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List of Contributors

Scott Atran, Centre National de la Recherche Scientifique, Paris, and Department of Psychology, University of Michigan

H. Clark Barrett, Department of Anthropology, University of California at Los Angeles

Robert Boyd, Department of Anthropology, University of California at Los Angeles

Peter Carruthers, Department of Philosophy, University of Maryland

Susan Dwyer, Department of Philosophy, University of Maryland Baltimore County.

Daniel M. T. Fessler, Department of Anthropology, University of California at Los Angeles

Marcus Giaquinto, Department of Philosophy, University College London

Paul Griffiths, Biohumanities Project, University of Queensland

Annerieke Heuvelink, Department of Artificial Intelligence, Vrije University, Amsterdam

Lawrence Hirschfeld, Departments of Psychology and Anthropology, New School for Social Research

Richard Joyce, Philosophy Program (RSSS), Australian National University

Stephen Laurence, Department of Philosophy, University of Sheffield

David Papineau, Department of Philosophy, King's College London

Peter J. Richerson, Department of Environmental Science and Policy, University of California at Davis

Paul Rozin, Department of Psychology, University of Pennsylvania

Michael Siegal, Department of Psychology, University of Sheffield

Tom Simpson, Higher Education Academy Psychology Network, University of York

Dan Sperber, Institut Jean Nicod, Centre National de la Recherche Scientifique, Paris

Chandra Sekhar Sripada, Departments of Philosophy and Psychiatry, University of Michigan

Kim Sterelny, Department of Philosophy, Victoria University in Wellington, and Philosophy Program (RSSS), Australian National University

Stephen Stich, Department of Philosophy and Center for Cognitive Science, Rutgers University

Luca Surian, Department of Psychology, University of Trieste

Peter M. Todd, Program in Cognitive Science and Department of Psychology, Indiana University at Bloomington

David Sloan Wilson, Department of Biological Sciences, Binghamton University

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ROBERT BOYD & PETER J. RICHERSON

Culture, Adaptation, and Innateness

It is almost 30 years since the sociobiology controversy burst into full bloom. The modern theory of the evolution of animal behavior was born in the mid-1960s with Bill Hamilton's seminal essays on inclusive fitness and George Williams's book *Adaptation and Natural Selection*. The following decade saw an avalanche of important ideas on the evolution of sex ratio, animal conflicts, parental investment, and reciprocity, setting off a revolution in our understanding of animal societies, a revolution that is still going on today. By the mid-1970s, Richard Alexander, E. O. Wilson, Napoleon Chagnon, Bill Irons, and Don Symons, among others, began applying these ideas to understand human behavior. Humans are evolved creatures, and quite plausibly the same evolutionary forces that shaped the behavior of other animals also molded our behavior. Moreover, the new theory of animal behavior—especially kin selection, parental investment, and optimal foraging theory—seemed to fit the data on human societies fairly well.

The reaction from much of the social sciences was, to put it mildly, negative. While the causes of this reaction are complex (Segerstråle, 2000), one key is that most social scientists thought about these problems in terms of nature versus nurture. On this view, biology is about nature; culture is about nurture. Some things, like whether you have sickle-cell anemia, are determined by genes—nature. Other things, like whether you speak English or Chinese, are determined by the environment—nurture. Evolution shapes innate genetically determined behaviors, but not behaviors acquired through learning. Social scientists knew that culture plays an overwhelmingly important role in shaping human behavior, and since culture is learned, evolutionary theory has little to contribute to the understanding of human behavior. This conclusion, and the reasoning behind it, remains the conventional wisdom in much of social science.

It is also deeply mistaken. Traits *do* vary in how sensitive they are to environmental differences, and it is sensible to ask whether differences in traits are mainly due to genetic differences or differences in the environment. However, the answer you get to this question tells you *nothing* about whether the traits in question have been shaped by natural selection. Every aspect of phenotype of every organism results from the interaction of genetic information stored in the developing organism and the properties of its environment. If we want to know why the organism develops one way in one environment and a different way in a different environment, we have to find out how natural selection and other evolutionary processes have shaped the developmental process of the organism. This logic applies to any trait, learned or not, and has been successful when applied to understand learned behavior in a wide range of species.

As a consequence, the evolutionary social science community by and large rejected the idea that culture makes any fundamental difference in the way that evolutionary thinking should be applied to humans. The genes underlying the psychological machinery that gives rise to human behavior were shaped by natural selection, so the machinery *must* have led to fitness-enhancing behavior, at least in ancestral environments. If it goes wrong in modern environments it is not culture that is the culprit, but the fact that our evolved, formerly adaptive psychology "misfires" these days. Over the last 20 years, two healthy research traditions have grown up in evolutionary social science, human behavioral ecology and evolutionary psychology, which study human behavior with little attention to the effects of culture.

In this essay we argue that both sides in this debate got it wrong. Culture profoundly alters human evolution, but not because culture is learned. Rather, culture entails a novel evolutionary trade-off. Social learning allows human *populations* to accumulate reservoirs of adaptive information over many generations, leading to the cumulative cultural evolution of highly adaptive social institutions and technology. Because this process is much faster than genetic evolution, it allows human populations to evolve cultural adaptations to local environments, an ability that was a masterful adaptation to the chaotic, rapidly changing world of the Pleistocene. However, the same psychological mechanisms that create this benefit *necessarily* come with a built-in cost. To get the benefits of social learning, humans have to be credulous, for the most part accepting the ways they observe in their society as sensible and proper. Such credulity opens up human minds to the spread of maladaptive beliefs. Tinkering with human psychology can lessen this, but it cannot be eliminated without also losing the adaptive benefits of cumulative cultural evolution.

