Culture Is Essential

The American South has long been more violent than the North. Colorful descriptions of duels, feuds, bushwhackings, and lynchings feature prominently in visitors' accounts, newspaper articles, and autobiographies from the eighteenth century onward. Statistics bear out these impressions. For example, over the period 1865–1915, the homicide rate in the South was ten times the current rate for the whole United States, and twice the rate in our most violent cities. Modern homicide statistics tell the same story.

In their book, *Culture of Honor*, psychologists Richard Nisbett and Dov Cohen argue that the South is more violent than the North because southern people have culturally acquired beliefs about personal honor that are different from their northern counterparts.¹ Southerners, they argue, believe more strongly than Northerners that a person's reputation is important and worth defending even at great cost. As a consequence, arguments and confrontations that lead to harsh words or minor scuffles in Amherst or Ann Arbor often escalate to lethal violence in Asheville or Austin.

What else could explain these differences? Some feature of the southern environment, such as its greater warmth, could explain why Southerners are more violent. Such hypotheses are plausible, and Nisbett and Cohen are at pains to test them. Northerners and Southerners might differ genetically, but this hypothesis is not very plausible. The settlers of the North and South came mostly from the British Isles and adjacent areas of northwestern Europe.² Human populations are quite well mixed on this scale.

Nisbett and Cohen support their hypothesis with an impressive range of evidence. Let's start with statistical patterns of violence. In the rural and small-town South, murder rates are elevated for arguments among friends and acquaintances, but not for killings committed in the course of other felonies. In other words, in the South men are more likely than Northerners to kill an acquaintance when an argument breaks out in a bar, but they are no more likely to kill the guy behind the counter when they knock off a liquor store. Thus, Southerners seem to be more violent than other Americans only in situations that involve personal honor. Competing hypotheses don't do so well: neither white per-capita income nor hot climate nor history of slavery explain this variation in homicide.

Differences in what people say about violence also support the "culture of honor" hypothesis. For example, Nisbett and Cohen asked people to read vignettes in which a man's honor was challenged—sometimes trivially (for example, by insults to his wife), and in other cases seriously (for example, by stealing his wife). Southern respondents were more likely than Northerners to say that violent responses were justified in all cases, and that one would "not be much of a man" unless he responded violently to insults. In the case of more serious affronts, southern respondents were almost twice as likely to say that shooting the perpetrator was justified.

Interestingly, this difference in behavior is not just talk; it can also be observed under the controlled conditions of the psychology laboratory. Working at the University of Michigan, Nisbett and Cohen recruited participants from northern and southern backgrounds, ostensibly to participate in an experiment on perception. As part of the procedure, an experimenter's confederate bumped some participants and muttered "Asshole!" at them. This insult had very different effects on southern and northern participants, as revealed by the next part of the experiment. Sometime after being bumped, participants encountered another confederate walking toward them down the middle of a narrow hall, setting up a little game of chicken. This confederate, a six-foot, three-inch, 250-pound linebacker on the UM football squad, was much bigger and stronger than any participant, and had been instructed to keep walking until either the participant stepped aside and let him pass or a collision was immanent. Northerners stepped aside when the confederate was six feet away, whether or not they had been insulted. Southerners who had not been insulted stepped aside when they were nine feet away from the confederate, while previously insulted Southerners continued walking until they were just three feet away. Polite, but

prepared to be violent, uninsulted Southerners take more care, presumably because they attribute a sense of honor to the football player and are careful not to test it. When their own honor is challenged, however, they are willing to challenge someone at considerable risk to their own safety. These behavioral differences have physiological correlates. In a similar confederateinsulter experiment, Nisbett and Cohen measured levels of two hormones, cortisol and testosterone, in participants before and after they had been insulted. Physiologists know that cortisol levels increase in response to stress, and testosterone levels rise in preparation for violence. Insulted Southerners showed much bigger jumps in cortisol and testosterone than insulted Northerners.

