CHAPTER 7

From Genes to Culture

The natural sciences have constructed a webwork of causal explanation that runs all the way from quantum physics to the brain sciences and evolutionary biology. There are gaps in this fabric of unknown breadth, and many of the strands composing it are as delicate as spider's silk. Predictive syntheses, the ultimate goal of science, are still in an early stage, and especially so in biology. Yet I think it fair to say that enough is known to justify confidence in the principle of universal rational consilience across all the natural sciences.

The explanatory network now touches the edge of culture itself. It has reached the boundary that separates the natural sciences on one side from the humanities and humanistic social sciences on the other. Granted, for most scholars the two domains, commonly called the scientific and literary cultures, still have a look of permanence about them. From Apollonian law to Dionysian spirit, prose to poetry, left cortical hemisphere to right, the line between the two domains can be easily crossed back and forth, but no one knows how to translate the tongue of one into that of the other. Should we even try? I believe so, and for the best of reasons: The goal is both important and attainable. The time has come to reassess the boundary.

Even if that perception is disputed—and it will be—few can deny that the division between the two cultures is a perennial source of misunderstanding and conflict. "This polarisation is sheer loss to us all,"

wrote C. P. Snow in his defining 1959 essay *The Two Cultures and the Scientific Revolution*. "To us as people, and to our society. It is at the same time practical and intellectual and creative loss."

The polarization promotes, for one thing, the perpetual recycling of the nature-nurture controversy, spinning off mostly sterile debates on gender, sexual preferences, ethnicity, and human nature itself. The root cause of the problem is as obvious today as it was when Snow ruminated on it at Christ College high table: the overspecialization of the educated elite. Public intellectuals, and trailing close behind them the media professionals, have been trained almost without exception in the social sciences and humanities. They consider human nature to be their province and have difficulty conceiving the relevance of the natural sciences to social behavior and policy. Natural scientists, whose expertise is diced into narrow compartments with little connection to human affairs, are indeed ill prepared to engage the same subjects. What does a biochemist know of legal theory and the China trade? It is not enough to repeat the old nostrum that all scholars, natural and social scientists and humanists alike, are animated by a common creative spirit. They are indeed creative siblings, but they lack a common language.

There is only one way to unite the great branches of learning and end the culture wars. It is to view the boundary between the scientific and literary cultures not as a territorial line but as a broad and mostly unexplored terrain awaiting cooperative entry from both sides. The misunderstandings arise from ignorance of the terrain, not from a fundamental difference in mentality. The two cultures share the following challenge. We know that virtually all of human behavior is transmitted by culture. We also know that biology has an important effect on the origin of culture and its transmission. The question remaining is how biology and culture interact, and in particular how they interact across all societies to create the commonalities of human nature. What, in final analysis, joins the deep, mostly genetic history of the species as a whole to the more recent cultural histories of its far-flung societies? That, in my opinion, is the nub of the relationship between the two cultures. It can be stated as a problem to be solved, the central problem of the social sciences and the humanities, and simultaneously one of the great remaining problems of the natural sciences.

At the present time no one has a solution. But in the sense that no one in 1842 knew the true cause of evolution and in 1952 no one knew the nature of the genetic code, the way to solve the problem may lie within our grasp. A few researchers, and I am one of them, even think they know the approximate form the answer will take. From diverse vantage points in biology, psychology, and anthropology, they have conceived a process called *gene-culture coevolution*. In essence, the conception observes, first, that to genetic evolution the human lineage has added the parallel track of cultural evolution, and, second, that the two forms of evolution are linked. I believe the majority of contributors to the theory during the past twenty years would agree to the following outline of its principles:

Culture is created by the communal mind, and each mind in turn is the product of the genetically structured human brain. Genes and culture are therefore inseverably linked. But the linkage is flexible, to a degree still mostly unmeasured. The linkage is also tortuous: Genes prescribe epigenetic rules, which are the neural pathways and regularities in cognitive development by which the individual mind assembles itself. The mind grows from birth to death by absorbing parts of the existing culture available to it, with selections guided through epigenetic rules inherited by the individual brain.

To visualize gene-culture coevolution more concretely, consider the example of snakes and dream serpents, which I used earlier to argue the plausibility of complete consilience. The innate tendency to react with both fear and fascination toward snakes is the epigenetic rule. The culture draws on that fear and fascination to create metaphors and narratives. The process is thus:

As part of gene-culture coevolution, culture is reconstructed each generation collectively in the minds of individuals. When oral tradition is supplemented by writing and art, culture can grow indefinitely large and it can even skip generations. But the fundamental biasing influence of the epigenetic rules, being genetic and ineradicable, stays constant.