In this essay, we begin by sketching the view of culture that is current among many in the evolutionary social science community. Then we summarize the evidence that human adaptation depends crucially on the cumulative cultural adaptation. Next we expand on our argument that cumulative cultural adaptation entails an unavoidable trade-off. We conclude by discussing how cumulative cultural evolution may breathe some new life into the idea of innateness.

1 Evolutionary Psychology: Culture as a Library of Works Written by Adapted Minds

In their critique of the "standard social science model," John Tooby and Leda Cosmides (1992, pp. 115–6) introduced the distinction between "epidemiological" and "evoked" culture. "Epidemiological culture" refers to what most people mean by the word *culture*—differences between people that result from different ideas or values acquired from the people around them. "Evoked culture" refers to differences that are not transmitted at all, but rather are evoked by the local environment. Cosmides and Tooby argue that much of what social scientists call culture is evoked. They ask their readers to imagine a jukebox with a large repertoire of records and a program that causes a certain record to be played under particular local conditions. Then, all the jukeboxes in Brazil will play one tune, and all those in England will play another tune, because the same program orders up different tunes in different places. Tooby and Cosmides believe that anthropologists and historians overestimate the importance of epidemiological culture, and emphasize that much human variation results from genetically transmitted information that is evoked by environmental cues.

They are led to this conclusion by their belief that learning requires a modular, information-rich psychology. Tooby and Cosmides (1992) and some other evolutionary psychologists (Gallistel, 1990) argue that "domain-general" learning mechanisms like classical conditioning and other forms of correlation detection are inefficient. When the environment confronts generation after generation of individuals with the same range of adaptive problems, selection will favor special-purpose, domain-specific cognitive modules that focus on particular environmental cues and then map these cues onto a menu of adaptive behaviors. Evidence from developmental cognitive psychology provides support for this picture of learning—small children seem to come equipped with a variety of preconceptions about how the physical, biological, and social worlds work, and these preconceptions shape how they use experience to learn about their environments (Hirschfeld & Gelman, 1994). Evolutionary psychologists (and others; see Sperber & Hirschfeld, 2004) think the same kind of modular psychology shapes social learning. They argue that culture is not "transmitted"—children make *inferences* by observing the behavior of others, and the kind of inferences they make are strongly constrained by their evolved psychology. Linguist Noam Chomsky's argument that human languages are shaped by a genetically transmitted universal grammar is the best known version of this idea, but evolutionary psychologists think virtually all cultural domains are similarly structured.

Anthropologist Pascal Boyer's (1994) account of the nature of religious belief provides a good example. Boyer worked among the Fang, a group in Cameroon and Gabon, who have elaborate beliefs about ghosts. For the Fang, ghosts are malevolent beings that want to harm the living; they are invisible, they can pass through solid objects, and so on. Boyer argues that most of what the Fang believe about ghosts is not transmitted; rather it is based on the innate, epistemological assumptions that underlie all cognition. Once young Fang children learn that ghosts are sentient beings, they don't need to learn that ghosts can see or that they have beliefs and desires—these components are provided by cognitive machinery that reliably develops in every environment. Like Cosmides and Tooby, Sperber, Atran, and others, Boyer thinks that many putatively cultural religious beliefs arise because different environmental cues evoke different innate information. Our California neighbors believe in angels instead of ghosts because they grew up in an environment in which people talked about angels. However, most of what they know about angels comes from the same cognitive machinery that gives rise to Fang beliefs about ghosts, and the information that controls the development of this machinery is stored in the genome.

Understand that these authors do not deny that epidemiological culture plays a role in shaping human behavioral variation. They are clear that some differences between groups are due to beliefs and values that are stored in human minds and transmitted from person to person and thus preserved through time, and agree that models from epidemiology and population genetics may help explain how ideas spread through populations. However, to explain the *content* of such ideas, evolutionary psychologists emphasize the information processing properties of human minds. For example, Steve Pinker writes:

> The striking features of cultural products, namely their ingenuity, beauty, and truth (analogous to an organism's complex design), comes from the mental computations that "direct"—that is, invent—the "mutations", and that "acquire"—that is, understand, the "characteristics." . . . Models of cultural transmission do offer insight on other features of cultural change, particularly their demographics. . . . They explain how ideas become popular, but not where ideas come from. (1997, pp. 209–10)

The idea here is that complex cultural adaptations do not arise gradually, as they do in genetic evolution. New symphonies don't appear bit by bit as a consequence of the differential spread and elaboration of slightly better and better melodies. Rather they emerge from people's minds, and their functional complexity arises from the action of those minds. The same goes for all aspects of culture—art, ritual, and technology—or at least so Pinker thinks. Culture is useful and adaptive because populations of human minds store the best efforts of previous generations of minds.