Nisbett and Cohen argue that the difference in beliefs between northern and southern people can be understood in terms of their cultural and economic histories. Scots-Irish livestock herders were the main settlers of the South, while English, German, and Dutch peasant farmers populated the North. States historically have had considerable difficulty imposing the rule of law in the sparsely settled regions where herding is the dominant occupation, and livestock are easy to steal. Hence in herding societies a culture of honor often arises out of necessity as men seek to cultivate reputations for willingly resorting to violence as a deterrent to theft and other predatory behavior. Of course, bad men may also subscribe to the same code, the better to intimidate their victims. As this arms race escalates, arguments over trivial acts can rapidly get out of hand if a man thinks his honor is at stake. This account is supported by the fact that Southern white homicide rates are unusually high in poor regions with low population density and a historically weak presence of state institutions, not in the richer, more densely settled, historically slave-plantation districts. In such an environment the Scots-Irish honor system remained adaptive until recent times.

This fascinating study illustrates the two main points we want to make in this book.

Culture is crucial for understanding human behavior. People acquire beliefs and values from the people around them, and you can't explain human behavior without taking this reality into account. Murder is more common in the South than in the North. If Nisbett and Cohen are right, this difference can't be explained in terms of contemporary economics, climate, or any other external factor. Their explanation is that people in the South have acquired a complex set of beliefs and attitudes about personal honor that make them more polite, but also more quick to take offense than people in the North. This complex persists because the beliefs of one generation are learned by the next. This is not an isolated example. We will present several other similar well-studied examples demonstrating that culture plays an important role in human behavior. These are only the tip of the iceberg—a complete scholarly rehearsal of the evidence would try the patience of all but the most dedicated reader. Culturally acquired ideas are crucially important for explaining a wide range of human behavior—opinions, beliefs, and attitudes, habits of thought, language, artistic styles, tools and technology, and social rules and political institutions.

Culture is part of biology. An insult that has trivial effects in a Northerner sets off a cascade of physiological changes in a southern male that prepare him to harm the insulter and cope with the likelihood that the insulter is prepared to retaliate violently. This example is merely one strand in a skein of connections that enmesh culturally acquired information in other aspects of human biology. Much evidence suggests that we have an evolved psychology that shapes what we learn and how we think, and that this in turn influences the kind of beliefs and attitudes that spread and persist. Theories that ignore these connections cannot adequately account for much of human behavior. At the same time, culture and cultural change cannot be understood solely in terms of innate psychology. Culture affects the success and survival of individuals and groups; as a result, some cultural variants spread and others diminish, leading to evolutionary processes that are every bit as real and important as those that shape genetic variation. These culturally evolved environments then affect which genes are favored by natural selection. Over the evolutionary long haul, culture has shaped our innate psychology as much as the other way around.

Few who have thought much about the problem would dispute either of these claims in principle. Beliefs and practices that we learn from one another are clearly important, and like all human behavior, culture must in some way be rooted in human biology. However, in practice most social scientists ignore at least one of them. Some scholars, including most economists, many psychologists, and many social scientists influenced by evolutionary biology, place little emphasis on culture as a cause of human behavior. Others, especially anthropologists, sociologists, and historians, stress the importance of culture and institutions in shaping human affairs, but usually fail to consider their connection to biology. The success of all these disciplines suggests that many questions can be answered by ignoring culture or its connection to biology. However, the most fundamental questions of how humans came to be the kind of animal we are can only be answered by a theory in which culture has its proper role *and* in which it is intimately intertwined with other aspects of human biology. In this book we outline such a theory.