Hence the prominence of dream serpents in the legends and art of the Amazonian shamans enriches their culture across generations under the guidance of the serpentine epigenetic rule.

Some individuals inherit epigenetic rules enabling them to survive and reproduce better in the surrounding environment and culture than individuals who lack those rules, or at least possess them in weaker valence. By this means, over many generations, the more successful epigenetic rules have spread through the population along with the genes that prescribe the rules. As a consequence the human species has evolved genetically by natural selection in behavior, just as it has in the anatomy and physiology of the brain.

Poisonous snakes have been an important source of mortality in almost all societies throughout human evolution. Close attention to them, enhanced by dream serpents and the symbols of culture, undoubtedly improves the chances of survival.

The nature of the genetic leash and the role of culture can now be better understood, as follows. Certain cultural norms also survive and reproduce better than competing norms, causing culture to evolve in a track parallel to and usually much faster than genetic evolution. The quicker the pace of cultural evolution, the looser the connection between genes and culture, although the connection is never completely broken. Culture allows a rapid adjustment to changes in the environment through finely tuned adaptations invented and transmitted without correspondingly precise genetic prescription. In this respect human beings differ fundamentally from all other animal species.

Finally, to complete the example of gene-culture coevolution, the frequency with which dream serpents and serpent symbols inhabit a culture is seen to be adjusted to the abundance of real poisonous snakes in the environment. But owing to the power of fear and fascination given them by the epigenetic rule, they easily acquire additional mythic meaning; they serve in different cultures variously as healers, messengers, demons, and gods.

Gene-culture coevolution is a special extension of the more general process of evolution by natural selection. Biologists generally agree that the primary force behind evolution in human beings and all other organisms is natural selection. That is what created *Homo sapiens* during the five or six million years after the ancestral hominid species split off from a primitive chimpanzeelike stock. Evolution by natural selection is not an idle hypothesis. The genetic variation on which selection acts is well understood in principle all the way down to the molecular level. "Evolution watchers" among field biologists have monitored evolution by natural selection, generation by generation, in natural populations of animals and plants. The result can often be reproduced in the laboratory, even up to the creation of new species, for example by hybridization and the breeding of reproductively isolated strains. The manner in which traits of anatomy, physiology, and behavior adapt organisms to their environment has been massively documented. The fossil hominid record, from man-apes to modern humans, while still lacking many details, is solid in main outline, with a well established chronology.

In simplest terms, evolution by natural selection proceeds, as the French biologist Jacques Monod once put it (rephrasing Democritus), by chance and necessity. Different forms of the same gene, called alleles, originate by mutations, which are random changes in the long sequences of DNA (deoxyribonucleic acid) that compose the gene. In addition to such point-by-point scrambling of the DNA, new mixes of alleles are created each generation by the recombining processes of sexual reproduction. The alleles that enhance survival and reproduction of the carrier organisms spread through the population, while those that do not, disappear. Chance mutations are the raw material of evolution. Environmental challenge, deciding which mutants and their combinations will survive, is the necessity that molds us further from this protean genetic clay.

If given enough generations, mutations and recombination can generate a nearly infinite amount of hereditary variation among individuals in a population. For example, if even a mere thousand genes out of the fifty thousand to a hundred thousand in the human genome were to exist in two forms in the population, the number of genetic combinations conceivable is 10^{300}, more than all the atoms in the visible universe. So except for identical siblings the probability that any two human beings share identical genes, or have ever shared them throughout the history of the hominid line, is vanishingly small.

With each generation the chromosomes and genes of the parents are scrambled to produce new mixes. But this perpetual shearing and reconfiguration does not of itself cause evolution. The consistent guiding force is natural selection. Genes that confer higher survival and reproductive success on the organisms bearing them, through the prescribed traits of anatomy, physiology, and behavior, increase in the population from one generation to the next. Those that do not, decrease. Similarly, populations or even entire species with higher survival and reproductive success prevail over competing populations or species, to the same general end in evolution.