On this view, transmitted culture is like a library. Libraries preserve knowledge created in the past. Librarians shape the contents of libraries as they decide which books are bought and which are discarded. But knowing about libraries and librarians does not help us understand the complex details of plot, character, and style that distinguish a masterpiece from a potboiler. To understand these things, you have to understand the minds of the authors who have written these books. In the same way, cultures store ideas and inventions, and people's "decisions" (often unconscious) about which ideas to adopt and which to reject shape the content of a culture. Evolutionary theories may help explain why, for example, traditional Fang religious beliefs are replaced by alternative beliefs like Christianity or Islam. However, to understand the structures of complex, adaptive cultural practices, religious beliefs, tools, or institutions, you have to understand the evolved psychology of the mind that gave rise to that complexity, and how that psychology interacts with its environment.

Students of the history of biology will recognize this picture of cultural evolution as similar to a frequently popular, but incorrect, theory of genetic evolution. Very few of Darwin's contemporaries accepted (or even understood) his idea that adaptations arose through the gradual accumulation of small variations. Some of his most ardent supporters, like T. H. Huxley, thought that new types arose in big jumps, and then natural selection determined which types spread. In this century, Richard Goldschmidt and the late Steven J. Gould, among others, championed this theory of evolution. It is wrong, because the likelihood that a complex adaptation will arise by chance is nil. Of course, this objection does have not any force for cultural evolution, precisely because innovations are highly nonrandom, and thus it is quite plausible that cultural evolution mainly involves the culling of innovations, innovations whose adaptive complexity can be understood only in terms of human psychology.

2 Culture Often Evolves by the Accumulation of Small Variations

This picture is a useful antidote to the view that cultural evolution is just like genetic evolution. Cultural variation is not transmitted in the same way as genes—ideas are not poured from one head into another. These evolutionary psychologists are surely right that every form of learning, including social learning, requires an information-rich innate psychology, and that some of the adaptive complexity we see in cultures around the world stems from this information. Nor does culture evolve through the gradual accumulation of "memes," gene-like particles that arise through blind mutations and spread by natural selection. Innovations are not purely random, and our evolved psychology certainly must influence the rate and direction of cultural adaptation. Plausibly some cultural adaptations, especially relatively simple ones, are invented in one step by individuals. Only a few good easy ways to tie a knot that makes a loop in the end of a rope are currently known. Some individual might invent a new and perhaps better one.

However, we think that it is much less plausible that most complex cultural adaptations, things like kayaks and institutions like hxaro exchange, arise in this way. Isaac Newton famously remarked "If I have seen further it is by standing on the shoulders of giants." For most innovators in most places at most times in human history, a different metaphor is closer to the truth. Even the greatest human innovators are, in the great scheme of things, midgets standing on the shoulders of a vast pyramid of other midgets. Individual minds rarely give birth to complex cultural adaptations. The evolution of languages, artifacts, and institutions can be divided up into many small steps, and during each step, the changes are relatively modest. No single innovator contributes more than a small portion of the total, as any single gene substitution contributes only marginally to a complex organic adaptation.

The history of technology shows that complex artifacts like watches are not hopeful monsters created by single inventors (Basalla, 1988). The watchmakers' skills have been built up piecemeal by the cumulative improvement of technologies at the hands of many innovators, each contributing a small improvement to the ultimately amazing instrument. Many competing innovations have been tried out at each step, most now forgotten except by historians of technology. A little too loosely, we think, historians of technology liken invention to mutation because both create variation and compare the rise of the successful technology to prominence with the action of natural selection. Forget watches for a moment. The historian of technology Henry Petroski (1992) documents how even simple modern artifacts like forks, pins, paper clips, and zippers evolve haltingly through many trials, some to capture the market's attention and others to fall by the wayside. No one knows how many failed designs have languished on inventors' workbenches. Cultural evolution is more complicated than bare-bones random variation and selective retention. To anticipate our argument, the decisions, choices, and preferences of individuals act at the population level as forces that shape cultural evolution, along with other processes like natural selection. We urge great care with loose analogies to mutation and selection because there are several distinct processes rooted in human psychology that lead to the accumulation of beneficial cultural variations, each with a distinctive twist of its own and none exactly like natural selection.

While human innovations are not like random mutations, they have been, until recently, small, incremental steps. The design of a watch is not the work of an individual inventor but the product of a watchmaking tradition from which the individual watchmaker derives most, but not quite all, of his designs. This is not to take anything away from the real heroes of watchmaking innovation, like John Harrison. Harrison delivered a marine chronometer accurate enough to calculate longitude at sea to the British Board of Longitude in 1759. He used every device of the standard clockmaker's art and a number of clever tricks borrowed from other technologies of the time, such as using bimetallic strips (you have seen them coiled behind the needles of oven thermometers and thermostats) for compensating the critical temperature-sensitive timekeeping elements of his chronometers. His achievement is notable for the sheer number of clever innovations he made—the bimetallic temperature compensators, a superb escapement, jewel bearings requiring no lubrication, substitutes for the pendulum. Also notable is his extraordinary personal dedication to the task. By dint of 37 years of unremitting effort and a first-rate mechanical mind, sustained by incremental payments against a British Admiralty prize he was a good candidate to win, he made a series of ever smaller, better, more rugged seagoing clocks. Eventually he delivered "Number 4," with an accuracy of better than one-fortieth of a second per day, significant improvement over one minute per day for the best watches of his day (Sobel, 1995). Only the rarest of inventors makes an individual contribution of this magnitude. Yet, like every great inventor's machine, Number 4 is a beautiful homage to the art and craft of Harrison's predecessors and colleagues as much as to his own genius. Without a history of hundreds or thousands of ancient and mostly anonymous inventors, Harrison would not even have conceived the idea of building a marine chronometer, much less succeeded in doing so. William Paley's famous argument from design would better support a polytheistic pantheon than his solitary Christian Creator; it takes many designers to make a watch.