Culture can't be understood without population thinking

Eminent biologist Ernst Mayr has argued that "population thinking" was Charles Darwin's key contribution to biology.³ Before Darwin, people thought of species as essential, unchanging types, like geometric figures and chemical elements. Darwin saw that species were populations of organisms that carried a variable pool of inherited information through time. To explain the properties of a species, biologists had to understand how the day-to-day events in the lives of individuals shape this pool of information, causing some variant members of the species to persist and spread, and others to diminish. Darwin famously argued that when individuals carrying some variants were more likely to survive or have more offspring, these would spread through a process of natural selection. Less famously, he also thought that beneficial behaviors and morphologies acquired during an individual's lifetime were transmitted to the offspring, and that this process, which he called the "inherited effects of use and disuse," also shaped which variants were present. We now know that the latter process is unimportant in organic evolution, and that many processes Darwin never dreamed of are important in molding populations, including mutation, segregation, recombination, genetic drift, gene conversion, and meiotic drive. Nonetheless, modern biology is fundamentally Darwinian, because its explanations of evolution are rooted in population thinking; and if through some miracle of cloning Darwin were to be resurrected from his grave in Westminster Abbey, we think that he would be quite happy with the state of the science he launched.

Population thinking is the core of the theory of culture we defend in this book. First of all, let's be clear about what we mean by *culture*:

Culture is information capable of affecting individuals' behavior that they acquire from other members of their species through teaching, imitation, and other forms of social transmission.⁴

By *information* we mean any kind of mental state, conscious or not, that is acquired or modified by social learning and affects behavior. We will use everyday words like *idea, knowledge, belief, value, skill,* and *attitude* to describe this information, but we do not mean that such socially acquired information is always consciously available, or that it necessarily corresponds to folk-psychological categories. Our definition is rooted in the conviction that most cultural variation is caused by information stored in human brains—information that got into those brains by learning from others.⁵

People in culturally distinct groups behave differently, mostly because they have acquired different skills, beliefs, and values, and these differences persist because the people of one generation acquire their beliefs and attitudes from those around them. Hence Southerners are more likely to kill than Northerners because they hold different attitudes about personal honor. The same is true of many other aspects of culture. Different populations exhibit persistent variation in language, social customs, moral systems, practical skills and devices, and art. These and all the other dimensions of culture exist because people possess different socially acquired skills, beliefs, or values.

Population thinking is the key to building a causal account of cultural evolution. We are largely what our genes and our culture make us. In the same way that evolutionary theory explains why some genes persist and spread, a sensible theory of cultural evolution will have to explain why some beliefs and attitudes spread and persist while others disappear. The processes that cause such cultural change arise in the everyday lives of individuals as people acquire and use cultural information. Some moral values are more appealing and thus more likely to spread from one individual to another. These will tend to persist, while less attractive alternatives tend to disappear. Some skills are easy to learn accurately, while others are more difficult and are likely to be altered as we learn them. Some beliefs make people more likely to be imitated, because the people who hold those beliefs are more likely to survive or more likely to achieve social prominence. Such beliefs will tend to spread, while beliefs that lead to early death or social stigma will disappear. In the short run, a population-level theory of culture has to explain the net effect of such processes on the distribution of beliefs and values in a population during the previous generation. Over the longer run, the theory explains how these processes, repeated generation after generation, account for observed patterns of cultural variation. The heart of this book is an account of how the population-level consequences of imitation and teaching work.

Taking a population approach does not imply that cultural evolution is closely analogous to genetic evolution. For example, population thinking that does not require cultural information takes the form of *memes*, discrete, faithfully replicating, genelike bits of information. A range of models are consistent with the facts of cultural variation as they are presently understood, including models in which cultural information is not discrete and is never replicated. The same goes for the processes that give rise to cultural change. Natural selection–like processes are sometimes important, but processes that have no analog in genetic evolution also play important roles. Culture is interesting and important because its evolutionary behavior is distinctly different from that of genes. For example, we will argue that the human cultural system arose as an adaptation, because it can evolve fancy adaptations to changing environments rather more swiftly than is possible by genes alone. Culture would never have evolved unless it could do things that genes can't!

