common, if not ubiquitous (Keeley 1996; Otterbein 1970). Darwin's picture of a group selection process operating at the level of competing symbolically marked tribal units with the outcome determined by differences in "patriotism, fidelity, obedience, courage, sympathy" and the like can work, but only upon cultural — not genetic — variation for such traits.

Consistent with this argument, evidence suggests that people in late Pleistocene human societies cooperated on a tribal scale (Bettinger 1991, pp.203-205; Richerson and Boyd 1998). "Tribe" is sometimes used in a technical sense to include only societies with fairly elaborate institutions for organizing cooperation among distantly related and unrelated people. We apply the term to any institution that organizes interfamilial cooperation, even if it is rather simple and the amount of cooperation organized modest. Definitional issues aside, our claim is controversial because the archaeological record permits only weak inferences about social organization and because the spectrum of social organization in ethnographically known hunter-gatherers is very broad (Kelly 1995). At the simple end of the spectrum are "family-level" societies (Johnson and Earle 2000; Steward 1955), such as the Shoshone of the Great Basin and !Kung of the Kalahari. *Because* these two groups are so simply organized, some scholars used them as an archetypal model for Paleolithic societies (Kelly 1995, p. 2). However, such groups are likely poor examples of the "average" Paleolithic society because they inhabit and have adapted to marginal environments using subsistence strategies quite different from any known from the Paleolithic (R. Bettinger, pers. comm.). Also, we believe that the ethnographic societies used to exemplify the family level of organization actually have tribal institutions of some sophistication.

Much evidence suggests that typical Paleolithic societies were more complex than the Shoshone or the !Kung. Many late Pleistocene societies emphasized big game hunting, often in resource-rich environments, rather than the plant foods emphasized in the marginal environments inhabited by Kalahari foragers and the Shoshone. For example, the Kalahari foragers (along with the Aranda in the Australian Desert) anchor the low end of the distribution with respect to plant biomass found in regions of 23 ethnographically known nomadic foraging groups (Kelly 1995, p. 122). As Steward (1955) reports, big game hunting in ethnographic cases typically involves cooperation on a larger scale than plant collecting and small game hunting; thus we should expect societies in the late Pleistocene to be more, not less, socially complex than the !Kung and Shoshone. In any case we think it an error to try to identify an archetypal Pleistocene society; most likely last glacial societies spanned as large or large a spectrum of social organization as ethnographically known cases. Art and settlement size

(several hundred people) at upper Paleolithic sites in France and Spain suggest that these societies were toward the complex end of the foraging spectrum (Price and Brown 1985). In Czechoslovakia, the palisades and large housing structures look much more like the Northwest Coast Indians or Big-Men social forms of New Guinea than the !Kung or Shoshone (Johnson and Earle 2000).

However, despite the marginality of their environment, these archetypal family-level societies do have tribal-scale institutions for dealing with environmental uncertainty (Wiessner 1984). For example, the Shoshonean peoples of the North American Great Basin foraged for most of the year in nuclear family units. Resources in the Basin were not only sparse but widely scattered, militating against aggregation into larger units during much of the year. Although such bands were generally politically autonomous, they were at least tenuously linked into larger units. As Steward (1955, p. 109) remarks about the Shoshoneans "...nuclear families have always co-operated with other families in various ways. Since this is so, the Shoshoneans, like other fragmented family groups, represent the family level of sociocultural integration only in a relative sense." Winter encampments of 20 or 30 families were the largest aggregations among Shoshoneans; however, these were not formal organizations but rather aggregations of convenience. Aside from visiting, some cooperative ventures, such as dances (fandangos), rabbit drives, and occasional antelope drives, were organized during winter encampments. The number of families that a given family might camp with over a period of years was also not fixed, although people preferred to camp with people speaking the same dialect (R. Bettinger, pers. comm.). Steward's picture of the simplicity of Shoshone has been challenged. Thomas (1986, p. 278) observes that, at best, Steward's characterization applied only to limiting cases, as, indeed, his frank use of them to exemplify an ideal type imperfectly suggests. Murphy and Murphy (1986), citing the case of the Northern Shoshone and Bannock, argue that the unstructured fluidity of Shoshonean society conceals a sophisticated adaptation to the sparse and uncertain resources of the Great Basin. The Shoshoneans maintained peace among themselves over a very large region, enabling families and small groups of families to move over vast distances in response to local feast and famine. When local resources permitted and necessity required, they were able to assemble considerable numbers of people for collective purposes. Murphy and Murphy cite the formation of war parties numbering in the hundreds to contest bison hunting areas with the Blackfeet. Indeed, the Shoshone and their relatives were relatively recent immigrants to the Great Basin who pushed out societies that were probably socially more complex but less well adapted to the sparse Great Basin environment (Bettinger and Baumhoff 1982). Murphy and Murphy summarize by saying "the Shoshone are a 'people' in the truest sense of the word." Compared to our great ape relatives, and presumably our remoter ancestors, Shoshonean families maintained generally friendly relations with a rather large group of other families, could readily strike up cooperative relations with

strangers of their ethnic group, and organized cooperative activities on a considerable scale.