Such is the impersonal force that evidently made us what we are today. All of biology, from molecular to evolutionary, points that way. At the risk of seeming defensive, I am obliged to acknowledge that many people, some very well educated, prefer special creation as an explanation for the origin of life. According to a poll conducted by the National Opinion Research Center in 1994, 23 percent of Americans reject the idea of human evolution, and a third more are undecided. This pattern is unlikely to change radically in the years immediately ahead. Because I was raised in a predominantly antievolutionist culture in the Protestant southern United States, I am inclined to be empathetic to these feelings, and conciliatory. Anything is possible, it can be said, if you believe in miracles. Perhaps God did create all organisms, including human beings, in finished form, in one stroke, and maybe it all happened several thousand years ago. But if that is true, He also salted the earth with false evidence in such endless and exquisite detail, and so thoroughly from pole to pole, as to make us conclude first that life evolved, and second that the process took billions of years. Surely Scripture tells us He would not do that. The Prime Mover of the Old and New Testaments is variously loving, magisterial, denying, thunderously angry, and mysterious, but never tricky.

Virtually all biologists closely familiar with the details find the evidence for human evolution compelling, and give natural selection the commanding role. There is at least one other force, however, that must be mentioned in any account of evolution. By chance alone, the biologists agree, substitutions are occurring through long stretches of time in some of the DNA letters and the proteins they encode. The continuity of change is often smooth enough to measure the age of different evolving lines of organisms. But this genetic drift, as it is called, adds very little to evolution at the level of cells, organisms, and societies. The reason is that the mutants involved in drift have proven to be neutral, or nearly so: They have little or no effect on the higher levels of biological organization manifest in cells and organisms.

TO GENETIC EVOLUTION, putting the matter as concisely as possible, natural selection has added the parallel track of cultural evolution, and the two forms of evolution are somehow linked. We are trapped, we sometimes think, for ultimate good or evil, not just by our genes but also by our culture. What precisely is this superorganism, this strange creature called culture? To anthropologists, who have analyzed thousands of examples, should go the privilege of response. For them, a culture is the total way of life of a discrete society—its religion, myths, art, technology, sports, and all the other systematic knowledge transmitted across generations. In 1952 Alfred Kroeber and Clyde Kluckhohn melded 164 prior definitions pertaining to all cultures into one, as follows: "Culture is a product; is historical; includes ideas, patterns, and values; is selective; is learned; is based upon symbols; and is an abstraction from behavior and the products of behavior." As Kroeber had earlier declared, it is also holistic, "an accommodation of discrete parts, largely inflowing parts, into a more or less workable fit." Among the parts are artifacts, but these physical objects have no significance except when addressed as concepts in living minds.

In the extreme nurturist view, which has prevailed in social theory for most of the twentieth century, culture has departed from the genes and become a thing unto itself. Possessing a life of its own, growing like wildfire ignited by the strike of a match, it has acquired emergent properties no longer connected to the genetic and psychological processes that initiated it. Hence, *omnis cultura ex cultura*. All culture comes from culture.

Whether that metaphor is accepted or not, the undeniable truth is that each society creates culture and is created by it. Through constant grooming, decorating, exchange of gifts, sharing of food and fermented beverages, music, and storytelling, the symbolic communal life of the mind takes form, unifying the group into a dreamworld that masters the external reality into which the group has been thrust, whether in forest, grassland, desert, ice field, or city, spinning from it the webs of moral consensus and ritual that bind each tribal member to the common fate.

Culture is constructed with language that is productive, comprising arbitrary words and symbols invented purely to convey information. In this respect *Homo sapiens* is unique. Animals have communication systems that are sometimes impressively sophisticated, but they neither invent them nor teach them to others. With a few exceptions, such as bird song dialects, they are instinctive, hence unchanging across generations. The waggle dance of the honeybee and the odor trails of ants contain symbolic elements, but the performances and meanings are tightly prescribed by genes and cannot be altered by learning.

Among animals true linguistic capacity is most closely approached by the great apes. Chimpanzees and gorillas can learn the meanings of arbitrary symbols when trained to use signaling keyboards. Their champion is Kanzi, a bonobo, or pygmy chimpanzee (*Pan paniscus*), arguably the smartest animal ever observed in captivity. I met this primate genius when he was a precocious youngster at the Yerkes Regional Primate Center of Emory University in Atlanta. He had been studied intensively since birth by Sue Savage-Rumbaugh and her colleagues. As I played games and shared a cup of grape juice with him, I was more than a bit disoriented by his general demeanor, which I found uncannily close to that of a human two-year-old. More than a decade later, as I write, the adult Kanzi has acquired a large vocabulary, with which he signals his wishes and intentions on a picture-symbol keyboard. He constructs sentences that are lexically if not grammatically correct. On one occasion, for example, *Ice water go* ("Bring me some ice water") got him the drink. He has even managed to pick up about 150 spoken English words spontaneously, listening to conversation among humans, without the kind of training needed by border collies and other smart breeds of dogs to go through their many tricks. On another occasion Savage-Rumbaugh, pointing to a companion chimpanzee nearby, said, "Kanzi, if you give Austin your mask, I'll let you have some of Austin's cereal." Kanzi promptly gave Austin the mask and pointed to the cereal box. He has acted upon words in a focused and specific manner too frequently for the connection to be due to chance alone. Even so, Kanzi uses only words and symbols supplied him by human beings. His linguistic powers have not yet risen to the level of early human childhood.