Population thinking makes it easy to link cultural and genetic evolution

Many social scientists have treated culture as a "superorganic" phenomenon. As one of the founders of modern anthropology, A. L. Kroeber, put it,

[P]articular 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 organic endowment of the human personality, even though cultural phenomena must always conform to the frame of this endowment.⁶

Social scientists in Kroeber's tradition have long dismissed the need to incorporate biology in any serious way into their study of human behavior. Humans cannot fly by flapping their arms or breathe underwater, but outside of such obvious constraints, biology has little to do with culture. 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.⁷

Superorganicism is wrong because it ignores the rich interconnections between culture and other aspects of our behavior and anatomy. Culture is as much a part of human biology as walking upright. Culture causes people to do many weird and wonderful things. Nonetheless, the equipment in human brains, the hormone-producing glands, and the nature of our bodies play a fundamental role in how we learn and why we prefer some ideas to others. 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, brains that have been shaped by natural selection to learn and manage culture. 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 period, culture must have increased the reproductive success of our ancestors; otherwise, the features of our brain that make culture possible would not have evolved.⁸ The operational products of this evolution are innate predispositions and organic constraints that influence the ideas that we find attractive, the skills that we can learn, the emotions that we can experience, and the very way we see the world. To take an exceedingly simple example, why are the doorways of houses in many cultures usually a little above head high? Because the human skull, for obvious adaptive reasons, is rather well endowed with pain sensors. Those who emphasize the role that organic evolution plays in explaining human behavior are surely correct to emphasize that a plethora of such innate adaptations strongly affect how culture evolves, although we still know little about the details. Why did Southerners need a *culture* of honor? Perhaps because on average, human males are *neither* innately sufficiently sensitive to insults *nor* sufficiently ready to respond violently to them in an environment where self-help violence is the chief means of protecting one's livelihood.

Thinking about culture as something that is acquired, stored, and transmitted by a population of individuals enables us to explore interactions between culture and other aspects of human biology. Individual psychologies determine which ideas are likely to be easy to learn and remember and which kinds of people are likely to be imitated. Of course, individuals do not behave in isolation. Individual psychologies may interact in interesting and complex ways, and we have to be careful to make sure that such structure finds its way into our theories. Individuals are also the main locus of genetic variation within the human species; to a first approximation, selection has acted over time to increase the fitness of individuals. A populationbased theory of cultural change tells us how the details of individual psychology affect what kinds of skills, beliefs, and values that individuals acquire. In concept, modeling the evolution of the innate psychological machinery that gives rise to social learning is easy—you just allow individual psychology to be genetically variable. Individuals with different psychologies will acquire different beliefs and values that will lead to different fitness outcomes. Of course, many complications can arise, so making such theory can be very hard work indeed. This is, however, straightforward scientific labor—when you use population thinking to conceptualize culture, intriguing questions appear where paradoxes and confusion once reigned.

Culture changes the nature of human evolution in fundamental ways

Although we do not doubt that culture is deeply intertwined with other aspects of human biology, we also believe that the evolution of culture has led to fundamental changes in the way that our species responds to natural selection. Over the last forty years or so, behavioral evolutionists have developed a rich theory predicting how natural selection will shape social behavior under various conditions. This theory explains a great deal about different aspects of behavior-mating and parenting, signaling, and cooperation—and has been fairly successful in explaining the differences between species throughout the animal kingdom. In the 1970s a group of scientists, then called human sociobiologists, created an intense controversy by applying the same body of theory to humans.9 Two contemporary research traditions have grown out of this work: human behavioral ecology and evolutionary psychology. Human behavioral ecologists typically use evolutionary theory to understand contemporary human behavior. Evolutionary psychologists use it to generate hypotheses about the evolved structure of human psychology. While both traditions have been quite successful, their application of evolutionary theory to humans is still the cause of much debate.¹⁰

Some of the opposition to evolutionary approaches to human behavior comes from thinking about these issues in terms of nature versus nurture. 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. Evolutionary biology, many opponents of evolutionary explanations believe, can explain genetically determined behaviors, but not behaviors that are learned or are the result of contact with the environment. Since most human behavior is learned, they conclude evolutionary theory has little to contribute toward shaping or understanding it.