We believe that the human capacity to live in larger-scale forms of tribal social organization evolved through a coevolutionary ratchet generated by the interaction of genes and culture. Rudimentary cooperative institutions favored genotypes that were better able to live in more cooperative groups. Those individuals best able to avoid punishment and acquire the locally relevant norms were more likely to survive. At first, such populations would have been only slightly more cooperative than typical nonhuman primates. However, genetic changes, leading to moral emotions like shame, and a capacity to learn and internalize local practices would allow the cultural evolution of more sophisticated institutions that in turn enlarged the scale of cooperation. These successive rounds of coevolutionary change continued until eventually people were equipped with capacities for cooperation with distantly related people, emotional attachments to symbolically marked groups, and a willingness to punish others for transgression of group rules. Mechanisms by which cultural institutions might exert forces tugging in this direction are not far to seek. People are likely to discriminate against genotypes that are incapable of conforming to cultural norms (Richerson and Boyd 1989; Laland et al. 1995). People who cannot control their self-serving aggression ended up exiled or executed in small-scale societies and imprisoned in contemporary ones. People whose social skills embarrass their families will have a hard time attracting mates. Of course, selfish and nepotistic impulses were never entirely suppressed; our genetically transmitted evolved psychology shapes human cultures, and as a result cultural adaptations often still serve the ancient imperatives of inclusive genetic fitness. However, cultural evolution also creates new selective environments that *build cultural imperatives to be built into our genes*.

Paleo-anthropologists believe that human cultures were essentially modern by the Upper Paleolithic, 50,000 years ago (Klein 1999, Chapter 7) if not much earlier (McBrearty and Brooks 2000). Thus, even if the cultural group selection process began as late as the Upper Paleolithic, such social selection could easily have had extensive effects on the evolution of human genes through this process. More likely, Upper Paleolithic societies were the culmination of a long period of coevolutionary increases in a tendency toward tribal social life.⁶

We suppose that the resulting “tribal instincts” are something like principles in the Chomskian linguists’ “principles and parameters” view of language

⁶ It would be a mistake to assume that complex technology is a prerequisite for tribal-level forms of social organization. At the time of European discovery, the Tasmanians had a technology substantially simpler than many upper Paleolithic peoples: they lacked bone tools, composite spears, bows, arrows, spear throwers and fish hooks, etc. Yet, they lived in multiband groups which controlled territories. Intertribal trade, warfare, and raiding were all commonplace (Jones 1974). The last 4,000 years of the Tasmania archaeologically record do not look much different from many middle Paleolithic sites.

(Pinker 1994). Innate principles furnish people with basic predispositions, emotional capacities, and social dispositions that are implemented in practice through highly variable cultural institutions, the parameters. People are innately prepared to act as members of tribes, but culture tells us how to recognize who belongs to our tribes, what schedules of aid, praise, and punishment are due to tribal fellows, and how the tribe is to deal with other tribes: allies, enemies, and clients. The division of labor between innate and culturally acquired elements is poorly understood, and theory gives little guidance about the nature of the synergies and tradeoffs that must regulate the evolution of our psychology (Richerson and Boyd 2000). The fact that even human-reared apes cannot be socialized to behave like humans guarantees that some elements are innate. Contrariwise, the diversity and sometimes-rapid change of social institutions guarantees that much of our social life is governed by culturally transmitted rules, skills, and even emotions. We beg the reader's indulgence for the necessarily brief and assertive nature of our argument here. The rationale and ethnographic support for the tribal instincts hypothesis are laid out in more detail in Richerson and Boyd (1998, 1999); for a review of the broad spectrum of empirical evidence supporting the hypothesis, see Richerson and Boyd (2001, 2002).