Bonobos and other great apes possess high levels of intelligence by animal standards but lack the singular human capacity to invent rather than merely to use symbolic language. It is further true that common chimpanzees are humanlike in guile and deception, the animal masters of "Machiavellian intelligence." As Frans de Waal and his fellow primatologists have observed in the African wild and the Arnhem zoo in the Netherlands, they form and break coalitions, manipulate friends, and outwit enemies. Their intentions are conveyed by voiced signals and postures, body movements, facial expressions, and the bristling of fur. But in spite of the great advantage a productive, humanlike language would bestow, chimpanzees never create anything resembling it, or any other form of free-ranging symbolic language.

In fact, the great apes are completely silent most of the time. The primatologist Allen Gardner described his experience in Tanzania as follows: "A group of ten wild chimpanzees of assorted ages and sexes feeding peacefully in a fig tree at Gombe may make so little sound that an inexperienced observer passing below can altogether fail to detect them."

Homo sapiens, by contrast, can rightfully be called the babbling ape. Humans communicate vocally all the time; it is far easier to start them talking than to shut them up. They begin in infancy during exchanges with adults, who urge them on with the slow, vowel-heavy, emotionally exaggerated singsong called motherese. Left alone, they continue with "crib speech," composed of squeaks, coos, and nonsense monosyllables, which evolve over a few months into a complex play of words and phrases. These early verbal repertories, conforming more or less to adult vocabularies, are repeated *ad nauseam*, modified, and combined in experimental mixtures. By the age of four the average child has mastered syntax. By six, in the United States at least, he has a vocabulary of about fourteen thousand words. In contrast, young bonobos play and experiment freely with movements and sounds and sometimes with symbols, but so far progress toward the Kanzi level depends on the rich linguistic environment provided by human trainers.

Even if the great apes lack true language, is it possible they possess culture? From evidence in the field it appears they do, and many expert observers have so concluded. Wild chimps regularly invent and use tools. And the particular kinds of artifacts they invent, just as in human culture, are often limited to local populations. Where one group breaks nuts open with a rock, another cracks them against tree trunks. Where some groups use twigs to fish ants and termites from the nests for food, others do not. Among those that fish, a minority first peel the bark off the twigs. One chimp group has been observed using long hooked branches to pull down branches of fig trees to obtain fruit.

It is natural to conclude from such observations that chimpanzees have the rudiments of culture, and to suppose that their capability differs from human culture by degree alone. But that perception needs to be accepted with caution. Chimpanzee inventions may not be culture in any sense. The still scanty evidence on the subject suggests that while chimps pick up the use of a tool more quickly when they see others using one, they seldom imitate the precise movements employed or show any clear sign of understanding the purpose of the activity. Some observers have gone so far as to claim that they are merely stirred into greater activity by watching others. This kind of response, which zoologists call social facilitation, is common in many kinds of social animals, from ants to birds and mammals. Although the evidence is inconclusive, social facilitation alone, combined with trial-and-error manipulation of materials conveniently at hand, might guide the chimps to tool-using behavior in the free-ranging African populations.

Human infants, on the other hand, do engage in precise imitation and with astonishing precocity. As early as forty minutes after birth, to cite the ultimate example, they stick out their tongues and move their heads from side to side in close concert with adults. By twelve days they imitate complex facial expressions and hand gestures. By two years they can be verbally instructed in the use of simple tools.

In summary, the language instinct consists of precise mimicry, compulsive loquacity, near-automatic mastery of syntax, and the swift acquisition of a large vocabulary. The instinct is a diagnostic and evidently unique human trait, based upon a mental power beyond the reach of any animal species, and it is the precondition for true culture. To learn how language originated during evolution would be a discovery of surpassing importance. Unfortunately, the evidences of behavior rarely fossilize. All the millennia of campsite chattering and gesticulation, and with them all the linguistic steps up from our chimplike ancestors, have vanished without trace.