Although this way of thinking is common, it is deeply mistaken. To ask whether behavior is determined by genes or environment does not make sense. *Every bit* of the behavior (or physiology or morphology, for that matter) of every single organism living on the face of the earth results from the interaction of genetic information stored in the developing organism and the properties of its environment. To think of genes like blueprints that specify the adult properties of the organisms—one gene says you are tall, the other short—is wrong. A much better analogy is that genes are like a recipe, but one in which the ingredients, cooking temperature, and so on are set by the environment. Different traits *do* vary in how sensitive they are to environmental differences. Some traits aren't much affected by the normal range of environments—humans develop five fingers on each hand in almost all environments¹¹—while others are highly sensitive—genetically similar people may end up with very different body sizes depending on nu-

trition and health during their childhood. Asking whether observed *differences* are due to genetic differences, differences in the environment, or some combination of these factors is sensible. However, the answer you get will tell you nothing about whether the traits in question are adaptations shaped by natural selection.

The reason is that natural selection shapes the way that developmental processes respond to environmental variation. Environment plays only a proximate role.12 Differences in the environment may cause genetically identical individuals to behave differently, and in this sense environmental differences are immediate causes of behavior. However, 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 has shaped the developmental process of the organism so that it responds to the environment as it does. Or, as biologists put it, the ultimate determinant of behavior is natural selection on genes. Learning and other developmental processes that cause individuals to respond differently to different environments implement structures built into the genes.¹³ In the natural world, proximate causes are typically physiological. Birds migrate toward the equator when days shorten because their brain converts changes in day length to hormonal signals that activate migratory behavior. Ultimate causes are evolutionary. Migration is an evolved strategy to exploit the favorable season at higher latitude while passing the harsh winter in less demanding habitats. Selection has shaped the reaction of the brain to day length and all the downstream physiological and behavioral machinery in order to motivate geese to fly from the Yukon River delta to central California before Arctic winter weather arrives.

While evolutionary social scientists reject the naïve idea that genes and environment can be independent causes, many accept that culture can be lumped with other environmental influences. They think that the psychological mechanisms that govern the acquisition of culture are just another form of behavioral plasticity whose structure can be understood in terms of natural selection acting on genes.¹⁴ As a result, many in the evolutionary social science community rejected the idea that culture makes any *fundamental* difference in the way that evolutionary thinking should be applied to humans. Because the psychological machinery that molds human culture was shaped by natural selection, so, at least in ancestral environments, the machinery *must have* led to fitness-enhancing behavior. If it goes wrong in modern environments, culture is not the culprit but the fact that our evolved, formerly adaptive psychology "misfires" these days. While the sort of adaptationist thinking inherent in this approach has many famous critics, we are not among their number.¹⁵

Instead, our concern is that lumping culture with other environmental influences leads people to ignore the novel evolutionary processes that are created by culture. Selection shapes individual learning mechanisms so that interaction with the environment produces adaptive behavior. For example, many plants contain toxic substances. Selection makes these chemicals taste bitter to herbivores so that they learn not to consume the toxic plant species. Culture adds something quite new and different to this scenario. Like other animals, humans normally use bitter taste as a signal that a plant is inedible. However, some bitter plant compounds (like salicylic acid in willow bark) have medicinal value, so we also learn from others that we can override the aversive bitter taste of certain plants when we have the need to cure an ailment. The genes making the plant taste bitter don't change at all, but the behavior of a whole population can change anyway as the belief in the bitter plant's medicinal value spreads. We take our medicine in spite of its bitter taste, not because our sensory physiology has evolved to make it less bitter, but because the idea that it has therapeutic value has spread through the population. In the distant past, some inquisitive and observant healer discovered the curative properties of a bitter plant. Then a number of processes that we describe in this book might cause this belief to increase in frequency, despite its horrible taste. You can't understand this process by asking how individuals interact with their environment. Instead, you have to understand how a population of individuals interact with their environments *and* each other over time.

Thus, culture is neither nature nor nurture, but some of both. It combines inheritance and learning in a way that cannot be parsed into genes or environment.¹⁶ This fact has two important consequences for human evolution, consequences to which we now turn.