Work-around Hypothesis

Contemporary human societies differ drastically from the societies in which our social instincts evolved. Pleistocene hunter-gatherer societies were likely comparatively small, egalitarian, and lacking in powerful institutionalized leadership. By contrast, modern societies are large, inegalitarian, and have coercive leadership institutions (Boehm 1993). If the social instincts hypothesis is correct, social instincts furnish the building blocks for the evolution of complex social systems, while simultaneously constraining the shape of these systems (Salter 1995). To evolve large-scale, complex social systems, cultural evolutionary processes, driven by cultural group selection, take advantage of whatever support these instincts offer. For example, families willingly take on the essential roles of biological reproduction and primary socialization, reflecting the ancient and still powerful effects of selection at the individual and kin level. At the same time, cultural evolution must cope with a psychology evolved for life in quite different sorts of societies. Appropriate larger-scale institutions must regulate the constant pressure from smaller groups (coalitions, cabals, cliques) to subvert rules favoring large groups. To do this cultural evolution often makes use of "work arounds," i.e., mobilizing tribal instincts for new purposes. For example, large national and international (e.g., great religions) institutions develop ideologies of symbolically marked inclusion that often fairly successfully engage the tribal instincts on a much larger scale. Military and religious organizations (e.g., Catholic Church), for example, dress recruits in identical clothing (and haircuts) loaded with symbolic markings, and then

subdivide them into small groups with whom they eat and engage in long-term repeated interaction. Such work-arounds are often awkward compromises, as is illustrated by the existence of contemporary societies handicapped by narrow, destructive loyalties to small tribes (West 1941) and even just to families (Banfield 1958). In military and religious organizations, for example, excessive within-group loyalty often subverts higher-level goals. If this picture of the innate constraints on current institutional evolution is correct, it is evidence for the existence of tribal social instincts that buttresses the uncertain inferences from ethnography and archaeology about late Pleistocene societies. Complex societies are, in effect, grand natural social-psychological experiments rather stringently test the limits of our innate dispositions to cooperate. We expect the social institutions of complex societies to simulate life in tribal-scale societies in order to generate cooperative “lift.” We also expect that complex institutions will accept design compromises to achieve such “lift,” which would be unnecessary if innate constraints of a specifically tribal structure were absent.

Coercive Dominance

The cynics’ favorite mechanism for creating complex societies is command backed up by force. The conflict model of state formation has this character (Carneiro 1970), as does Hardin’s (1968) recipe for commons management.

Elements of coercive dominance are no doubt necessary to make complex societies work. Tribally legitimated self-help violence is a limited and expensive means of altruistic coercion. Complex human societies have to supplement the moralistic solidarity of tribal societies with formal police institutions. Otherwise, the large-scale benefits of cooperation, coordination, and division of labor would cease to exist in the face of selfish temptations to expropriate them by individuals, nepotists, cabals of reciprocators, organized predatory bands, greedy capitalists, and classes or castes with special access to means of coercion. At the same time, the need for organized coercion as an ultimate sanction creates roles, classes, and subcultures with the power to turn coercion to narrow advantage. Social institutions of some sort must police the police so that they will act in the larger interest to a measurable degree. Indeed, Boehm (1993) notes that the egalitarian social structure of simple societies is itself an institutional achievement by which the tendency of some to try to dominate others on the typical primate pattern is frustrated by the ability of the individuals who would be dominated to collaborate to enforce rules against dominant behavior. Such policing is never perfect and, in the worst cases, can be very poor. The fact that leadership in complex systems always has at least some economic inequality suggests that narrow interests, rooted in individual selfishness, kinship, and, often, the tribal solidarity of the elite, always exert an influence. The use of coercion in complex societies offers excellent examples of the imperfections in social arrangements traceable to the ultimately irresolvable tension of more narrowly selfish and more inclusively altruistic instincts.

While coercive, exploitative elites are common enough, we suspect that no complex society can be based purely on coercion for two reasons: (a) coercion of any great mass of subordinates requires that the elite class or caste be itself a complex, cooperative venture; (b) defeated and exploited peoples seldom accept subjugation as a permanent state of affairs without costly protest. Deep feelings of injustice generated by manifestly inequitable social arrangements move people to desperate acts, driving the cost of dominance to levels that cripple societies in the short run and often cannot be sustained in the long run (Insko 1983; Kennedy 1987). Durable conquests, such as those leading to the modern European national states, Han China, or the Roman Empire, leaven raw coercion with other institutions. The Confucian system in China and the Roman legal system in the West were far more sophisticated institutions than the highly coercive systems sometimes set up by predatory conquerors and even domestic elites.