What paleontologists have instead are fossil bones, which tell of the downward migration and lengthening of the voice box, as well as possible changes in the linguistic regions of the brain impressed upon the inner cranial case. They also have steadily improving evidence of the evolution of artifacts, from the controlled use of fire 450,000 years ago, presumably by the ancestral species *Homo erectus*, to the construction of well-wrought tools by early *Homo sapiens* 250,000 years ago in Kenya, then elaborate spearheads and daggers 160,000 years later in the Congo, and finally elaborate painting and the accouterments of ritual 30,000 and 20,000 years ago in southern Europe.

This pace in the evolution of artifactual culture is intriguing. We know that the modern *Homo sapiens* brain was anatomically fully formed by no later than 100,000 years before the present. From that time forward the material culture at first evolved slowly, later expanded, and then exploded. It passed from a handful of stone and bone tools at the beginning of the interval to agricultural fields and villages at the 90 percent mark, and then—in a virtual eyeblink—to prodigiously elaborate technologies (example: five million patents so far in the United States alone). In essence, cultural evolution has followed an exponential trajectory. It leaves us with a mystery: When did symbolic language arise, and exactly how did it ignite the exponentiation of cultural evolution?

TOO BAD, but this great puzzle of human paleontology seems insoluble, at least for the time being. To pick up the trail of gene-culture coevolution, it is better to defer reconstruction of the prehistoric record and proceed to the production of culture by the contemporary human brain. The next best approach, I believe, is to search for the basic unit of culture. Although no such element has yet been identified, at least to the general satisfaction of experts, its existence and some of its characteristics can be reasonably inferred.

Such a focus may seem at first contrived and artificial, but it has many worthy precedents. The great success of the natural sciences has been achieved substantially by the reduction of each physical phenomenon to its constituent elements, followed by the use of the elements to reconstitute the holistic properties of the phenomenon. Advances in the chemistry of macromolecules, for example, led to the exact characterization of genes, and the study of population biology based on genes has refined our understanding of biological species.

What then, if anything, is the basic unit of culture? Why should it be supposed even to exist? Consider first the distinction made by the Canadian neuroscientist Endel Tulving in 1972 between episodic and semantic memory. Episodic memory recalls the direct *perception* of people and other concrete entities through time, like images seen in a motion picture. Semantic memory, on the other hand, recalls *meaning* by the connection of objects and ideas to other objects and ideas, either directly by their images held in episodic memory or by the symbols denoting the images. Of course, semantic memory originates in episodes and almost invariably causes the brain to recall other episodes. But the brain has a strong tendency to condense repeated episodes of a kind into concepts, which are then represented by symbols. Thus, "Proceed to the airport this way" yields to a silhouette of an airplane and arrow, and "This substance is poisonous" becomes a skull and crossbones on the side of a container.

With the two forms of memory distinguished, the next step in the search for the unit of culture is to envision concepts as "nodes," or reference points, in semantic memory that ultimately can be associated with neural activity in the brain. Concepts and their symbols are usually labeled by words. Complex information is thus organized and transmitted by language composed of words. Nodes are almost always linked to other nodes, so that to recall one node is to summon others. This linkage, with all the emotional coloring pulled up with it, is the essence of what we refer to as meaning. The linkage of nodes is assembled as a hierarchy to organize information with more and more meaning. "Hound," "hare" and "chasing" are nodes, each symbolizing collectively a class of more or less similar images. A hound chasing a hare is called a proposition, the next order of complexity in information. The higher order above the proposition is the schema. A typical schema is Ovid's telling of Apollo's courtship of Daphne, like an unstoppable hound in pursuit of an unattainable hare, wherein the dilemma is resolved when Daphne, the hare and a concept, turns into a laurel tree, another concept reached by a proposition.

I have faith that the unstoppable neuroscientists will encounter no such dilemma. In due course they will capture the physical basis of mental concepts through the mapping of neural activity patterns. They already have direct evidence of "spreading activation" of different parts of the brain during memory search. In the prevailing view of the researchers, new information is classified and stored in a similar manner. When new episodes and concepts are added to memory, they are processed by a spreading search through the limbic and cortical systems, which establishes links with previously created nodes. The nodes are not spatially isolated centers connected to other isolated centers. They are typically complex circuits of large numbers of nerve cells deployed over wide, overlapping areas of the brain.

Suppose, for example, you are handed an unfamiliar piece of fruit. You automatically classify it by its physical appearance, smell, taste, and the circumstances under which it is given. A large amount of information is activated within seconds, not just the comparison of the fruit in hand with other kinds but also the emotional feelings, recollections of previous discoveries of similar nature, and memories of dietary customs that seem appropriate. The fruit—all its characteristics compounded—is given a name. Consider the durian of Southeast Asia, regarded by aficionados as the greatest of all tropical fruits. It looks like a spiny grapefruit, tastes sweet with a transient custardlike nuance, and when held away from the mouth smells like a sewer. The experience of a single piece establishes, I assure you, the concept "durian" for a lifetime.