Consider a much simpler nautical innovation, the mariners' magnetic compass. Its nameless innovators must have been as clever as James Watt, Thomas Edison, Nikola Tesla, and the other icons of the Industrial Revolution whose life stories we know so much better. First, someone had to notice the tendency of small magnetite objects to orient in the earth's weak magnetic field in nearly frictionless environments. The first known use of this effect was by Chinese geomancers, who placed polished magnetite spoons on smooth surfaces for purposes of divination. Later, Chinese mariners built small magnetite objects or magnetized needles that could be floated on water to indicate direction at sea. Ultimately, Chinese seamen developed a dry compass with the needle mounted on a vertical pin bearing, like a modern toy compass. Europeans acquired this form of compass in the late medieval period. European seamen developed the card compass, in which a large disk was attached to the magnets and marked with 32 points. This compass was not merely used to indicate direction but was rigidly mounted at the helmsman's station, with the position of the bow of the ship marked on the case. Now the helmsman could steer a course as accurate as one sixty-fourth of a circle by aligning the bow mark on the case with the appropriate compass point. Compass makers learned to adjust iron balls near the compass to zero out the magnetic influence from the ship, an innovation that was critical after steel hulls were introduced. The first such step was a small one, replacing the iron nails of the compass box with brass screws. Later, the compass was filled with a viscous liquid and gimbaled to damp the ship's motion, making the helmsman's tracking of the correct heading still more accurate. Even such a relatively simple tool as the mariner's compass was the product of numerous innovations over centuries and in space across the breadth of Eurasia (Needham, 1979).

Other aspects of culture are similar. Take churches. Modern American churches are sophisticated organizations for supplying certain kinds of social services to their parishioners. The successful ones derive from a long tradition of incorporating good ideas and abandoning bad ones. Surprisingly, one of the unsuccessful ideas turns out to be hiring educated clergy. College-educated clergy are good intellectuals but too frequently deadly dull preachers, consumed with complex doubts about the traditional verities of Christian faith. In the United States, successful religious innovation is handsomely rewarded, due to the free-market character of Protestant religious institutions. Many ambitious religious entrepreneurs organize small sects mostly drawing upon a set of stock themes called Fundamentalism. Only a tiny fraction of sects expand beyond the original cohort recruited by the initial innovator. The famous celibate Shakers are an example of a sect that failed to recruit followers, but there have been many others. A much smaller number are successful and have grown to become major religious institutions, largely replacing traditional denominations. The Methodists and the Mormons are examples of very successful sects that became major churches.

Religious innovators build in small steps. Mormon theology is very different from that of most of American Protestantism. Nevertheless, John Brooke (1994) shows how Joseph Smith's cosmology mixes frontier Protestantism with hermetic ideas, Masonry, divination schemes for finding treasure, and spiritual wifery (polygamy). He traces the spread of these ideas from Europe to specific families in Vermont and New York where Smith and his family resided. Smith invented little and borrowed much, although we properly credit him with being a great religious innovator. His innovations were, like Harrison's, large compared to those introduced by most other ambitious preachers.

Individuals are smart, but most of the cultural artifacts that we use, the social institutions that shape our lives, and the languages that we speak, are far too complex for even the most gifted innovator to create from scratch. Religious innovations are a lot like mutations, and successful religions are adapted in sophisticated ways beyond the ken of individual innovators. The small frequency of successful innovations suggests that most innovations degrade the adaptation of a religious tradition and only a lucky few improve it. We don't mean to say at that complex cultural institutions can't ever be improved by the application of rational thought. Human innovations are not *completely* blind, and if we understood cultural evolutionary processes better, they would be less blind. But human cultural institutions are very complex and rarely have been improved in large steps by individual innovators.

3 Culture Permits Adaptation to a Wide Range of Environments without Domain-Specific Modules

Cultural adaptation has played a crucial role in human evolution. Human foragers adapted to a vast range of environments. The archeological record indicates that Pleistocene foragers occupied virtually all of Africa, Eurasia, and Australia. The data on historically known hunter-gatherers suggests that to exploit this range of habitats, humans used a dizzying diversity of subsistence practices and social systems. Consider just a few examples. The Copper Inuit lived in the high Arctic, spending summers hunting near the mouth of the MacKenzie River and the long dark months of the winter living on the sea ice and hunting seals. Groups were small and highly dependent on men's hunting. The !Xo lived in the central Kalahari. Women's collecting of seeds, tubers, and melons accounted for most of their calories. Men hunted impala and oryx. They survived fierce heat and lived without surface water for months at time. Both the !Xo and the Copper Inuit lived in small, nomadic bands linked together in large band clusters by patrilineally reckoned kinship. The Chumash lived on the productive California coast around present-day Santa Barbara, gathering shellfish and seeds and fishing the Pacific from great plank boats. They lived in large permanent villages with division of labor and extensive social stratification.