Segmentary Hierarchy

Late Pleistocene societies were undoubtedly segmentary in the sense that supra-band ethnolinguistic units served social functions (e.g., the Shoshone). The segmentary principle can serve the need for more command and control by hardening up lines of authority without disrupting the face-to-face nature of proximal leadership present in egalitarian societies. The Polynesian ranked lineage system illustrates how making political offices formally hereditary according to a kinship formula can help deepen and strengthen a command and control hierarchy (Kirch 1984). A common method of deepening and strengthening the hierarchy of command and control in complex societies is to construct a nested hierarchy of offices, using various mixtures of ascription and achievement principles to staff the offices. Each level of the hierarchy replicates the structure of a hunting and gathering band. A leader at any level interacts mainly with a few near-equals at the next level down in the system. New leaders are usually recruited from the ranks of subleaders, often tapping informal leaders at that level. As Eibl-Eibesfeldt (1989) remarks, even high-ranking leaders in modern hierarchies adopt much of the humble headman's deferential approach to leadership. Henrich and Gil-White's (2001) work on prestige provides a coevolutionary explanation for this phenomenon.

The hierarchical nesting of social units in complex societies gives rise to appreciable inefficiencies (Miller 1992). In practice, brutal sheriffs, incompetent lords, venal priests, and their ilk degrade the effectiveness of social organizations in complex societies. Squires (1986) dissects the problems and potentials of modern hierarchical bureaucracies to perform consistently with leaders' intentions. Leaders in complex societies must convey orders downward, not just seek consensus among their comrades. Devolving substantial leadership responsibility to subleaders far down the chain of command is necessary to create small-scale leaders with face-to-face legitimacy. However, it potentially generates great friction if lower-level leaders either come to have different objectives

than the upper leadership or are seen by followers as equally helpless pawns of remote leaders. Stratification often creates rigid boundaries so that natural leaders are denied promotion above a certain level, resulting in inefficient use of human resources and a fertile source of resentment to fuel social discontent.

On the other hand, failure to articulate properly tribal-scale units with more inclusive institutions is often highly pathological. Tribal societies often must live with chronic insecurity due to intertribal conflicts. One of us once attended the *Palio*, a horse race in Sienna in which each ward, or *contrada*, in this small Tuscan city sponsors a horse. Voluntary contributions necessary to pay the rider, finance the necessary bribes, and host the victory party amount to a half a million dollars. The *contrada* clearly evoke the tribal social instincts: they each have a totem — the dragon, the giraffe, etc., special colors, rituals, and so on. The race excites a tremendous, passionate rivalry. One can easily imagine medieval Sienna in which swords clanged and wardmen died, just as they do or did in warfare between New Guinea tribes (Rumsey 1999), Greek city-states (Runciman 1998), inner city street gangs (Jankowski 1991), and ethnic militias.

Exploitation of Symbolic Systems

The high population density, division of labor, and improved communication made possible by the innovations of complex societies increased the scope for elaborating symbolic systems. The development of monumental architecture to serve mass ritual performances is one of the oldest archaeological markers of emerging complexity. Usually an established church or less formal ideological umbrella supports a complex society's institutions. At the same time, complex societies extensively exploit the symbolic ingroup instinct to delimit a quite diverse array of culturally defined subgroups, within which a good deal of cooperation is routinely achieved. Ethnic group-like sentiments in military organizations are often most strongly reinforced at the level of 1,000–10,000 or so men (British and German regiments, U.S. divisions) (Kellett 1982). Typical civilian symbolically marked units include nations, regions (e.g., Swiss cantons), organized tribal elements (Garthwaite 1993), ethnic diasporas (Curtin 1984), castes (Srinivas 1962; Gadgil and Guha 1992), large economic enterprises (Fukuyama 1995), and civic organizations (Putnam et al. 1993).

How units as large as modern nations tap into the tribal social instincts is an interesting issue. Anderson (1991) argues that literate communities, and the social organizations revolving around them (e.g., Latin literates and the Catholic Church), create “imagined communities,” which in turn elicit significant commitment from members of the community. Since tribal societies were often large enough that some members were not known personally to any given person, common membership would sometimes have to be established by the mutual discovery of shared cultural understandings, as simple as the discovery of a shared language in the case of the Shoshone. The advent of mass literacy and print media — Anderson stresses newspapers — made it possible for all

speakers of a given vernacular to have confidence that all readers of the same or related newspapers share many cultural understandings, especially when organizational structures such as colonial government or business activities really did give speakers some institutions in common. Nationalist ideologists quickly discovered the utility of newspapers for building of imagined communities, typically several contending variants of the community, making nations the dominant quasi-tribal institution in most of the modern world.

