EVOLUTIONARY THEORY AND THE SOCIAL SCIENCES

INCREASINGLY A MUTUAL EXCHANGE

Ever since the constitution of sociality as a matter sui generis, social scientists have, at best, ignored the biological sciences as irrelevant or, at worst, fought against them for fear of reductionism and/or racist underpinnings. As a consequence, social scientists avoided to meet the challenge of seriously considering the biological aspects of culture. Repelled by the bold claims of sociobiologists (instigated be E.O. Wilson in 1975), they failed to realize the more substantive contributions among biologists as well as the usages made by their fellow social scientists: Among these were Donald Campbell (psychologist), Napoleon Chagnon and William Irons (anthropologists), Richard Nelson and Sydney Winter (economists). Notably in the last 15 years the efforts have become ever-more intense and less exploratory (for overviews, cf. Barkow/Cosmides/Tooby 1992, Smith/Winterhalder 1992; Weingart/Richerson/Mitchell/Maasen 1997).

Basically, scholars pursue two different research strategies: either a homological or an analogical strategy. On the homological account, one argues that culture does have a direct impact on genetic fitness and one appeals to the theoretical resources developped in the biological investigation of nonhuman behavior. As the genetical bases of human social behaviors are not (well) known, two assumptions are required: first, the phenotypic gambit (Grafen 1991) according to which for each trait under study there is some mapping onto the genetic level. Hence, one can ignore the latter and still presume that fitness consequences will have evolutionary effects. The second assumption is called the natural origin argument: It holds that even the most clearly culturally variable behavior that is not directly genetically controlled, can be treated as if it were. According to this perspective, any cultural learning mechanism that survived an initial selective competition will lead to behaviors that increase genetic fitness. Another way to make use of biology is its theoretical structure in order to build analogous models for cultural change. The analogical strategy rests on the assumption that evolution is a historical process: Human cultures are historical entities, changing over time, but they also carry with them vestiges of their past. Analogous reasoning acknowledges that the relation between culture and evolution is one of similarity, and not identity, thus illuminating both the similarities and differences between biological and cultural processes.

Most prominent accounts along the line of dual inheritance or co-evolutionary models have been given by William Durham (1991) as well as Robert Boyd and Peter Richerson (1985), respectively. In the following chapter Richerson and Boyd will argue that cultural evolution can indeed create social institutions that in the long run shape important aspects of even the innate components of human biology. The long-cherished division between the biological and the cultural (or nature / nurture) is seriously challenged by this type of evolutionary reasoning and so are the boundaries between the biological and the social sciences.

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CULTURE IS PART OF HUMAN BIOLOGY. WHY THE SUPERORGANIC CONCEPT SERVES THE HUMAN SCIENCES BADLY

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Introduction

Rates of violence in the American South have long been much greater than in the North. Accounts of duels, feuds, bushwhackings, and lynchings occur prominently in visitors' accounts, newspaper articles, and autobiography from the eighteenth century onward. According to crime statistics these differences persist today. In their book, Culture of Honor, Richard Nisbett and Dov Cohen (1996) argue that the South is more violent than the North because Southerners have different, culturally acquired beliefs about personal honor than Northerners. The South was disproportionately settled by Protestant Scotch-Irish, people with an animal herding background, whereas Northern settlers were English, German and Dutch peasant farmers. Most herders live in thinly settled, lawless regions. Since livestock are easy to steal, herders seek reputations for willingness to engage in violent behavior as a deterrent to rustling and other predatory behavior. Of course, bad men come to subscribe to the same code, the better to intimidate their victims. As this arms race proceeds, arguments over trivial acts can rapidly escalate if a man – less often a woman – thinks his honor is at stake, and the resulting 'culture of honor' leads to high rates of violence. Nisbett and Cohen support their hypothesis with an impressive range of data including, laboratory data, attitude surveys, field experiments, data on violence, and differences in legal codes.

Their laboratory experiments are most relevant to our argument here. Cohen and Nisbett recruited subjects with Northern and Southern backgrounds from the University of Michigan student body, ostensibly to work on an psychological task dealing with perception. During the experiment, a confederate bumped some subjects and muttered "asshole" at them. Cortisol (a stress hormone) and testosterone (rises in preparation for violence) were measured before and after the insult. Insulted Southerners showed big jumps in both cortisol and testosterone compared to uninsulted Southerners and insulted Northerners. The difference in psychological and physiological responses to insults was manifest in behavior. Nisbett and Cohen recruited a 6'3" 250 lb (190 cm, 115 kg) American style football player whose task was to walk down the middle of a narrow hall as subjects came the other direction. The experimenters measured how close subjects came to the football player before stepping aside. Northerners stepped aside at around 6 feet regardless of whether they had been insulted. Un-insulted Southerners stepped aside at an average distance of 9 feet, whereas insulted Southerners approached to an average of about 3 feet. Polite but prepared to be violent, un-insulted Southerners take more care, presumably because they attribute a sense of honor to the football player and are normally respectful of others' honor. When their honor is challenged, they are prepared and willing to challenge someone at considerable risk to their own safety.

Nisbett and Cohen's study illustrates the two main points we want to make in this essay.

- *Culture is fundamental to understanding human behavior.* The high rates of violence in the American South are a product of a social heritage. The Southern culture of honor arose and was for a long time maintained by an environment that made it an efficacious means of protecting a family's livelihood. Nowadays, few Southerners are pastoralists, and few Notherners are peasant farmers. Nonetheless, these striking differences in behavior persist.
- *Culture causes behavior by causing changes in our biology.* An insult that has trivial effects in a Northerner sets of a cascade of physiological changes in a Southerner that prepare him do violent harm to the insulter and to cope with the likelihood that the insulter is prepared to do equal harm in return. We argue that this example is merely a single strand in mass of connections that so thoroughly web culture into other aspects of human biology that any separation of them into distinct phenomena is impossible.

We can certainly make an analytical distinction between genetic and cultural influences on our behavior, and the influences of non-cultural forms of environmental influences. However useful, this analytical distinction emphatically does not license is an ontological separation of culture and biology separate levels of organization with only simple biological 'constraints' on cultural evolution and diversity. Culture is as much part of human biology as bipedal locomotion, and cultural and genetic influences on human behavior are thoroughly intertwined.