This range of habitats, ecological specializations, and social systems is much greater than that of any other animal species. Big predators like lions and wolves have very large ranges compared to other animals, but lions never extended their range beyond Africa and the temperate regions of western Eurasia; wolves were limited to North America and Eurasia. The diet and social systems of such large predators are similar throughout their range. They typically capture a small range of prey species using one of two methods: they wait in ambush, or combine stealthy approach and fast pursuit. Once the prey is captured, they process it with tooth and claw. The basic simplicity of the lives of large carnivores is captured in a Gary Larson cartoon in which a *Tyrannosaurus rex* contemplates its monthly calendar—every day has the notation "Kill something and eat it." In contrast, human hunters use a vast number of methods to acquire and process a huge range of prey species, plant resources, and minerals. For example, Hillard Kaplan, Kim Hill, and their coworkers at the University of New Mexico have observed the Aché, a group of foragers who live in Paraguay, take 78 different species of mammals, 21 species of reptiles, 14 species of fish, and over 150 species of birds using an impressive variety of techniques that depend on the prey, the season, the weather, and many other factors. Some animals are tracked—a difficult skill that requires a great deal of ecological and environmental knowledge. Others are called by imitating the prey's mating or distress calls. Still others trapped with snares or traps or smoked out of burrows. Animals are captured and killed by hand, shot with arrows, clubbed, or speared (Kaplan et al., 2000).

And this is just the Aché—if we included the full range of human hunting strategies, the list would be much longer. The lists of plants and minerals used by human foragers are similarly long and diverse. Making a living in the Arctic requires specialized knowledge: how to make weatherproof clothing, how to provide light and heat for cooking, how to build kayaks and umiaks, how to hunt seals through holes in the sea ice. Life in the central Kalahari requires equally specialized but quite different knowledge: how to find water in the dry season, which of the many kinds of plants can be eaten, which beetles can be used to make arrow poison, and the subtle art of tracking game. Survival might have been easier on the balmy California coast, yet specialized social knowledge was needed to succeed in hierarchical Chumash villages, compared to the small egalitarian bands of the Copper Inuit and the !Xo.

So maybe humans are more variable than lions, but what about other primates? Don't chimpanzees have culture? Don't different populations use different tools and foraging techniques? There is no doubt that great apes do exhibit a wider range of foraging techniques, more complex processing of food, and more tool use than other mammals (Byrne, 1999). However, these techniques play a much smaller role in great ape economy than they do in the economies of human foragers. Anthropologists Kaplan, Hill, and their coworkers (2000) compare the foraging economies of a number of chimpanzee populations and human and human foraging groups. They categorize resources according to the difficulty of acquisition: *Collected foods* like ripe fruit and leaves can be simply collected from the environment and eaten. *Extracted foods* must be processed before they can be eaten. Examples include fruits in hard shells, tubers or termites that are buried deep underground, honey hidden in hives in high in trees, and plants that contain toxins that must be extracted before they can be eaten. *Hunted foods* come from animals, usually vertebrates, that must be caught or trapped. Chimpanzees are overwhelmingly dependent on collected resources, while human foragers get almost all of their calories from extracted or hunted resources.

Humans can live in a wider range of environments than other primates because culture allows the relatively rapid accumulation of better strategies for exploiting local environment compared to genetic inheritance. Consider "learning" in the most general sense; every adaptive system "learns" about its environment by one mechanism or another. Learning involves a tradeoff between accuracy and generality. Learning mechanisms generate contingent behavior based on "observations" of the environment. The machinery that maps observations onto behavior is the "learning mechanism." One learning mechanism is more accurate than another in a particular environment if it generates more adaptive behavior in that environment. A learning mechanism is more general than another if it generates adaptive behavior in a wider range of environments. Typically, there is a trade-off between accuracy and generality, because every learning mechanism requires prior knowledge about which environmental cues are good predictors of the actual state of the environment and what behaviors are best in each environment. The more detailed and specific such knowledge is for a particular environment, the more accurate is the learning rule. Thus for a given amount of stored knowledge, a learning mechanism can either have detailed information about a few environments, or less detailed information about many environments.

In most animals, this knowledge is stored in the genes, including, of course, the genes that control individual learning. Consider the following thought experiment. Pick a wide-ranging primate species, let's say baboons. Then capture a group of baboons, and move them to another part of the natural range of baboons in which the environment is as different as possible. You might, for example, transplant a group from the lush wetlands of the Okavango Delta to the harsh desert of western Namibia. Next, compare their behavior to the behavior of other baboons living in the same environment. We believe that after a little while, the experimental group of baboons would be quite similar to their neighbors. The reason that the local and transplanted baboons would be similar, we think, is the same reason that baboons are less variable than humans: they acquire a great deal of information about how to be a baboon genetically—it is hard wired. To be sure, they have to learn where things are, where to sleep, which foods are desirable, and which are not, but they can do this without contact with already knowledgeable baboons because they have the basic knowledge built in. They can't learn to live in temperate forests or arctic tundra, because their learning systems don't include enough innate information to cope with those environments.