Many problems and conflicts revolve around symbolically marked groups in complex societies. Official dogmas often stultify desirable innovations and lead to bitter conflicts with heretics. Marked subgroups often have enough tribal cohesion to organize at the expense of the larger social system. The frequent seizure of power by the military in states with weak institutions of civil governance is probably a byproduct of the fact that military training and segmentation, often based on some form of patriotic ideology, are conducive to the formation of *relatively* effective large-scale institutions. Wherever groups of people interact routinely, they are liable to develop a tribal ethos. In stratified societies, powerful groups readily evolve self-justifying ideologies that buttress treatment of subordinate groups, ranging from neglectful to atrocious. American White Southerners had elaborate theories to justify slavery, and pioneers everywhere found the brutal suppression of Indian societies legitimate and necessary. The parties and interest groups that vie to sway public policy in democracies have well-developed rationalizations for their selfish behavior. A major difficulty with loyalties induced by appeals to shared symbolic culture is the very language-like productivity possible with this system. Dialect markers of social subgroups emerge rapidly along social fault-lines (Labov 2001). Charismatic innovators regularly launch new belief and prestige systems, which sometimes make radical claims on the allegiance of new members, sometimes make large claims at the expense of existing institutions, and sometimes grow explosively. Contrariwise, larger loyalties can arise, as in the case of modern nationalisms overriding smaller-scale loyalties; sometimes for the better, sometimes for the worse. The ongoing evolution of social systems can develop in unpredictable, maladaptive directions by such processes (Putnam 2000). The worldwide growth of fundamentalist sects that challenge the institutions of modern states is a contemporary example (Marty and Appleby 1991). If T. Wolfe (1965) is right, mass media can be the basis of a rich diversity of imagined sub-communities using such vehicles as specialized magazines, newsletters, and, nowadays, web sites. The potential of deviant subgroups, such as sectarian terrorist organizations, to use modern media to create small but highly motivated imagined communities is an interesting variant on Anderson's theory. Ongoing cultural evolution is impossible to control wholly in the larger interest, at least impossible to control completely, and forbidding such evolution tends to deprive societies of the "civic culture" that spontaneously produces so many collective benefits.

Legitimate Institutions

In small-scale egalitarian societies, individuals have substantial autonomy, considerable voice in community affairs, and can enforce fair, responsive — even self-effacing — behavior and treatment from leaders (Boehm 1999). At their most functional, symbolic institutions, a regime of tolerably fair laws and customs, effective leadership, and smooth articulation of social segments can roughly simulate these conditions in complex societies. Rationally administered bureaucracies, lively markets, the protection of socially beneficial property rights, widespread participation in public affairs, and the like provide public and private goods efficiently, along with a considerable amount of individual autonomy. Many individuals in modern societies feel themselves part of culturally labeled tribal-scale groups, such as local political party organizations, that have influence on the remotest leaders. In older complex societies, village councils, local notables, tribal chieftains, or religious leaders often hold courts open to humble petitioners. These local leaders, in turn, represent their communities to higher authorities. To obtain low-cost compliance with management decisions, ruling elites have to convince citizens that these decisions are in the interest of the larger community. As long as most individuals trust that existing institutions are reasonably legitimate and that any felt needs for reform are achievable by means of ordinary political activities, there is considerable scope for large-scale collective social action.

Legitimate institutions, however, and trust of them, are the result of an evolutionary history and are neither easy to manage nor engineer. Social distance between different classes, castes, occupational groups, and regions is objectively great. Narrowly interested tribal-scale institutions abound in such societies. Some of these groups have access to sources of power that they are tempted to use for parochial ends. Such groups include, but are not restricted to, elites. The police may abuse their power. Petty administrators may victimize ordinary citizens and cheat their bosses. Ethnic political machines may evict historic elites from office but use chicanery to avoid enlarging their coalition.

Without trust in institutions, conflict replaces cooperation along fault lines where trust breaks down. Empirically, the limits of the trusting community define the universe of easy cooperation (Fukuyama 1995). At worst, trust does not extend outside family (Banfield 1958), and potential for cooperation on a larger scale is almost entirely foregone. Such communities are unhappy as well as poor. Trust varies considerably in complex societies, and variation in trust seems to be the main cause of differences in happiness across societies (Inglehart and Rabier 1986). Even the most efficient legitimate institutions are prey to manipulation by small-scale organizations and cabals, the so-called special interests of modern democracies. Putnam's (1993) contrast between civic institutions in Northern and Southern Italy illustrates the difference that a tradition of functional institutions can make. The democratic form of the state, pioneered by

Western Europeans in the last couple of centuries, is a powerful means of creating generally legitimate institutions. Success attracts imitation all around the world. The halting growth of the democratic state in countries ranging from Germany to sub-Saharan Africa is testimony that legitimate institutions cannot be drummed up out of the ground just by adopting a constitution. Where democracy has struck root outside of the European cultural orbit, it is distinctively fitted to the new cultural milieu, as in India and Japan.