Most of the important threads of twentieth-century social science have rejected one of these two principles. Some traditions within the social sciences, for example rational choice theorists, many psychologists, and human sociobiologists, place little emphasis on culture as a cause of human behavior, and sometimes view cultural explanations as limited to historical-descriptive accounts devoid of real explanatory power. While we sympathize with critics of current culture studies, this state of affairs is not inherent in the culture concept. The effects of culture on human behavior can readily be addressed with the methods of the so-called hard sciences (e. g., Cavalli-Sforza / Feldman 1973, 1981; Lumsden / Wilson 1981; Boyd / Richerson 1985; Richerson / Boyd 1989). We want to convince you that a Darwinian science of culture is a respectable and promising pursuit and that the easiest way to see why is to place culture squarely in the middle of human biology.

Many social scientists have objected to moves of this ilk for fear that the result would be to 'reduce' culture to biology. Many biologists interested in humans have encouraged such fears. E.O. Wilson (1975, 1998) argues that disciplines stand in a reductionistic relation to one another, and that the ultimate fate of the social sciences is to be reduced to sociobiology. The project we champion differs significantly from Wilson's. Part of the payoff for locating culture in biology is that we can model the influence that culture has on genes as well as the 'reductionistic' influence of genes on culture. If we imagine that genes and culture are two inheritance systems that interact on the *same level* to produce human behavior we can make 'coevolutionary' or 'dual inheritance' models of the basic processes by which this interaction takes place. These models have the virtue of reducing to more conventional positions such as rational choice theory, various kinds of human sociobiology, and, most interestingly, Sahlins' (1976) cultural reason, under different simplifying assumptions (Boyd / Richerson 1985: chapter 8). Under a broad and reasonable range of assumptions, evolving genes, evolving culture and environmental contingencies all conspire to affect human behavior.

For some students of culture, locating culture in biology may still seem a risky strategy. The powerful theories and intimidating empirical methods of the natural sciences might overwhelm culture as if science is somehow inherently biased against cultural explanations. We believe the opposite. Cultural explanations of human behavior are likely to prove exceedingly robust. Human nature itself may be substantially socially constructed by the processes of cultural evolution, not just our ideas about it. Culture, on this hypothesis, has the fundamental role in human behavior long claimed for it by cultural anthropologists and many other social scientists and humanists. Cultural evolution can create social institutions that in the long run shape important aspects of even the innate components human biology. Innatists run a real risk that some of their genes will be 'reduced' to culture!

The Poverty of Superorganicism

Most social scientists treat culture as a "super-organic" phenomenon. As A.L. Kroeber put it in trying to explicate the superorganic concept "particular manifestations of culture find their primary significance in other cultural manifestations, and can be most fully understood in terms of these manifestations; whereas they cannot be specifically explained from the generic endowment of the human personality, even though cultural phenomena must always conform to the frame of this endowment" (Kroeber 1948: 62). Theodosius Dobzhansky, an evolutionary biologist very sympathetic to the twentieth-century social sciences of culture, states it: "In producing the genetic basis of culture, biological evolution has transcended itself – it has produced the superorganic" (Dobzhansky 1962: 20). Social scientists have long used rhetoric like this to dismiss the need to incorporate biology in any serious way into their study of human behavior. Humans cannot fly by flapping their arms or swim naked in polar seas, but outside of obvious framing constraints of this type, things biological had no explanatory role in explaining things cultural. On this view, biology is important, of course, because we need bodies and brains to have culture. But biology just furnishes the blank slate on which culture and personal experience write. This idea goes back to the turn-of-the-twentieth-century pioneers of the sociology and anthropology. For example, the French sociologist Gabriel Tarde's (1903) book *The Laws of Imitation* prefigures in many ways the ideas in this essay, but he rejected any considerations of biology as a practical matter of disciplinary specialization. Dobzhansky's usage was probably inspired

Kroeber and kindred influential social scientists of his period. Dobzhansky was recognizing a *fait accompli* we believe. If biologists of his day wanted harmonious relations with social scientists rather than destructive nature-nurture disputes, they had to make obeisance to the superorganic concept. Yet Dobzhansky went right on to say: "Yet the super-organic has not annulled the organic" (1962: 20). He never satisfactorily resolves the tension between these two statements. Ingold provides a discussion of three different senses of "superorganic" used by social scientists over the years about which he summarizes "the superorganic has become a banner of convenience under which have paraded anthropological and sociological philosophies of the most diverse kinds" (Ingold 1986: 223ff.).

In our view, superorganicism is wrong because it cannot deal with the rich interconnections between culture and other aspects of our phenotype, as exemplified by the Southern culture of honor. Superorganicism may have served a useful function in helping the social sciences get on their feet (after a couple of beers – you buy the first round – we'll be happy to dispute even that). Better to grasp the nettle: *Culture is a part of human biology,* as much a part as bipedal locomotion or thick enamel on our molars. Because of culture people can do many weird and wonderful things. But in all cases the equipment in human brains, the hormone producing glands, our hands, and the rest of our bodies play a fundamental role in how we learn our cultures and why we prefer some ideas to others. This is a minority, even heretical, position among human scientists, albeit one with a long pedigree. Freud was a defender of it (Sulloway 1979) as are many modern psychologists, some of whom we discuss below.

Suppose we define culture like this:

> Culture is information capable of affecting individuals' phenotypes which they acquire from other conspecifics by teaching or imitation.

In the taxonomy of definitions of culture, ours is in a category that emphasizes the psychological aspects of the phenomenon (Kroeber / Kluckhohn 1952). Culture is taught by motivated human teachers, acquired by motivated learners, and stored and manipulated in human brains. Culture is an evolving product of populations of human brains. Humans are adapted to learn and manage culture by the way natural selection has arranged our brains. Human social learners in turn arrange features of their brains as they learn from others and the environment. Culture is a major aspect of what the human brain does, just in the same way as smelling and breathing are what noses do. Culture-making brains are the product of more than two million years of more or less gradual increases in brain size and cultural complexity. During this evolution, culture must have increased genetic fitness or the psychological capacities for it would not have evolved. Indeed, anthropologists long interpreted much of culture in adaptive terms (e.g., Steward 1955). Rather than a neat, narrow boundary between innate and cultural processes that can be characterize by a short list of simple biological constraints on human behavior, we imagine a wide, historically contingent, densely intertwined set of phenomena *with causal arrows operating in both directions.* If we think of human culture as a part of human biology in this way we simply don't need to try to unpack what 'superorganic' could possibly mean.