Culture is a necessary part of the design problem for human psychology

One of the key steps in an adaptationist analysis of human behavior is to decide on the design problem that natural selection had to solve. Most students of human evolution begin by asking, how should evolution have shaped the psychology of a group-living, foraging hominid? From there, they ask how the evolved psychology will shape human culture. The implicit evolutionary scenario seems to be that Pleistocene hominids were just extra-smart chimpanzees, clever social animals in which learning from each other played a negligible role until the evolution of our brain was complete, at which point the souped-up chimpanzee was able to take up culture. *First* we got human nature by genetic evolution; *then* culture arose as an evolutionary byproduct.

This way of thinking neglects the inevitable feedback between the nature of human psychology and the kind of social information that this psychology should be designed to process. For us to take bitter medicine, our psychology must have evolved both to learn from others and to let this culturally acquired information override aversive stimuli. Culture is adaptive because the behavior of other individuals is a rich source of information about which behaviors are adaptive and which are not. We all know that plagiarism is often easier than the hard work of writing something by ourselves; imitating the behavior of others can be adaptive for the same reason. The trick is that once culture becomes important, the nature of the behavior that is available to imitate is itself strongly affected by the psychology that shapes how we learn from others. To take an extreme example, if everyone relied completely on imitation, behavior would become decoupled from the environment. With any environmental change, imitation would no longer be adaptive. To understand the evolution of the psychology that underlies culture, we must take this population-level feedback into account. We want to know how evolving psychology shapes the ideas and behaviors that can be acquired from others, and how natural selection shapes how we think and learn in an environment featuring direct information from personal experience and the potential to use the behavior of others at a lower cost but perhaps greater risk of error.

This kind of reasoning leads to conclusions quite different from other evolutionary theories of human behavior. Under the right conditions, selection can favor a psychology that causes most people most of the time to adopt behaviors "just" because the people around them are using those behaviors. The last 800,000 years or so have seen especially large, rapid fluctuations in world climate; the world average temperature sometimes changed more than 10 degrees Celsius in a century, leading to massive shifts in ecosystem structure.¹⁷ A group of hominids living in a habitat something like contemporary Madrid could find themselves in a habitat like Scandinavia one hundred years later. You might think that such rapid and extreme environmental changes would put a premium on individual learning over imitation. Odd as it may seem, in many kinds of variable environments, the best strategy is to rely mostly on imitation, not your own individual learning. Some individuals may discover ways to cope with the new situation, and if the not-so-smart and not-so-lucky can imitate them, then the lucky or clever of the next generation can add other tricks. In this way the ability to imitate can generate the cumulative cultural evolution of new adaptations at blinding speed compared with organic evolution. A population of purely individual learners would be stuck with what little they can learn by themselves; they can't bootstrap a whole new adaptation based on cumulatively improving cultural traditions. This design for human behavior depends on people adopting beliefs and technologies *largely* because other people in their group share those beliefs or use these technologies. When lots of imitation is mixed with a little bit of individual learning, *populations* can adapt in ways that outreach the abilities of any individual genius.

Thinking about the population properties of culture helps us understand the psychology of social learning. For example, we will see that selection can favor a psychology that causes people to conform to the majority behavior even though this mechanism sometimes prevents populations from adapting to a change in the environment. Evolution also favors a psychology that makes people more prone to imitate prestigious individuals and individuals who are like themselves even though this habit can easily result in maladaptive fads. These psychological mechanisms in turn give rise to important patterns of behavior, like the symbolic marking of social groups that would not evolve unless their culture had certain populationlevel consequences.