CONCLUSIONS

The processes of cultural evolution quite plausibly led to group selection being a more powerful force on cultural rather than genetic variation. The cultural system of inheritance probably arose in the human lineage as an adaptation to the increasingly variable environments of the recent past (Richerson and Boyd 2000). Theoretical models show that the specific structural features of the cultural systems, such as conformist transmission, have ordinary adaptive advantages. We imagine that these adaptive advantages favored the capacity for a system that could respond rapidly and flexibly to environmental variation in an ancestral creature that was not particularly cooperative. As a byproduct, cultural evolution happened to favor large-scale cooperation. Over a long period of coevolution, cultural pressures reshaped “human nature,” giving rise to innate adaptations to living in tribal-scale social systems. Humans became prepared to use systems of legitimate punishment to lower the fitness of deviants, for example. We believe that the cultural explanation for human cooperation is in accord with much evidence, as summarized by stylized facts about human cooperation with which we introduced our remarks. More detailed surveys of the concordance of our conjectures with various bodies of data may be found in Richerson and Boyd (1999, 2001) and Richerson (2002).

Regardless of the fate of any particular proposals, we think that explanations of human cooperation have to thread some rather tight constraints. They have to somehow finesse the awkward fact that humans, at least partly because of our ability to cooperate with distantly related people in large groups, are a huge success yet quite unique in our style of social life. If a mechanism like indirect reciprocity works, why have not many social species used it to extend their range of cooperation? If finding self-reinforcing solutions to coordination games is mostly what human societies are about, why do not other animals have massive coordination-based social systems? If reputations for pairwise cooperation are easy to observe or signal (but unexploitable by deceptive defectors), why have we found no other complex animal societies based on this principle? By contrast, we do find plenty of complex animal societies built on the principle of inclusive fitness.

The unique pattern of cooperation of our species suggests that human cooperation is likely to derive from some other unique feature or features of human life.

Advanced capacities for social learning are also unique to humans; thus culture is, *prima facie*, a plausible key element in the evolution of human cooperation. Our argument depends upon the existence of culture and group selection on cultural variation. Since sophisticated culture is unique to humans, we do not expect this mechanism to operate in other species. Ours is not the only hypothesis that passes this basic test. For example, E. Smith's (this volume) signaling hypothesis depends upon language, another unique feature of the human species. E. Hagen made a similar proposal in his comment on our background paper. He argued that the inventiveness of humans combined with language as a cheap communication device adapts us to solve problems of cooperation. We think that hypotheses in this vein, like Alexander's proposed indirect bias mechanism, cannot be decisively rejected, but they are far from completely specified. What is it that biases invention and cheap talk in favor of cooperative rather than selfish ends? The intuition that cheap talk, symbolic rewards, and clever institutions are in themselves sufficient to explain human cooperation probably comes from the common experience that people do find it rather easy use such devices to cooperate (e.g., Ostrom et al. 1994). The difficult question is whether these are backed up by unselfish motives on the part of at least some people. A literal interpretation of experiments such as those of Fehr and Gächter (2002) and Batson (1991) suggests that unselfish motives play important roles. However, unselfish motives may be a proximal evolutionary result of an ultimate indirect reciprocity sort of evolutionary process rather than result of a group selection mechanism. Those who attempt deception in a world of clever cooperators may simply expose their lack of cleverness, so that the best strategy in an unfeigned willingness to cooperate. The data that cultural group selection is an appreciable process (Soltis et al. 1995) is also not definitive, since it could be weak relative to some competing process of the indirect reciprocity sort.

Another complication is that hypotheses leaning on language, technology, and intelligence are appealing to phenomena with considerable cultural content. The evolution of technology and the diffusion of innovations are cultural processes that depend upon institutions and a sophisticated social psychology (Henrich, pers. com). Both the cultural and genetic evolution of our cognitive capacities (some of which gave rise to language) likely emerged from a culture-gene coevolutionary process (Henrich and McElreath 2002; Tomasello 1999). Thus, these hypotheses are not, we submit, clean alternatives to the cultural group selection hypothesis, absent further specification. In the future, we hope our critics will fully specify these vague proposals into such alternatives so to provide for comparative empirical tests.