We are a bit sensitive on this point because the style of analysis of the cultural phenomenon we advocate has collected its share of brickbats from both sides of the superorganic divide. From the evolutionary biology side, Richard Alexander (1979: 79–81) and others have supposed that the analysis of culture as an inheritance system is an attempt to defend the superorganic concept against evolutionary analyses of human behavior. On the other, some social scientists have treated our work as yet another attempt to 'reduce' culture to biology (e.g., Ingold 1986: chapter 7). In our view, culture and the rest of human biology interacted in complex ways in the evolutionary past to produce an extraordinary ability to imitate. Genes and culture continue to interact in the everyday world of human behavior in most complex ways. Functional MRI and the other brain scanning techniques are even beginning to give us a real-time picture of how these interactions take place in the brain. In some ways these processes resemble the claims of the conventional social sciences, and in some ways the proposals of human sociobiologists and innatist psychologists. Very often the processes don't resemble the proposals of either. There are some fascinating scientific puzzles to solve here. We doubt there will ever be any use for the superorganic concept, but if one is found we'll take it in stride. In the meantime, we find it liberating just to drop it from our vocabulary. If you'll try it, we think you'll like it too!

Culture is a Derived Human Trait

We as yet know precious little about exactly how genes, culture and external environment play upon the brain to produce our behavior. We do know that without a human brain, you can't acquire human culture. Recent comparative primatology is beginning to describe the nature of our capacity for imitation relative to other apes in some detail. Groups led by Andrew Whiten and Michael Tomasello have studied the social learning of apes and human children in a tightly comparative framework (Whiten/Custance 1996; Tomasello 1996). For example Tomasello's group used human demonstrators of a raking technique to test the social learning of juvenile and adult chimpanzees and 2-year-old children. The demonstrators used two different techniques of raking to obtain otherwise unreachable, desirable objects. Control groups saw no demonstrator. The demonstrator had a big effect on the use of the rake by both children and chimpanzees compared to control groups, but the interspecific difference was also large. The children tended to imitate the exact technique used by the demonstrator but the chimpanzees did not. In similar experiments with older children Whiten and Custance report rapid increase in the fidelity of imitation by children over the age range 2–4 years, with adult chimpanzees generally not quite achieving the fidelity of 2 year old humans. Human children already at quite young ages are far more imitative than any other animal so far tested, although a very few other animals, such as parrots, are also about as good as chimpanzees at imitative tasks (Pepperberg 1999).

What is the biological underpinning of our hypertrophied social learning system? Tomasello (1999) gives an account based on a considerable body of observational and experimental evidence. He argues that the most important unique feature of human cognition is what is called 'joint attention.' Human children, beginning at about nine months of age, begin to pay attention to the attention of other people and to call the attention of others to things of interest to themselves. For example, in Western cultures, children interact with their caregivers in little word-games where both the child and the adult pay attention to the same object, typically a toy. The child may hand the toy to the adult and then look to the adult for some reaction or vice versa. The adult often articulates the word for the toy – 'ball,' 'dolly,' 'truck.' In this way children learn their first words and use the joint attention situation to try out their new words. Or the adult operates the toy – throws the ball, dresses the doll, runs the truck on its wheels – and the child learns these skills. Tomasello dissects joint attention into nine separate skills emerging between nine and twelve months of age. The early maturation of these skills and the apparent necessity of having them before substantial imitation can occur argue for a large element of innate specification of the joint attention system. All of these skills are specific to normal humans and are sufficient to account for the differences in imitative capacities of children and chimpanzees. Autistic children seem to have specific deficits in joint attention and are greatly handicapped in learning language and acquiring other culturally transmitted skills. At the end of the normal developmental sequence, children understand that other people are intentional agents with motivations like their own. Thus, the actions of other are cues as to how one can take advantage of the experiences and skills of others to accomplish one's own goals. From this age onward children are efficient imitators, and begin to rapidly build their cultural repertoires. According to Tomasello's hypothesis, the same joint attention skills underpin the learning of all aspects of culture from language to subsistence skills. Many evolutionary psychologists prefer modular hypotheses, imagining many separate mental 'organs,' most famously for language learning (Pinker 1994). The evidence on these problems is far from conclusive. The very existence of a seemingly rather unusual and highly organized capacity (or capacities) for imitation does argue that an understanding of it (them) is part of evolutionary psychology correctly considered.

Evolved Human Nature Versus Gene-Culture Coevolution

Most evolutionary theories of *human* behavior inspired by Darwin underestimate the importance of culture in the evolution of human behavior, much as superorganicists underestimate the role of genes. Typically, biological theorists assume that natural selection first built human biology and then that this evolved biology controls human behavior. In such theories, the ultimate determinants of human behavior are the product of selection on genes. Any role for culture is proximate and can be thought of as implementing structures built into the genes. The distinction between proximate and ultimate causation is Ernst Mayr's (1961) borrowing from Aristotle. Mayr argues that in biology, proximate causes are typically physiological. Birds migrate equatorward when day lengths shorten because the brain converts short day length into hormonal signals that activate migratory behavior. The ultimate cause of migratory behavior is natural selection. Migration is an evolved strategy to exploit the favorable season at higher latitude while passing the harsh winter in undemanding habitats. Selection has shaped the reaction of the brain to daylength and all the downstream physiological and behavioral machinery to accomplish the migratory adaptation. Much of the dispute over the role of culture in human behavior is understandable in terms of the proximate / ultimate distinction.

Most Human Sociobiology Unduly Neglects Culture

Most students of human behavior inspired by evolutionary biology prefer to keep things simple and neglect or deny the possibility that culture has a fundamental role to play in human adaptation and especially that it has any component of ultimate causality. The classic paper by Richard Alexander in 1974 and the final chapter on humans in Edward Wilson's landmark treatise *Sociobiology* in 1975 caused considerable interest in applying evolutionary ideas to human behavior. Two traditions that grew up in the wake of Alexander's and Wilson's work are human behavioral ecology and evolutionary psychology. The bedrock of the evolutionary analysis conducted by scholars in these traditions is the concept of natural selection acting on genes. They argue that selection over the course of human evolution would have favored decision-making capacities, including decisions about what cultural behaviors to adopt, that increased genetic fitness. How could our large, complex, expensive brain have evolved to support human capacities for learning, including the learning of culture, unless the resulting behaviors increased fitness? Natural selection is the only process of design operating in the world, and the complex capacities of the human brain must therefore have arisen by its operation.