The natural elements of culture can be reasonably supposed to be the hierarchically arranged components of semantic memory, encoded by discrete neural circuits awaiting identification. The notion of a culture unit, the most basic element of all, has been around for over thirty years, and has been dubbed by different authors variously as mnemotype, idea, idene, meme, sociogene, concept, culturgen, and culture type. The one label that has caught on the most, and for which I now vote to be winner, is meme, introduced by Richard Dawkins in his influential work *The Selfish Gene* in 1976.

The definition of meme I suggest is nevertheless more focused and somewhat different from that of Dawkins. It is the one posed by the theoretical biologist Charles J. Lumsden and myself in 1981, when we outlined the first full theory of gene-culture coevolution. We recommended that the unit of culture—now called meme—be the same as the node of semantic memory and its correlates in brain activity. The level of the node, whether concept (the simplest recognizable unit), proposition, or schema, determines the complexity of the idea, behavior, or artifact that it helps to sustain in the culture at large.

I realize that with advances in the neurosciences and psychology the notion of node-as-meme, and perhaps even the distinction between episodic and semantic memory, are likely to give way to more sophisticated and complex taxonomies. I realize also that the assignment of the unit of culture to neuroscience might seem at first an attempt to short-circuit semiotics, the formal study of all forms of communication. That objection would be unjustified. My purpose in this exposition is the opposite, to establish the plausibility of the central program of consilience, in this instance the causal connections between semiotics and biology. If the connections can be established empirically, then future discoveries concerning the nodes of semantic memory will correspondingly sharpen the definition of memes. Such an advance will enrich, not replace, semiotics.

I CONCEDE that the very expression "genes to culture," as the conceptual keystone of the bridge between science and the humanities, has an ethereal feel to it. How can anyone presume to speak of a gene that prescribes culture? The answer is that no serious scientist ever has. The web of causal events comprising gene-culture coevolution is more complicated—and immensely more interesting. Thousands of genes prescribe the brain, the sensory system, and all the other physiological processes that interact with the physical and social environment to produce the holistic properties of mind and culture. Through natural selection, the environment ultimately selects which genes will do the prescribing.

For its implications throughout biology and the social sciences, no subject is intellectually more important. All biologists speak of the interaction between heredity and environment. They do not, except in laboratory shorthand, speak of a gene "causing" a particular behavior, and they never mean it literally. That would make no more sense than its converse, the idea of behavior arising from culture without the intervention of brain activity. The accepted explanation of causation from genes to culture, as from genes to any other product of life, is not heredity alone. It is not environment alone. It is interaction between the two.

Of course it is interaction. But we need more information about interaction in order to encompass gene-culture coevolution. The central clarifying concept of interactionism is the *norm of reaction*. The idea is easily grasped as follows. Choose a species of organism, whether animal, plant, or microorganism. Select either one gene or a group of genes that act together to affect a particular trait. Then list all the environments in which the species can survive. The different environments may or may not cause variation in the trait prescribed by the selected gene or group of genes. The total variation in the trait in all the survivable environments is the norm of reaction of that gene or group of genes in that species.

The textbook case of a norm of reaction is leaf shape in the arrowleaf, an amphibious plant. When an individual of the species grows on the land, its leaves resemble arrowheads. When it grows in shallow water, the leaves at the surface are shaped like lily pads; and when submerged in deeper water, the leaves develop as eelgrasslike ribbons that sway back and forth in the surrounding current. No known genetic differences among the plants underlie this extraordinary variation. The three basic types are variations in the expression of the same group of genes caused by different environments. Together they compose the norm of reaction of the genes prescribing leaf form. They embrace, in other words, the full variation in expression of the genes in all known survivable environments.

When some of the variation within a species is due to differences in genes possessed by separate members of the species, and not just different environments, norms of reaction can still in principle be defined for each of the genes or set of genes in turn. The relation of variation in a trait to variation in genes and their norms of reaction is illustrated by human body weight. There is abundant evidence that body form is influenced by heredity. A person genetically predisposed to obesity by heredity can diet to moderate slimness, although he is prone to slide back when off the diet. A hereditarily slender person, on the other hand, is likely to stay that way, and only persistent overeating or endocrine imbalance can push him into obesity. The relevant genes of the two individuals have different norms of reaction. They produce different results when both individuals occupy identical environments, including diet and exercise. The more familiar way to express the matter is in reverse, noting that hereditarily distinct individuals require different environments, in particular different diets and regimes of exercise, in order to produce the same result.