Human culture allows learning mechanisms to be both more accurate and more general, because *cumulative* cultural adaptation provides accurate and more detailed information about local environments. Evolutionary psychologists argue that our psychology is built of complex, information-rich, evolved modules that are adapted for the hunting and gathering life that almost all humans pursued up to a few thousand years ago. Fair enough, but *individual* humans can't learn how to live in the Arctic, the Kalahari, or anywhere else. The reason is that our information-rich, evolved psychology doesn't contain the necessary information. Think about being plunked down on an Arctic beach with a pile of driftwood and sealskins and trying to make a kayak. You already know a lot—what a kayak looks like, roughly how big it is, and something about its construction. Nonetheless, you would almost certainly fail. (We're not trying to belittle you; we've read a lot about kayak construction, and we'd make poor specimens, if we were lucky.) And, supposing you did make a passable kayak, you'd still have a dozen or so similar tools to master before you could make a contribution to the Inuit economy. And then there are the social mores of the Inuit to master. The Inuit could make kayaks, and do all the other things that they needed to do to stay alive, because they could make use of a vast pool of useful information available in the behavior and teachings of other people in their population.

The reason the information contained in this pool is adaptive is that combination of learning and cultural transmission leads to relatively rapid, cumulative adaptation. Populations of people connected over time by social learning can accumulate the solutions to problems that no individual could do on his or her own. Individuals don't have to be too smart, because simple heuristics like correlation detection and imitation of the successful can produce clever adaptations when averaged over a population of individuals and over generations of time. Even if most individuals imitate with only the occasional application of some simple heuristic, many individuals will be giving traditions a nudge in an adaptive direction, on average. Cultural transmission preserves the many small nudges, and exposes the modified traditions to another round of nudging. Very rapidly by the standards of ordinary evolutionary time, and more rapidly than evolution by natural selection alone, weak, general-purpose decision-making forces generate new adaptations. The complexity of cultural traditions can explode to the limits of our capacity to imitate or be taught them, far past our ability to make careful, detailed decisions about them. We let the population-level process of cultural evolution do the heavy lifting for us.

4 Cumulative Cultural Adaptation Involves a Trade-Off

As far as many evolutionary social scientists are concerned, Richard Dawkins is way up in the pantheon of contemporary evolutionary thinkers. (For sure, he makes most top five lists.) Nonetheless, most place little stock in Dawkins's argument about rogue memes, regarding it as an imaginative device for explaining the nature of replicators rather than a serious proposal about human cultural evolution. Instead, most evolutionary social scientists tend to think that all forms of learning are processes whereby the organism exploits statistical regularities in the environment so as to develop a phenotype that is well suited to the existing environment. Over time, selection shapes psychology so that it uses predictive cues to generate adaptive behavior. Social learning is just another learning mechanism that exploits cues available in the social environment. As a result, to oversimplify just a bit, most evolutionary social scientists expect people to learn things that were good for them in the Pleistocene and perhaps in the smaller scale human societies that resemble those of the Pleistocene. Adaptation arises from the information-processing capacities built into the human brain by natural selection acting on genes. These mechanisms may give rise to maladaptive behaviors nowadays, but it's got nothing to do with culture and everything to with the fact that "environments" are far outside of the parameters to which our innate decision-making talents are calibrated.

We think this argument neglects an important trade-off. Selection cannot create a psychology that gets you only the adaptations and always rejects maladaptive variants. Why not? Because of the accuracy–generality trade-off. General-purpose learning has to be inaccurate to have bearable costs. Individuals, having let the population do the thinking, are in no position to accurately assess the results. Think of using the taste of a substance as a guide to whether it is edible or not. Many toxic plant compounds have a bitter taste. If you are tempted to eat something, and it is bitter, you are well advised to reject it as food. On the other hand, many toxins do not taste bitter, so bitterness is no infallible guide to edibility. Further, many bitter plants, for example acorns, can be rendered edible by cooking or leaching. Further still, some bitter-tasting plant compounds have medicinal value. People can actually grow fond of some bitter-tasting food and drink. Think gin-and-tonic. A bitter taste is only a rough-and-ready guide to what is edible and what is not. In principle, you could do much better if you had a modern food chemist's laboratory on the tip of your tongue, one that could separately sense every possible harmful and helpful plant compound rather than having just four very general taste senses. Some animals are much better at these things than humans—we have a rather poor sense of smell, for example. But the number of natural organic compounds is immense, and selection favors compromises that *usually* result in adaptive behavior and don't cost too much. A fancy sense of smell requires a long muzzle to contain the sensory epithelium where all those fancy sensory neurons are deployed, and plenty of blood flow to feed them. Bitter taste is a reasonably accurate and reasonably general sense for screening substances for edibility, but it is far from a food chemist's laboratory or a dog's nose. To get the good, you have to risk adopting the bad, because the evaluative machinery the brain deploys to exercise the various biases is necessarily limited. Let's see why.