We call this the 'principle of natural origins.' In our view, the principle of natural origins is an exceedingly important idea. It has been attacked vigorously by critics from Darwin's time forward and has proved quite robust (Dawkins 1985). Most Darwinians no longer think detailed defense of it is necessary and just use natural origins as a metatheoretical precept to use to discover adaptations. That is, Darwinians very frequently use the principle of natural origins to formulate hypotheses about what would be adaptive if it is true, rather than testing the dominant role of selection as a hypothesis. This usage has famous critics among evolutionists not to mention anti-evolutionists (Gould / Lewontin 1979), but we are not among their number. The alternative metatheory of the evolutionist critics has not enjoyed much success (e.g., Carroll 1997) compared, say, to the universal Darwinism of Campbell (1965), Dawkins (1976), Dennett (1995), Cziko (1995), and Sober and Wilson (1998). Universal Darwinists see selection as producing adaptations on diverse heritable substrates, including culture, and at diverse levels ranging from individual genes and memes to groups. Some of the most exciting recent work in population genetics is that showing how wide a variety of Dawkins' selfish genes exist in the genome. Given selection falling at different levels or on different sexes, intragenomic conflicts of various kinds arise, giving adaptationism a neat, built-in theory of maladaptations (Rice 1994). Selection at one level can produce maladaptations at another. The creation of new levels on which selection might act occasionally lead to breakthrough adaptations like multicellularity, when formerly intensely competing individuals are welded into larger units (Maynard Smith / Szathmáry 1995).

Our problem is not with the principle of natural origins itself but with its persistent misapplication in the human case. Human sociobiologists with otherwise diverse beliefs have taken certain contingent generalizations from evolutionary biology on board as metatheoretical presuppositions to guide hypothesis formation that we believe should be left in the realm of hypothesis to be tested (cf. Miller 2000 for a view something like ours). Among the most problematical are: (1) we can deduce adaptations directly from what would maximize individual or inclusive genetic fitness, (2) cultural causes are always proximate, and (3) group selection plays no role in the evolution of human social institutions. We think the proper use of the principle of natural origins is *methodological*, not substantive. If culture itself has the attributes of an inheritance system, then it makes sense to apply Darwinian analytical methods to that system of inheritance as well as to the genetic and see where the exercise leads. Will cultural evolution generally lead to genetic fitness maximization? Can cultural variation itself create heritable variation on which selection can act? Can enough of this variation be expressed at the group level for group selection to be an important force? These are among the most interesting *hypotheses* we want to use the analysis to address and to imagine that the principle of natural origins dictates certain answers to them is, in the human case, to badly mis-locate the boundary of Darwinian metatheory and hypothesis. The human/chimpanzee comparative data on imitation, not to mention a mass other data indicating how important culture is in humans, makes importing the unvarnished adaptationist metatheory from evolutionary biology a very risky proposition.

Human behavioral ecologists start with the idea that natural selection ensures that humans act, to a decent first approximation, as general-purpose genetic fitness maximizers. Considerations of cultural evolution and gene-culture coevolution have a strictly secondary role, and for most practical purposes they can be neglected in the view of most human behavioral ecologists. As Alexander puts it, "Cultural novelties do not replicate or spread themselves, even indirectly. They are replicated as a consequence of the behavior of vehicles of gene replication" (Alexander 1979: 80). Or, as Betzig says in reaction to claims for the importance of culture: "[E]verything we think, feel, and do might be better understood as a means to the spread of our own – or of our ancestors – genes", and "I personally, find culture unnecessary" (Betzig 1997: 2, 17).

Very often the strategy of asking what behavior would optimize fitness leads to useful insights. For example, consider mating strategies. When should females mate polygynously with a male that already has a mate, and when should they seek an unmarried mate? In the case of species where males defend territories with resources on them, females should mate polygynously if the extra resources available on an already mated male's territory exceed those available on the best available unmated male's territory. Such 'polygyny threshold' models were first applied to birds and non-human mammals, and they often work quite well. Borgerhoff Mulder (1992) showed that one human population, Kipsigis farmers of Kenya, also followed the polygyny threshold model quite well. Women tend to select husbands on the basis of the land they can offer a new wife to cultivate rather than other criteria. The success of such models should not surprise us. Humans are a successful species and much of our behavior must be pretty adaptive most of the time to account for this success. At minimum, fitness optimizing models provide a convenient benchmark against which to judge competing hypotheses. But cultural evolutionary competing hypotheses exist! For example, the basic subsistence adaptations of humans have been evolving rapidly, relatively speaking throughout the history of our species. Most of these adaptations seem to have a large cultural component and how we get from one to another, optimally or not, is certainly of interest. To ignore our most dynamic system for achieving our adaptations on an 'argument' such as Betzig's is stubborn and willful ignorance!

A second important branch of human sociobiology is evolutionary psychology. The influential school of evolutionary psychology represented by the authors in Barkow, Cosmides and Tooby (1992) argues that fitness optimizing arguments are directed at the wrong target by human behavioral ecologists. The real adaptations to focus upon are the attributes of the mind that optimally adapted us to live in the Pleistocene environments of the past. Contemporary environments have changed so radically that it is vain to hope that behavior will be fitness maximizing today. Evolution is too slow to readapt the human mind significantly in the last few thousand years. The human mind is best conceived of as a collection of adaptations designed to solve specific adaptive problems of Pleistocene life, our 'environments of evolutionary adaptedness,' not a general-purpose fitness maximization system. (The fact that people are even more successful in the Holocene than the Pleistocene is puzzling on this argument, but the fact that we did evolve under Pleistocene conditions is likely important.) These scholars model the mind as a large collection of rather narrowly specialized content rich algorithms that solve a series of narrow problems. For example, human adaptations to the Pleistocene were social. To judge from contemporary hunter-gatherers and from archaeology, small bands of people collaborated to gain subsistence, with a great deal of sharing within and between the constituent families of the band. Bands were linked into a larger social sphere, the tribe among whom mates were sought and help elicited in emergencies. The exchange economies of even the simplest human societies are greatly expanded compared to ancestral primates. Among the adaptations to life in such societies must have been the ability to detect violators of complex social contracts.