Culture is an ultimate cause of human behavior

If the only processes shaping culture arose from our innate evolved psychology, then culture would be a strictly proximate cause of human behavior. Understanding how natural selection gave rise to our psychology would be more complicated than for other forms of behavioral plasticity, but in the end we could, at least in principle, reduce human culture to the actions of evolution by natural selection to increase genetic fitness.¹⁸

However, not all of the processes shaping culture *do* arise from our innate psychology—culture itself is subject to natural selection. Much as a child resembles her parents, people resemble those from whom they have acquired ideas, values, and skills. Culturally acquired ideas, values, and skills affect what happens to people during their lives—whether they are successful, how many children they have, and how long they live. These events in turn affect whether their behavior will be culturally transmitted to the next generation. If successful people are more likely to be imitated, then those traits that lead to becoming successful will be favored. Even more obviously, if living people are more likely to be imitated than the dead, then ideas, values, and skills that promote survival will tend to spread. Consequently, a culture of honor arises, at least in part, because in lawless societies, men who are not aggressive in protecting their herds and their families tend to fall victim to tough, ruthless predators. If these advantages to a culture of honor have disappeared in the modern South, the higher death rate of those who cling to the custom will eventually extinguish it.

Such selective processes can often favor quite different behaviors from those favored by selection on genes. For example, beliefs and values that lead to prestige and economic success in modern societies may also reduce fertility. Such beliefs spread because the prestigious are more likely to be imitated, even though this lowers genetic fitness. Opening our minds to ideas in the environment allows rapid adaptation, but it also leads to the evolution of pathological cultural maladaptations. Our psychology has a delicately balanced set of mechanisms designed to exclude harmful ideas in the environment yet not attack the beneficial ones.

Natural selection acting on culture is an ultimate cause of human behavior, just like natural selection acting on genes. Consider an example we will return to repeatedly. Much cultural variation exists at the group level. Different human groups have different norms and values, and the cultural transmission of these traits can cause such differences to persist for long periods of time. Now, the norms and values that predominate in a group plausibly affect the probability that the group is successful, whether it survives, and whether it expands. For the purposes of illustration, suppose that groups having norms that promote group solidarity are more likely to survive than groups lacking this sentiment. This creates a selective process that leads to the spread of solidarity. Of course, this process may be opposed by an evolved innate psychology that biases what we learn from others, making us more prone to imitate and invent selfish or nepotistic beliefs rather than ones favoring group solidarity, like patriotism. The long-run evolutionary outcome would then depend on the balance of the processes favoring and disfavoring patriotism. Again for the sake of illustration, let us suppose that net effect of these opposing processes causes patriotic beliefs to predominate. In this case, the population behaves patriotically *because* such behavior promotes group survival, in exactly the same way that the sicklecell gene is common in malarial areas because it promotes individual survival. Human culture participates in ultimate causation.

Cultural scientists, we believe, should not fear a reunion with biology. Culture is a brawny phenomenon and is in no real danger of being "reduced" to genes. Of course genetic elements of our evolved psychology shape culture—how could it be otherwise? But at the same time, natural selection acting on cultural variation shaped the environments in which our psychology evolved (and is evolving). The coevolutionary dynamic makes genes as susceptible to cultural influence as vice versa. We will argue that the phenomenon of group selection on cultural variation described above could have produced institutions encouraging more cooperation with distantly related people than would be favored by our original evolved psychology. These cooperators would have discriminated against individuals who carried genes that made them too belligerent to conform to the new cooperative norms. Then the cultural rules could expand cooperation a bit further, generating selection for still more-docile genes. Eventually, innate elements of human social psychology became tolerably well adapted to promote living in tribes, not just families.

Culture makes us odd

Thinking about cultural evolution at the population level leads to a picture of a powerful adaptive system that is necessarily accompanied by some exotic side effects. Some of our evolutionist friends take a dim view of this notion, seeing it as giving aid and comfort to those who would deny the relevance of evolution to human affairs. We prefer to think that populationbased theories of cultural evolution strengthen the Darwinian's grasp on the human species by providing a picture of the engine that powered the furious pace of human evolution over the last few hundred thousand years. Our ape cousins still live in the same tropical forests in the same small social groups, and eat the same fruits, nuts, and bits of meat as our common ancestors did. By the late Pleistocene (say, 20,000 years ago), human foragers already occupied a much wider geographical and ecological range than any other species, using a remarkable range of subsistence systems and social arrangements. Over the last ten millennia we have exploded to become the earth's dominant organism by dint of deploying ever moresophisticated technology and ever more-sophisticated social systems. The human species is a spectacular evolutionary anomaly, so we ought to expect that the evolutionary system behind it is pretty anomalous as well. Our quest is for the evolutionary motors that drove our divergence from our ancestors, and we believe that the best place to hunt is among the anomalies of cultural evolution. This does not mean that gene-based evolutionary reasoning is worthless. To the contrary, human sociobiologists and their successors have explained a lot about human behavior even though most work ignores the novelties introduced by cultural adaptation. However, there is still much to explain, and we think that the population properties of culture are an essential ingredient of a satisfactory theory of human behavior.