The same kind of interaction between genes and environment occurs in every category of human biology, including social behavior. In his important 1996 work *Born to Rebel*, the American social historian Frank J. Sulloway has demonstrated that people respond powerfully during personality development to the order in which they were born and thus the roles they assume in family dynamics. Later-borns, who identify least with the roles and beliefs of the parents, tend to become more innovative and accepting of political and scientific revolutions than do first-borns. As a result they have, on average, contributed more than first-borns have to cultural change throughout history. They do it by gravitating toward independent, often rebellious roles, first within the family and then within society at large. Because first- and later-borns do not differ genetically in any way correlated with their birth order, the genes influencing development can be said to spread their effects among various niches available in the environment. The birth-order effect documented by Sulloway is their norm of reaction.

In some categories of biology, such as the most elementary molecular processes and properties of gross anatomy, almost everyone has the same genes affecting traits in these categories and hence the same norms of reaction. Long ago in geological time, when the truly universal traits were evolving, there probably was variation in the prescribing genes, but natural selection has since narrowed the variation almost to

zero. All primates, for example, have ten fingers and ten toes, and there is virtually no variation due to environment; so the norm of reaction is exactly the single state, of ten fingers and ten toes. In most categories, however, people differ genetically to a considerable degree, even in traits consistent enough to be regarded as cultural universals. In order to make the most of the variation, to cultivate health and talent and realize human potential, it is necessary to understand the roles of both heredity and environment.

By environment I do not mean merely the immediate circumstances in which people find themselves. A snapshot will not suffice. The required meaning is that used by developmental biologists and psychologists. It is nothing less than the myriad influences that shape body and mind step by step throughout every stage of life.

Because human beings cannot be bred and reared under controlled conditions like animals, information about the interaction of genes and environment comes hard. Relatively few genes affecting behavior (some of which I will describe later) have been located on chromosomes, and the exact pathways of development they influence have seldom been traced. In the interim the preferred measure of interaction is *heritability*, the percentage of variation in the trait due to heredity. Heritability does not apply to individuals; it is used only for populations. It is incongruous to say, "This marathoner's athletic ability is 20 percent due to his genes and 80 percent to his environment." It *is* correct to make a statement such as, to use an imaginary example, "Twenty percent of the variation in performance of Kenyan marathoners is due to their heredity and 80 percent to their environment." For the reader who would like more precise definitions of heritability and variance, the measure of variation used by statisticians and geneticists, I will add them here:

> Heritability, minus mathematical refinements, is estimated as follows. In a sample of individuals from the population, measure the trait in a standardized way, say aerobic performance on a treadmill to represent endurance. Take the variation in the measure among the individuals in the sample, and estimate the amount of the variation due to heredity. That fraction is the heritability. The measure of variation used is the variance. To get it, first take the average score obtained from individuals in the sample. Subtract each individual's score in turn from the average and square the difference. The variance is the average of all the squared differences.

The principal method of estimating the fraction of variation due to the genes—the heritability—is by studies of twins. Identical twins, which have exactly the same genes, are compared with fraternal twins, which on average share only the same number of genes as the number shared by siblings born at different times. Fraternal twins are consistently less alike than identical twins, and the difference between pairs of fraternal twins and pairs of identical twins serves as an approximate measure of the contribution of heredity to the overall variation in the trait. The method can be considerably enhanced by studies of those special pairs of identical twins who were separated in infancy and adopted by different families, thus possessing the same heredity but reared in different environments. It is further improved by multiple correlation studies, in which the key environmental influences are identified and their contributions to the overall variation individually assessed.

Heritability has been a standard measure for decades in plant and animal breeding. It has gained recent controversial attention for its human applications through *The Bell Curve*, the 1994 book by Richard J. Herrnstein and Charles Murray, and other popular works on the heredity of intelligence and personality. The measure has considerable merit, and in fact is the backbone of human behavioral genetics. But it contains oddities that deserve close attention with reference to the consilience between genetics and the social sciences. The first is the peculiar twist called "genotype-environment correlation," which serves to increase human diversity beyond the ambit of its immediate biological origins. The twist works as follows. People do not merely select roles suited to their native talents and personalities. They also gravitate to environments that reward their hereditary inclinations. Their parents, who possess similar inborn traits, are also likely to create a family atmosphere nurturing development in the same direction. The genes, in other words, help to create a particular environment in which they will find greater expression than would otherwise occur. The overall result is a greater divergence of roles within societies due to the interaction of genes and environment. For example, a musically gifted child, receiving encouragement from adults, may take up an instrument early and spend long hours practicing. His classmate, innately thrill-seeking, persistently impulsive and aggressive, is drawn to fast cars. The first child grows up to be a professional musician, the second (if he stays out of trouble) a successful racing-car driver. The hereditary differences in talent and personality between the classmates may be small, but their effects have been amplified by the diverging pathways into which they were guided by the differences. To put genotype-environment correlation in a phrase, heritability measured at the level of biology reacts with the environment to increase heritability measured at the level of behavior.