Evolutionary psychologists want to use this Pleistocene-limited version of the natural origins principle to inspire hypotheses about evolved cognitive architecture that can be tested experimentally (Tooby/Cosmides 1989). As with the empirical program of human behavioral ecologists, the results of these experiments are often quite convincing. For example, the classic work of Cosmides (1989, cf. also Gigerenzer / Hug 1992) showed that humans are much better at solving logical problems posed as violations of social rules than posed as abstract logical problems, *and* better at solving the social rule problems than with other familiar, concrete content. Cosmides argues that this data is consistent with the hypothesis that humans' social adaptation has equipped them with a powerful innate mental organ for detecting cheaters.

The main problem, from our point of view, with this form of evolutionary psychology is again that the principle of natural origins has been misapplied. Now it seems to be licensing as metatheoretical assumptions the innateness of the important adaptations as well as fitness optimization (in past but not present environments). Several of the leading figures in evolutionary psychology are radical innatists who believe that the role of culture is greatly exaggerated by most social scientists. John Tooby and Leda Cosmides, for example, argue that social scientists have failed to distinguish between what they call *evoked* and *transmitted* culture (Thornhill et al. 1997: 230–234). Transmitted culture is what we call culture here, the product of human social learning. Evoked culture is the innate information that resides in human heads and which is expressed contingently in different environments. Tooby and Cosmides (1989) introduced the term evoked culture to make the point that innate mental organs can be environment-contingent rules, and hence can produce patterns of variation in space that would be difficult to distinguish from transmitted culture. As a hypothesis to explain any given pattern of human behavior, 'evoked culture' is a perfectly good candidate. No doubt, adapted genes play a large role in human behavior much along the lines such innatists suggest. For example the impressive rate at which we can encode and decode speech is the product of specialized auditory and motor pathways (Friederici 1996). In general, however, testing ideas about less peripheral aspects of speech processing and language learning, such as how grammar develops, has proven rather difficult, and hypotheses like Tomasello's (1999) giving a large role to transmitted culture are currently as viable as much more innatist views, such as those of Pinker (1994). Given that humans live in intensely social groups structured by culturally transmitted institutions, and given that culture and individual learning generally lead to adaptive behavior, the bare finding that people are very good at social tasks does not speak very loudly about the proximal causes of social behaviors. The innatist interpretation of the results of Cosmides' experiments seems to based upon the assumption that at least in the ultimate sense, the products of natural selection all reside in the genes on the principle of natural origins. This application of the principle at the psychological level makes no more sense than at the phenotypic. Experimental work by psychologists such as Nisbett, Cohen, and Tomasello shows that culture is an important part of human psychology and to attempt to marginalize it *a priori* is just not a good bet as a research strategy, much less a legitimate deduction from the principle of natural origins.

We think that psychobiology brings plenty of evidence to the table to rule out an extreme *tabula rasa* hypothesis but not nearly enough to rule out an important role for culture. Cultural scientists bring plenty of evidence to the table to rule out a strong version of the evoked culture argument but not nearly enough to rule out a detailed role for evolved innate mechanisms in the acquisition and management of culture. For example, even if the diversity of human behavior in space is explicable on the basis of only an innate human nature and environment, its diversity in time is harder to account for in this way. Over the last 10,000 years, human subsistence behavior and social organization have changed quite radically even though neither genes nor environments have not changed much at all. Even if almost all of the middle ground where the failure of the extreme hypotheses shows the real answers to lie is poorly understood, we know that they are not very close to either extreme.

In the remainder of this essay, the nettle of biology tightly in our grasp, we illustrate the consequences of taking both the principle of natural origins and the importance of culture seriously with two example hypotheses. The classic claim of mid-twentieth-century cultural ecologists (e.g., Steward 1955) was that the human adaptation has two basic components, technology and social organization. Humans adapt to environments by evolving elegant tools to exploit the most diverse sorts of resources the earth has to offer. Human adaptations are social. Human populations take advantage of the principles of cooperation, coordination, and division of labor to a degree otherwise only known among the social insects and a few other lineages. Even by the Middle Pleistocene we were an unusually widely distributed species and for the last 50,000 years or so we have been fairly abundant over most of our range. Let us imagine our nearly acultural chimpanzee like ancestors. What sort of selective pressures would have led to the evolution of accurate imitation of food-gathering strategies? What sort of adaptation is technology? Why is it rare? In this example, we stick to conventional sociobiological assumption that culture is a proximal system of adaptation. Even so, to understand how culture works as a genetic adaptation requires taking the properties of cultural evolution seriously. What of the evolution of the social component of our adaptation? How might we come to cooperate in groups composed of distantly related individuals? Evolutionary theory makes strong predictions about cooperation and the standard sociobiological theory well predicts all but a handful of cases. We are perhaps the most glaring exception, cooperating in large groups of distantly (genetically) related individuals. Our hypothesis is that natural selection has a stronger purchase on cultural than genetic variation and that the social component of our behavior is substantially the result of culture participating in evolution as an ultimate cause, not just a proximate one.

How Technology Works

The principle of natural origins encourages us to ask why natural selection might have favored our capacity for culture. The imitative capacity psychologists have described, and the cultural traditions the capacity it apparently supports, could only have evolved if they were adaptive. The capacity to acquire, store, manage and use technological practices is at least one of the functions of our large brain. Most accounts of human origins take our current ecological dominance as evidence of a qualitatively new and superior form of adaptation and ask what evolutionary breakthrough led to this revolutionary new adaptation. For example, Lumsden and Wilson (1981: 330) remark that "[*Homo*] overcame the resistance to advanced cognitive evolution by the cosmic good fortune of being in the right place at the right time." Our current ecological dominance is undeniable, although perhaps precarious, but the principle of natural origins encourages to ask quite detailed questions about just what selection pressures would have operated leading up to any breakthroughs.