For example, even if innatist linguists are correct that much of what we need to know to speak is innate, we wonder why more is not innate? Why is it that mutually unintelligible languages arise so rapidly? Would not we be better off if everyone spoke the some common entirely innate language? Not necessarily. Very often people from distant places are likely to have evolved different ways of

doing things that are adaptive at home but not abroad. Similarly, avoiding listening to people proposing a behavior deviant from locally prevailing coordination equilibria is a wise idea. Cultural evolution can run up adaptive *barriers* to communication quite readily if listening to foreigners makes you liable to acquire erroneous ideas (McElreath et al., in press). Dialect evolution seems to be a highly nuanced system for regulating communication within languages as well as between them, although the adaptive significance of dialect is hardly well worked out (Labov 2001). Interestingly, in McElreath et al.'s model, using a symbolic signal to express a willingness to cooperate cannot support the evolution of a symbolic marker of group membership because defectors as well as potential cooperators will be attracted by the signal. A symbolic system can be used to communicate intention to cooperate only if potential cooperative partners can exchange trustworthy signals. Once symbolic markers became sufficiently complex as to be unfakable by defectors *and* a sufficiently large pool of relatively anonymous but trustworthy signalers exist, *then* cheap signals will be useful. Dialect is difficult to fake although cheap to use, and once some level of cooperation on a proto-tribal scale was possible, proto-languages might have come under selection to create unfakable signals of group membership that imply an intention to cooperate. We suspect that language could only evolved in concert with a measure of trust of other speakers rather than being an unaided generator of trust. To the extent that cooperation is the game, one has no interest in listening to speakers whose messages are self-serving. Think of how annoying we find telemarketer's speech acts. Sociolinguists make much of the concept that speech is a cooperative system and argue that the empirical structure of conversation is consistent with this assumption (Wardhaugh 1992). Language seems to presuppose cooperation as much as it in turn facilitates cooperation.

That technology, like language, is one of the major components of the human adaptation is undeniable. It opens up opportunities to gain advantage to cooperation in hunting and defense, and to exploit the possibilities of the division of labor. What is less well understood is the extent to which technology is likely a product of large-scale social systems. Henrich (pers. comm.) has analyzed models of the "Tasmanian Effect." At the time of European contact, the Tasmanians had the simplest tool kit ever recorded in an extant human society; it was substantially simpler than the toolkits of many upper Paleolithic peoples. Archaeological evidence shows that Tasmanian simplicity resulted from both the gradual loss of items from their own pre-Holocene toolkit and the failure to develop many of the technologies that subsequently arose only 150 km to the north in Australia. The loss likely began after the Bass Strait was flooded by rising post-glacial sea levels (Jones 1995). At contact, the Tasmanians numbered about 4,000. Henrich's analysis indicates that imperfect inference of the practices of skilled technologists, rather than stochastic loss due to drift-like effects, is the most likely reason for this loss. To maintain an equilibrium toolkit as complex as those of late Pleistocene hunter-gatherers seems to have required a rather

large population of people who interacted fairly freely so that rare highly skilled performances, spread by selective imitation, could compensate for the routine loss of skills due to imperfect inference. Neanderthals and perhaps other archaic human populations had large brains but simple toolkits. The Tasmanian Effect may explain why. Archaeology suggests that Neanderthal population densities were lower than the modern humans that replaced them in Europe and that they had less routine contact with their neighbors, as evidenced by shorter distance movement of high-quality raw materials from their sources compared to modern humans (Klein 1999).