Tooby and Cosmides (1992, p. 104) define an adaptation as "a reliably developing structure in the organism, which, because it meshes with the recurrent structure of the world, causes the solution to an adaptive problem." They give behavioral examples like inbreeding avoidance, the avoidance of plant toxins during pregnancy, and the negotiation of social exchange. Evolutionary psychologists are prone to wax eloquent over marvelous cognitive adaptations created by natural selection. And they are right to marvel; everyone should. Natural selection has created brains and sensory systems that easily solve problems that stump the finest engineers. Making robots that can do anything sensible in a natural environment is exceedingly difficult, yet a tiny ant with a few thousand neurons can meander over rough ground hundreds of meters from its nest, find food, and return in a beeline to feed its sisters. Humans are able to solve many astoundingly difficult problems as they go through daily life because natural selection has created numerous adaptive information-processing modules in the human brain. Notably, the best examples involve tasks that have confronted every member of our lineage in every environment over tens of millions of years of evolution, things like visual processing and making inferences about causal processes. The list of well-documented examples that apply to humans alone is short, and once again these psychological adaptations that provide solutions to problems that every human, if not every advanced social vertebrate, faces—things like inbreeding avoidance, social contract reasoning, mate choice, and language learning.

Cultural evolution also gives rise to marvelous adaptations. However, they are typically solutions to problems posed by *particular* environments. Consider, once again, the kayaks built and used by the Inuit, Yupik, and Aleut foragers of the North American Arctic. By Tooby and Cosmides's definition, kayaks are clearly adaptations. These peoples' subsistence was based on hunting seals (and sometimes caribou) in Arctic waters. A fast boat was required to get close enough to these large animals to reliably hit and kill them with a harpoon or spear. Kayaks are a superb solution to this adaptive problem. Their slim, efficient hull design allows sustained paddling at up to 7 knots. They were extremely light (sometimes less than 15 kg), yet strong and seaworthy enough to safely navigate rough, frigid northern seas. They were also "reliably developing"—every successful hunter built or acquired one—until firearms allowed hunting from slower, but more stable, and more widely useful umiaks. For at least 80 generations, people born into these societies acquired the skills and knowledge necessary to construct these boats from available materials—bone, driftwood, animal skin, and sinew.

Certainly, no evolved "kayak module" lurks in the recesses of the human brain. People have to acquire the knowledge necessary to construct a kayak using the same evolved psychology that people use in other environments to master other crucial technologies. No doubt this *requires* an evolved "guidance system." People must be able to evaluate alternatives, to know that boats that don't sink and are easy to paddle are better than leaky, awkward designs. They have to be able to judge, to some significant degree, whose boats are best, and when and how to combine information from different sources. The elaborate psychological machinery that allows children to bootstrap any knowledge of the world is also clearly crucial. People can't learn to make kayaks unless they already understand something about the properties of materials, how to categorize plants and animals, the manual skills to make and use tools, and so on and on. This guidance system is not "domain general," in the sense that it allows people to learn *anything*. It is highly specific to life on earth, in a regime of middle-sized objects, relatively moderate temperatures, living creatures, humanmade artifacts, and small social groups. However, it *is* domain general in the sense that there is nothing in our evolved psychology that contains the specific details that make a difference in the case of kayaks—knowledge of the dimensions, materials, and construction methods that make the difference between constructing a 15-kilogram craft that safely skims across the arctic seas and death by drowning, hypothermia, or starvation. These crucial details were stored in the brains of each generation of Inuit, Yupik, and Aleut peoples. They were preserved and improved by the action of a population of evolved psychologies, but using mechanisms that are equally useful for preserving a vast array of other kinds of knowledge.

Such widely applicable learning mechanisms are necessarily more error prone than highly constrained, domain specific ones. As Tooby and Cosmides (1992, pp. 104–8) have emphasized, broad general problems are much more difficult to solve than simple constrained ones. A kayak is a highly complex object, with many different attributes or "dimensions." What frame geometry is best? Should there be a keel? How should the components of the frame be joined? What kind of animal provides the best skin? Which sex? Harvested at what time of year? Designing a good kayak means finding one of the very few combination of attributes that successfully produces this highly specialized boat. The number of combinations of attributes grows geometrically as the number of dimensions increases, rapidly exploding into an immense number. The problem would be much easier if we had a kayak module that constrained the problem, so we would have fewer choices to evaluate. However, evolution cannot adopt this solution, because environments are changing far too quickly and are far too variable spatially for selection to shape the psychologies of arctic populations in this way. The same learning psychology has to do for kayaks, oil lamps, waterproof clothing, snow houses, and all the other technology necessary to survive in the Arctic. It also has to do for birch bark canoes, reed rafts, dugout canoes, planked rowboats, rabbit drives, blowguns, hxaro exchange, and the myriad marvelous, specialized, environment-specific technologies that human hunter-gatherers have culturally evolved.

For the same reason that it is impossible to build a learning device that is both general purpose and powerful, selection cannot shape social learning mechanisms so that they reliably reject maladaptive beliefs over the whole range of human experience. A young Aleut cannot readily evaluate whether the kayaks he sees his father and cousins using are better than alternative designs. He can try one or two modifications and see how they work, and he can compare the performance of the different designs he sees. But small samples and noisy data will severely limit his ability to optimize kayak design by individual effort. From the point of view of an isolated individual, such general-purpose learning mechanisms are both costly and weak. The repeated action of weak domain-general mechanisms by a population of individuals connected by cultural inheritance over many generations can generate complex adaptations like kayaks, but individuals must adopt what they observe with only marginal modifications. As a result, we may often adopt maladaptive behaviors.