Cultural Evolution is Fast and Cumulative

The human brain is a serious adaptive puzzle. It is a very costly organ (Aiello / Wheeler 1995). Human brains account for about 10 percent of our total energy budget versus something like 1.5 percent for average mammals. Aiello and Wheeler argue that one consequence of our expensive brain is that to pay its overhead we evolved a smaller gut (gut tissue is also costly per unit weight). A short gut means that we have to eat more energy-intensive foods than our ancestors. A costly brain and a short gut meant that humans had to hunt, gather, and conduct their social life with some efficiency to support their brains under quite hostile physical conditions in competition with other predators, scavengers, and plant eaters with much more economical brains and more efficient guts. At least during the last glaciation, climates were not only colder, but drier and much more variable than during the Holocene. We believe that culture is most likely an adaptation to the Pleistocene climate variation (Richerson / Boyd 2000). During the last glacial, and by inference during most of the rest of the Pleistocene, climate did not vary only the 100,000 year time scale of the classic ice ages. Climates were also spectacularly variable on time scales ranging from a few years to a few thousand years. For example, from 80,000 to 10,000 years ago was punctuated more than 20 abrupt (~1° C per decade!) warmings to about half of interglacial temperatures, not to mention considerable variation at both shorter and longer time scales (Ditlevsen et al. 1996; Broecker 1995).

Our mathematical modeling studies show that a likely adaptive advantage of culture is the ability of this system of adaptation to respond more rapidly to changing environments better than genes (Boyd / Richerson 1985). This ability comes from coupling adaptive decision-making systems to the transmission system made possible by accurate, fast imitation. Take the two simplest kinds of models. One feature of culture is that it is a system for the inheritance of acquired variation. Individuals can imitate the behavior learned by others. If the rules that guide learning tend to be adaptive, then two forces, natural selection and learning, act together to favor the accumulation of adaptations. In the world of models at least, this system is especially suited to adapting to environments that vary a lot, but with an appreciable, but not too large, resemblance between parents' and offsprings' environments. If environments vary too fast, then Mom's and Dad's behavior may be out of date, and individuals should learn for themselves. If the vary too slowly, selection on genes keeps up well enough, and the costly overhead of brain tissue consumptive culture weighs against it. The Pleistocene was rich in just the kind of variation that favors the inheritance of acquired variation.

A second trick we can do with culture is use pre-existing cultural variants rather than our own random trials or inventions. Suppose we observe not only how Mom gathers, but also the techniques of several other gatherers. Suppose we observe two or three variants. As we begin to practice gathering we can try each variant a few times and retain the one that seems best. Further, throughout our life we may continue to observe and try out any likely variant techniques that seems promising. Depending upon how accurately people can discriminate among different techniques and on how many varying techniques one has an opportunity to observe, the biasing of imitation can be a weak or powerful force.

The neat result of the models is that even when decision-making effects are *weak* at the level of individuals, they can be *powerful* at the level of the population. This finding is closely related to the fact that natural selection is a powerful force at the population level even when so weak as to be impractical to measure at the individual level. When any directional force acts in the same direction in an entire population and consistently for more than a few generations, the evolutionary response is swift. For selective forces to operate including both biased imitation and natural selection, variation to select upon must exist. However, coupling individual learning to social learning means that trial and error learning can act as a source of new, generally partly adaptive, variation.

We believe (Boyd/Richerson 1996) that the evidence suggests that our adaptive success also rests decisively on our ability to create cultural adaptations that can accumulate complexity, eventually coming to rival genetic adaptations in the sophistication of their 'design.' Even relatively sophisticated social learners like chimpanzees get only a very general idea of a behavior using social cues. Using this general idea, they refine their actions to a functional behavior using individual learning. This limits the complexity of the socially learned behavior to that which can be supported by individual learning at the individual level. The human ability to imitate accurately means that we can adopt the precise variant of a previous innovator, perhaps tracing back to some long-dead genius, and then add a new wrinkle of our own, which can in turn be imitated and improved by our successors. Eventually human populations heap innovation upon innovation until we reach the limits of human minds to be taught the result. Even the cultures of simple societies accumulate far more genius than even the most brilliant individual innovator could muster. Most likely, the invention of language increased the number and sophistication of abstract concepts we could learn. In simple societies, memory places limits on complexity that more recently have been relieved by the invention of writing and numbers (Donald 1991). At the cutting edge, we again push right up against human cognitive limitations. Most of us now live by skills dearly won in classrooms by great mental exertion on both our and our teachers' parts. The relative rapidity with which we could build up and adaptively modify complex technology is one leg of the adaptation allowed us in the Pleistocene to chase the ephemeral niches left under-exploited as other species lagged behind the kaleidoscopic changes in resources caused by rapid climate change. In the Holocene, the invention of agriculture gave us the tools to deteriorate the environments of competing and pest species faster than they could adapt to our modifications (Richerson et al. 2001).

Thus, we suppose that the environmental deterioration of the Pleistocene is the specific environmental factor that humans exploited to support their large, costly brains (Richerson / Boyd 2000). Interestingly, many mammalian lineages show increased brain size in the Pleistocene. Other species may also have been using social learning to adapt to variable environments. However, no other mammalian species has developed the ability to use rapidly evolving complex tools to exploit variable environments. Probably, our bipedal posture, by freeing the hands to specialize in creating and using tools, was a decisive preadaptation (Tobias 1981). Coupling the capacity to imitate to the capacity to make tools allowed us to rapidly develop adaptations that would otherwise have required slow anatomical modifications. Lacking a flexible way to implement a diversity of cultural adaptations, no other species came to support such a radically enlarged and costly brain.

The promise of explicitly modeling and measuring the processes of cultural change is immense. For example, why has the Holocene witnessed a 10,000 year long raggedly progressive trend to fancier technology and larger societies? What currently regulates rates of change in various components of various cultures? Are current anthropogenic climate changes likely to stress our ability to adapt to them? Ice age climates will presumably return. Can complex societies adapt enough to cope with the very noisy climates that have prevailed during the last couple of million years? The extraordinary dynamism of human societies means that understanding our species using assumptions about equilibrium adaptations to given environments will be less productive than in other cases (Nelson / Winter 1982).