The proposal that human intelligence is at the root of human cooperation is difficult to evaluate because of the ambiguity in what we might mean by intelligence in a comparative context (Hinde 1970, pp. 659-663). As the Tasmanian Effect illustrates, *individual* human intelligence is only a part of, and perhaps only a small part, being able to create complex adaptive behaviors. In fact, we think “intelligence” plays little role in the emergence of many of human complex adaptations. Instead, humans seem to depend upon socially learned strategies to finesse the shortcomings of their cognitive capabilities (Nisbett and Ross 1980). The details of human cognitive abilities apparently vary substantially across cultures because culturally transmitted cognitive styles differ (Nisbett et al. 2001). Although we share the common intuition that humans are individually more intelligent than even our very clever fellow apes, we are not aware of any experiments that sufficiently control for our cultural repertoires to be sure that it is correct. The concept of “intelligence” in individual humans perhaps makes little sense apart from their cultural repertoires: humans are smart in part because they can bring a variety of “cultural tools” (e.g., numbers, symbols, maps, various kinematic models) to bear on problems. A hunter-gatherer would seem an incredibly stupid college professor, but college professors would seem equally dense if forced to try to survive as hunter-gatherers (a few knowledgeable anthropologists aside). Even abilities as seeming basic as those related directly to visual perception vary across cultures (Segall et al. 1966). Second, *intelligence* implies a means to an end, not an end in itself. Individual intelligence ought to serve the ends of both cooperation and defection. We suspect that actually defection, used for trickery and deception, is better served by intelligence than cooperation. Game theorists assuming perfect, but selfish, rationality predict that humans should defect in the one-shot anonymous prisoner’s dilemma, just as evolutionary biologists predict that dumb beasts using evolved predispositions will. Whiten and Byrne (1997) characterized our social intelligence as “Machiavellian,” implying that it does indeed serve deception equally with honesty. However, just as humans punish altruistically, they seem also to exert their political intelligence altruistically (e.g., Sears and Funk 1990), biasing the evolution of institutions accordingly. On the basis of our brain size compared to other apes Dunbar (1992) predicts that human groups ought to number around 50. Hunter-gatherer co-residential bands do number around 50, but culturally

transmitted *institutions* web together bands to create tribes typically numbering a few hundred to a few thousand people, as we have seen. Human political systems do seem to exceed in scale anything predicted on the basis of enhanced Machiavellian talents (supposing that such talents can on average increase social scale at all). The institutional basis of these systems is not far to seek. For example, Wiessner (1984) describes how institutions of ceremonial exchange of gifts knit the famous !Kung San bands into a much larger risk pooling cooperative. Australian aboriginal groups show similar functional patterns, which are built out of quite different and substantially more elaborate sets of cultural practices (Peterson 1979). Underpinning such individual-to-individual bond making is likely the kind of generalized trust that co-ethnics have for one another. If Murphy and Murphy (1986) are correct about the Northern Shoshone, a society of thousands, constituted a functional “people” engaging in mutual aid in a hostile and uncertain environment on the basis of little more than a common language. In his classic ethnography of the Nuer, Evans-Pritchard (1940) describes how simple tribal institutions can knit herding people into tribes numbering tens of thousands, much larger than was possible among hunter-gatherers. The size of hunter-gatherer societies was evidently limited by low population density, not by their relatively unsophisticated institutions. Third, Henrich and Gil-White (2001) propose that human prestige systems are an adaptation to facilitate cultural transmission. Social learning means that the returns to effort in individual learning potentially result in gains for many subsequent social learners who do not have to “reinvent the wheel.” If extra individual effort in acquiring better ideas pays off in prestige and if prestige leads to fitness advantages, then the social returns to effortful individual learning will in part be reflected in private returns to individual learners. Group selection on prestige systems may further enlarge the returns to investment individual learning and bring returns up to a level that reflects the group optimum amount of effort in individual learning. If this mechanism operates, human intelligence may have been enhanced by social selection emanating from institutions of prestige.⁷

We propose that group selection on cultural variation is at the heart of human cooperation, but we certainly recognize that our sociality is a complex system that includes many linked components. Surely, without punishment, language,

⁷ Similarly, as Smith (this volume) notes, Hawkes hypothesizes that men contribute to hunting success to “show off” and that showing off earns men reproductive success in terms of sexual favors from women. Contrary to what Hawkes supposes, this system is a possible focus of cultural group selection. In many hunter-gatherer groups, meat is very widely shared and hunters often do not control its distribution. Personal favors granted to a successful hunter as recompense for effort will benefit all who share his kills. Showing that individuals who contribute heavily to the common good are rewarded is not evidence that group-selected effects are absent. In the end, group selection can succeed only if altruistic individuals on average do better than selfish ones. The fact that hunters are not allowed to bargain with consumers of their kills and yet are rewarded by consumers anyway is at least as consistent with the operation of group selection as a competing individualist explanation.

technology, individual intelligence and inventiveness, ready establishment of reciprocal arrangements, prestige systems, and solutions to games of coordination, our societies would take on a distinctly different cast, to say the least. Human sociality no doubt has a number of components that were necessary to its evolution and are necessary to its current functions. If such is the case, prime mover explanations giving pride of place to a single mechanism are vain to seek. Thus, a major constraint on explanations of human sociality is its systemic structure. Explanations have to have a plausible historical sequence tracing how the currently interrelated parts evolved, perhaps piecemeal. And explanations have to account for the current functional and dysfunctional properties of human social systems. We are far from having completed this task.

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