The path not taken

In the preface to the second edition of the *Descent of Man* in 1874, Darwin noted that he

[took the] opportunity of remarking that my critics frequently assume that I attribute all changes of corporeal structure and mental power exclusively to the natural selection of such variations as are often called spontaneous; whereas, even in the first edition of the *Origin of Species* I distinctly stated that great weight must be attributed to the inherited effects of use and disuse, with respect both to the body and mind.¹⁹

From the biologists' point of view, Darwin's belief in the inheritance of acquired variation was his greatest error. Darwin thought "inherited habits," by which he meant something very close to human culture, were important in a wide variety of species. In a sense he was correct—simple forms of social learning are widespread in the animal kingdom.²⁰ However, Darwin imagined that even honeybees had humanlike imitative capacities, whereas the best modern evidence, as we shall see, suggests that all other animals, including our closest ape relatives, have rudimentary capacities for culture compared with ourselves.

Darwin's intuitions about "inherited habits" no doubt came from his observation that humans had such things, combined with his desire to minimize the gap between humans and other animals. He is sometimes said to have biologized human culture, but he is more accurately accused of culturizing biology.²¹ Darwin had a sophisticated, if erroneous, picture of the distribution of the inherited effects of use and disuse across traits. He thought that behavior was more susceptible to the inheritance of acquired variation and that anatomy was much more conservative in this regard, so he could account for the fact that human behavior was much more variable from place to place than were human bodies. As "On the Races of Man," chapter 7 of the *Descent*, shows, Darwin was not seduced into thinking that the huge behavioral differences he and other pioneering anthropologists observed among humans could be accounted for by differences in conservative—we would say today genetic—characters. Rather, he attributed them to the more labile characters that we would today label cultural.

We thus have an interesting historical paradox: Darwin's theory was a better starting point for humans than any other species, and required a major pruning to adjust to the rise of genetics. Nevertheless, the *Descent* had no lasting influence on the social sciences that emerged at the turn of the twentieth century.²² Darwin was pigeonholed as a biologist, and sociology, economics, and history all eventually wrote biology out of their disciplines. Anthropology relegated his theory to a subdiscipline, biological anthropology, behind the superorganic firewall. Since the midtwentieth century, many social scientists have treated Darwinian initiatives as politically tainted threats. If anything, the gulf between the social and natural sciences continues to widen as some anthropologists, sociologists, and historians adopt methods and philosophical commitments that seem to natural scientists to abandon the basic norms of science entirely.

In this book, we follow Darwin's path not taken. Beginning with psychologist Donald T. Campbell's work in the 1960s, we, and a few compatriots,²³ have sought to give cultural evolution its due weight without divorcing culture from biology. We hope to convince you that this approach to cultural evolution delivers new and powerful tools to dissect some of the enduring problems of the human sciences: How do genes and culture interact to influence our behavior? Why are humans so extraordinarily successful a species? How do individual processes and the institutional structures and functions of groups articulate? What are the sources of cultural diversity? Why, despite our success as a species, do our actions often seem mildly (or sometimes wildly) dysfunctional? Why does our behavior sometimes lead to colossal catastrophes? Why are we sometimes downright heroic in our concern for others' welfare while in other circumstances indifferent, callous, exploitative, or vicious? As far as we can see, the benefits of such a theory are large compared with the cost of abandoning certain cherished commitments to disciplines, methods, and hypotheses that it casts into doubt. We hope that by the time you finish this book you will agree.