When it is difficult to determine which cultural variant is best, natural selection favors heavy reliance on imitating others and low confidence in one's own experience (Boyd & Richerson, 1985, 1988). The natural world is complex and variable from place to place and time to time. Is witchcraft effective? What causes malaria? What are the best crops to grow in a particular location? Are natural events affected by human pleas to their governing spirits? The relationship between cause and effect in the social world is often equally hard to discern. What sort of person should one marry? How many husbands are best? Tibetan women often have two or three. What mixture of devotion to work and family will result in the most happiness or the highest fitness? Students of the diffusion of innovations note that "trialability" and "observability" are some of the most important regulators of the spread of ideas from one culture to another (Rogers 1983, pp. 231–2). Many important cultural traits, including things like family organization, have low trialability and observability and are generally rather conservative. We act as if we know that sensible choices about such behaviors are hard to make and that we are liable to err if we try to depart far from custom.

As the effects of biases weaken, social learning becomes more and more like a system of inheritance. Much of an individual's behavior is thus a product of beliefs, skills, ethical norms, and social attitudes that are acquired from others with little, if any, modification. To predict how individuals will behave, one must know something about their cultural milieu. This does not mean that the evolved predispositions that underlie individual learning become unimportant. Without the ability to taste and dislike bitter substances, and many similar innate senses and predilections, cultural evolution would be uncoupled from genetic evolution. It would provide none of the fitness-enhancing advantages that normally shape cultural evolution and produce adaptations. However, once cultural variation is heritable, it can respond to selection for behaviors that conflict with genetic fitness. Selection on genes that regulate the cultural system may still favor the ability and inclination to rely on imitation because it is beneficial on average. Selection will balance the advantages of imitation against the risk of catching pathological superstitions. Our propensity to adopt dangerous beliefs may be the price we pay for the marvelous power of cumulative cultural adaptation. As the saying goes, you get what you pay for.

5 Culture, Adaptation, and Innateness

We conclude by arguing that this way of thinking about cultural adaptation has implications for the topic of this book, the notion of innateness.

One of Darwinism's central accomplishments is the explanation of design—spectacularly improbable "organs of extreme perfection" like the eyes of animals are explained by the gradual accumulation of the genes that give rise to these traits through the process of natural election. While the development of such complex, highly functional traits always depends on the interaction of genes and environment, the design information that causes functional eyes to develop generation after generation comes from the genes. The eyes of a cod and an octopus are similar in design (Land & Nilsson, 2002): both have spherical lenses that are located about 2.5 lens radii from the retina; in both, the index of refraction of those lenses gradually increases toward their center. In both species, the eyes are oriented by six muscle groups, one pair for each independent axis of rotation, and in both, different muscles adjust the focus by moving the lens. These structures evolved independently, and develop quite differently. To be sure, environmental inputs will be crucial—the development of functional eyes depends on light input, for example. But the design of these eyes can only be explained in terms of natural selection acting on the genes that control this development. Put another way, design doesn't come from the environment; it is innate.

The same argument applies to complex, adaptive behavior in most organisms. Like the development of eyes, behavior arises from the interaction of the environment with innate, genetically transmitted developmental mechanisms, especially various forms of learning. Simple, relatively domain-general mechanisms such as classical conditioning can shape behavior in adaptive ways, but, if evolutionary psychologists are right, they are unlikely to generate the many forms of highly complex adaptive behavior seen in nature. Behaviors like the long-distance stellar navigation of indigo buntings or the spectacular feats of memory of acorn woodpeckers require a highly structured, information-rich psychology. The design latent in this psychology comes from the genes, and the details of this design are explained by the action of natural selection.

The cumulative cultural evolution of spectacular human adaptations like kayaks, bows and arrows, and the like complicates this picture. Now there are two processes that generate design, natural selection acting on genes, and a variety of processes acting on culturally transmitted variation. If we are right, cultural adaptation has allowed the human species to adapt to a wide range of environments *because* its design information is stored in brains, not genes. By linking the efforts of many people over many generations, relatively crude, relatively domain-general mechanisms can generate cultural adaptations to a wide range of environments much more rapidly than natural selection can generate genetic adaptations. True, cultural adaptation depends on the evolved psychological mechanisms that allow social learning, and, again if the evolutionary psychologists are right, the learning mechanisms that shape cultural adaptations over time depend on a large number of evolved psychological mechanisms. However, unlike other forms of learning, the design information that generates the adaptations is not stored in the genes.

Thus in cultural organisms it becomes interesting to ask, in any particular case, where does the design come from, "inside" from genes shaped by natural selection, or "outside" from adaptive, cumulatively evolved information stored in other human brains? The right question is not Is it nature or nurture? but Is it genes or culture? The answer to this question is interesting, because the dynamic processes that cause cultural adaptation can lead to systematically different outcomes from those of natural selection acting on genetic variation (Richerson & Boyd, 2005). Some of these differences are adaptive. Culture evolves faster than genes and can track more rapidly varying environments. Symbolic marking divides human populations up into semiisolated pseudospecies, as it were, that adapt finely to their local environment, resisting the cultural analog of gene flow from other environments. Some of these differences are maladaptive. The fact that much culture is transmitted nonparentally allows considerable scope for the evolution of selfish cultural variants. A theory of how evolving genes interact with environments to determine behavior is adequate for most organisms, but in humans, evolving culture is an essential part of the explanatory problem.

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