Why Humans Are Ultra-Social

Many critics of the orthodox schools of human sociobiology have argued that the problem is that these investigators leap to adaptation without considering the complexities raised by development. Our critique above is of this form if we take social learning to be a form of developmental process linking the evolving genes to the adaptive phenotypes. While true, this objection bites less sharply than it might otherwise because adaptationists commonly, and commonly successfully, neglect the details of genes and development when studying the evolution of adaptations. The tactic of taking genes and development lightly in the hope that progress can be made without needing to understand proximate causes is called the "phenotypic gambit" (Grafen 1991). The phenotypic gambit is generally necessary when one studies adaptations. Development is a complex and difficult topic all its own, and usually the only practical way to proceed is to assume that selection has managed the developmental processes well enough that adaptations close to what we'd predict from gross functional considerations. We endorse the judicious use of the phenotypic gambit; if *we* can't use it, we'd have to wait until developmental psychologists have delivered a Mercedes model of the imitation process rather than a pick-your-own collection of Amsterdam bicycles. Related scientific programs typically have to cope with weaknesses in their partners and with the intimidating complexity of even well known phenomena. The phenotypic gambit and allied strategies are necessary to finesse ignorance and complexity.

A critique that bites deeper is that human sociobiologists have generally neglected the ultimate role culture has played in human evolution. The coevolutionary concept of an ultimate-cause role for culture is very simple. Culture, like genes, creates patterns of heritable variation. Natural selection will inevitably play upon any pattern of heritable variation that arises in the world as Richard Dawkins (1976) noticed and Donald Campbell (e.g., 1965) had argued earlier. If cultural variation can respond to selection it is just as ultimate a cause as genes! Of course, culture does not stand in isolation; it lives in brains and is no doubt heavily shaped by influences having their roots in genes and selection on genes. But the proximal causal arrow runs both ways, as we've already seen. Our psychology is shaped by our culture. Culture acts as a selective environment to which our genes will, in the long run, adapt. The term coevolution classically derives from the interacting evolution of pairs of species like predators and prey, diseases and hosts, and mutualists. In the present case we imagine that our culture is something like a symbiont. It lives in the same body as our genes, but has a different life cycle and thus responds somewhat differently to evolutionary forces. In our species, culture and genes are obligate mutualists – an individual cannot even survive without tolerably good genes and tolerably good culture.

We hope that the gene-culture coevolutionary idea seems perfectly intuitive to most of our readers. Be warned, however, that you are being invited down what many evolutionary social scientists believe is a garden path. The issue is whether or not gene-culture interactions in humans are *fully* or *only partially* coevolutionary. The more prominent hypothesis is that the gene-culture system is a degenerate example of coevolution. Genes have no doubt evolved to constrain the evolution of cultural variants in ways that favor the fitness of the evolving gene. This dynamic is what Charles Lumsden and Edward O. Wilson called the "full coevolutionary circuit" (Lumsden/Wilson 1981: 303). They emphasized evolution of evolved genetic 'leashes' on cultural evolution. We think Lumsden and Wilson's dynamic is incomplete because selection also exists on the cultural variants *and thus evolved cultural institutions can cause changes in the genome that favor cultural fitness.* Culture is on a leash all right, but the dog on the end is big, smart, and independent not a well-trained toy poodle. On any given walk, who is leading whom is not a question with a simple answer (cf. Durham 1991: 223–225 for a similar argument).

Mechanisms by which culture might exert forces tugging in this direction are not far to seek. Cultural norms affect mate choice and people seeking mates are likely to discriminate against genotypes that are incapable of conforming to cultural norms (Richerson/Boyd 1989). Men who cannot control their testosterone storms end up exiled to the wilderness in small-scale societies and to prison in contemporary ones. Women who are an embarrassment in social circumstances are unlikely to find or keep husbands. We believe that with, at minimum, tens of thousands of years to work with, natural section on cultural variation could easily have had dramatic effects on the evolution human genes by this process. Some of these effects no doubt just energize Lumsden and Wilson's limb of the coevolutionary circuit, favoring better genetic leashes. Humans are still in part a wild animal; our cultural adaptations often still serve the ancient imperatives of genetic fitness. However, we think the evidence supports the hypothesis that the coevolutionary circuit is 'doubly full.' The leash works both ways. Humans, we might say, are a *semi-domesticated* species. *Cultural imperatives are built into our genes.* Not only can culture act proximally to constrain behavior via institutions, skills, values, and so forth, but by constraining behavior in similar ways over hundreds of millennia it is a major source of ultimate causes of human 'nature.'

Group Selection on Cultural Variation Selected New Social Instincts by Coevolution

The other major leg of the human adaptation is our complex social organization and our form of social organization is potentially a result for selection on cultural variation and coevolutionary adjustments on the genetic side. The residential bands that most ethnographically known hunter-gatherers lived in are only a little larger than those of chimpanzees (Dunbar 1992), but human social organization includes a tribal level that is unique to our species. In the simpler human societies, typically several residential units, numbering a few hundred to a few thousand people, speak the same dialect, participate in a common ceremonial system, maintain a level of internal peace and security against hostile groups, and aid one another in subsistence emergencies.

Other ultra-social animals, including to one other mammalian example, the naked mole rats of Africa, are based upon creating large societies by multiplying the number of close genetic relatives. The creation of reproductive and sterile castes in the social insects offers examples of several independent origins of this system. Humans have taken a quite different route to ultra-sociality (Campbell 1983). As Campbell observed, human societies have reproductive competition among the cooperators, leading to societies that exhibit considerable self-sacrificial altruism (e. g., heroism in war) and considerable within-group conflict (e. g., feuding). Some societies exhibit *both* extremes of warrior self-sacrifice *and* of extremes internal conflict rooted in sub tribal scale loyalties, a trick that seems to defy the evolutionary law of gravity (Hamilton 1964) as it applies to all other species. The proximal mechanisms by which cultural institutions can harness phenomena like Southerners' touchy sense of *personal* honor to functional large-scale organizations, like the excellent armies of the Confederacy in the American Civil War, are tolerably well understood (Boehm 1984; Salter 1995).

We have proposed what we call the "tribal social instincts hypothesis" to account for our peculiar pattern of social organization (Richerson / Boyd 1998, 1999, 2001). The tribal social instincts hypothesis is based on theoretical analyses suggesting that group selection plays a more important role in shaping culturally transmitted variation than it does in shaping genetic variation. In our simplest model of the process, we imagine that humans come to use conformist biases in acquiring culture (Boyd / Richerson 1985: chapter 7, cf. also Henrich / Boyd 1998). Conformity is adaptive under a wide range of conditions because the commonest thing people are doing in a given environment is frequently a very good thing to do relative to most easy-to-discover alternatives. When in Rome, do as the Romans do. As a *byproduct*, conformity has the effect of preserving between group variation and suppressing within group variation. Most evolutionists doubt that group selection on genes is very often important because it is so hard to maintain variation between groups, particularly variation for traits such as altruism that are selected against within groups.

Almost everyone agrees that human material culture was of essentially modern levels of sophistication by the Upper Paleolithic, 50,000 years ago (Klein 1999). Even if the cultural group selection process did not start until the Upper Paleolithic Transition 50,000 years ago, human minds have been selected for 2,000 generations in social environments in which the innate willingness to recognize, aid, and if necessary, punish fellow group members was favored by co-evolution. That is, cultural group selection produced traditional institutions that penalized genotypes that were hewed too tightly to individual selfishness, Hamilton's kin selection rules, or to reciprocity strategies to deal with non-relatives. If cultural institutions can generate sufficiently costly punishments for deviations from their rules or provide the benefits of group cooperation mainly to cooperators, any genetic variation underlying behavioral dispositions will fall under selection favoring genotypes that avoid the punishments and earn the rewards. We suppose that the resulting tribal instincts are something like principles in the Chomskian linguists' "principles and parameters" view of language (Pinker 1994). The innate principles furnish people with basic predispositions, emotional capacities, and social skills – the principles – that are implemented in practice through highly variable cultural institutions – the parameters. People are innately prepared 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.

Because the tribal instincts are of relatively recent origin and because our genes still fall under selection pressures obeying Hamilton's rule, they are not the sole regulators of human social life. The tribal instincts are laid on top of more ancient social instincts rooted in kin selection and reciprocal altruism. These ancient social instincts conflict with the tribal. We are simultaneously committed to tribes, family, and self, even though the conflicting demands very often cause us the great anguish as Freud (1930) described in *Civilization and Its Discontents* or Graham Greene portrayed in novels such as *The Honorary Consul*. So long as reproductive competition among the cooperators exists, people still have to look out for their personal fitness interests even as they try to do their civic duty.

We (Richerson/Boyd 2001) argue that a considerable mass of evidence from a number of domains of knowledge supports that tribal social instincts hypothesis and calls into question competing evolutionary explanations. Nevertheless, much more work needs to be done before any hypothesis regarding the evolutionary origins of human sociality should be accepted as well verified. What we do claim on the basis of the evidence we review is that the tribal social instincts hypothesis, with its active, ultimate role for the process of group selection on cultural variation, is at least as attractive as any current competing hypothesis.

Conclusion

The fast and cumulative hypothesis to explain the original adaptive advantage of imitation in humans is a straightforward application of adaptive analysis. It is a simple argument from the principle of natural origins. However, if it or hypotheses like it are true, culture plays, and has long played, a central role in human evolution and cannot be marginalized. For example, the time scale of cultural evolution is rapid, but not instantaneous. Indeed, 10,000 years after the end of the last big shift in the earth's environmental regime, the Pleistocene-Holocene transition, human cultural change has apparently not equilibrated. The processes of cultural evolution are fundamentally important to understanding human behavior but are comparatively little studied, especially with sophisticated quantitative methods.

The coevolutionary tribal instincts hypothesis, if it or anything in its genre are correct, means that coevolution with culture has driven the evolution of genes in directions genes would never have gone, left to their own devices. Cultural institutions achieved the tribal (and now larger) scale of organization by partly domesticating genes. The human achievement of ultrasociality seems to be one of those rare evolutionary transitions where a new level of organization emerges because some form of group selection, no doubt always tenuously in the beginning, unites previously fiercely competing entities into a larger scale cooperative system (Maynard Smith / Szathmáry 1995). This hypothesis is also perfectly consistent with natural origins. Large scale human societies are (so far) extraordinarily successful because they, on average, increase the fitness of both genes and culture, quite like other successful coevolved mutualisms.

The principle of natural origins is the fundamental building block of Darwinian metatheory. We have no competing metatheory that has much promise of giving us a truly deep and synthetic theory of human behavior. The trouble is not with the principle but its misapplication in the human case. It especially does not imply what cultural scientists have come to fear, a trivialization of the role of culture in human behavior. Culture, its evolutionary processes and coevolutionary effects are all straightforward topics for Darwinian investigation. A mass of evidence argues that we cannot understand human behavior without doing culture right. This same evidence argues that using concepts like the superorganic to separate the study of culture from the rest of human biology is equally flawed. The superorganic concept was a tribal ploy used by twentieth-century social scientists to create and maintain disciplinary boundaries with biology (cf. Campbell 1978 on the functions and dysfunctions of disciplinary boundaries). If we are correct, it never served a truly useful analytical role. Whatever useful function the concept and its boundaries served in the twentieth century, they are now utterly senescent. The task for twenty-first-century human science is to put culture back into human biology.

Culture operates through biological mechanisms – brains, hormones, hands – and the causal pathways by which it acts are certain to prove densely tangled with genetic causes. The difficulty we have in following the threads of genetic and cultural influences on human behavior is the best evidence we have on this point. If the relationship between genes and culture were simple, the case would have been cracked long ago. Scientists should not be faint-hearted in the face of complexity if that is where the real problem lies. Darwinism is rich in techniques for making progress in the face of intimidating complexity. The last 'tangled bank' paragraph of the *Origin of Species* is a lyrical passage that combines a downright mystical appreciation for the complexity of nature with a scientist's optimism that useful understanding is possible nonetheless. The extremes superorganicism and innatism are useless simplifications that lead human scientists to avoid the hard but central problem of the human species, the natural origin of the cultural system of inheritance and all the things that people can create because their biology includes the capacity for imitation.

Cultural scientists should not be timid about being reunited with biology. Culture is a brawny phenomenon in no danger of being 'reduced' to genes. Evolutionary biologists should not be timid about welcoming cultural scientists either, as biologists command the methods cultural scientists neglected because superorganicism especially stigmatized Darwinism. All sorts of borrowings and interchanges across the biology social science divide are likely to prove fruitful (Weingart et al. 1997). The only people with legitimate reason to fear a unified human biology with culture and genes playing their appropriate roles are those who want easy answers to hard questions.

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