Understanding genotype-environment correlation clarifies a second principle of the relation of genes to culture. There is no gene for playing the piano well, or even a particular "Rubinstein gene" for playing it extremely well. There is instead a large ensemble of genes whose effects enhance manual dexterity, creativity, emotive expression, focus, attention span, and control of pitch, rhythm, and timbre. All of these together compose the special human ability that the American psychologist Howard Gardner calls musical intelligence. The combination also inclines the gifted child to seize the right opportunity at the right time. He tries a musical instrument, likely provided by musically gifted parents, is then reinforced by deserved praise, repeats, is reinforced again, and soon embraces what is to be the central preoccupation of his life.

Another important peculiarity of heritability is its flexibility. By simply changing the environment, the percentage of variation due to heredity can be increased or decreased. Scores for heritability in IQ and measurable personality traits in white Americans, a segment of population typically chosen for convenience and in order to increase statistical reliability by making the sample more uniform, mostly fall around the 50 percent mark, at least closer to it than to zero or 100 percent.

Do we wish to change these numbers? I think not, at least not as a primary goal. Imagine the result if a society became truly egalitarian, so that all children were raised in nearly identical circumstances and encouraged to enter any occupation they chose within reach of their abilities. Variation in environment would thus be drastically reduced, while the original innate abilities and personality traits endured. Heritability in such a society would increase. Any socioeconomic class divisions that persisted would come to reflect heredity as never before.

Suppose instead that all children were tested for ability at an early age and put on educational tracks that reflected their scores, with the aim of directing them to occupations most appropriate to their gifts. Environmental variation in this Brave New World would rise and innate ability would stay the same. If the scores and hence environments reflected the genes, heritability would increase. Finally, imagine a society with the reverse policy: uniformity of outcome is valued above all else. Gifted children are discouraged and slow children provided with intensive personal training in an effort to bring everyone to the same level in abilities and achievement. Because a wide range of tailored environments is required to approach this goal, heritability would fall.

These idealized societies are posed not to recommend any one of them—all have a totalitarian stench—but to clarify the social meaning of this important phase of genetic research. Heritability is a sound measure of the influence of genes on variation in existing environments. It is invaluable in establishing the presence of the genes in the first place. Until the 1960s, for example, schizophrenia was thought to be a result of what parents, especially mothers, do to their children in the first three years of their lives. Until the 1970s autism was also thought to be an environmental disorder. Now, thanks to heritability studies, we know that in both disabilities genes play a significant role. In the reverse direction, alcoholism was once assumed to be largely inherited, so much so that careful heritability studies were not conducted until the 1990s. Now we know that alcoholism is only moderately heritable in males and scarcely at all in females.

Still, except for the rare behavioral conditions approaching total genetic determination, heritabilities are at best risky predictors of personal capacity in existing and future environments. The examples I have cited also illustrate the danger of using them as measures of the worth of either individuals or societies. The message from geneticists to intellectuals and policy-makers is this: Choose the society you want to promote, then prepare to live with its heritabilities. Never favor the reverse, of promoting social policies just to change heritabilities. For best results, cultivate individuals, not groups.

I HAVE PUT these ideas from genetics in play so as to clarify the vexing differences between nurturists and hereditarians, and to try to establish a common ground between them. Until that much is accomplished, the search for consilience risks being sidetracked by endless ideological bickering, with adversaries who promote different political and social agendas talking past one another. Nurturists traditionally emphasize the contributions of the environment to behavior, while hereditarians emphasize the genes. (Nurturists are sometimes called environmentalists, but that label has been preempted by protectors of the environment; and hereditarians cannot be called naturists, unless they hold their conferences in the nude.) Redefined with the more precise concepts of genetics, nurturists can now be seen to believe that human behavioral genes have very broad norms of reaction, while hereditarians think the norms are relatively narrow. In this sense the difference between the two opinions is thus one of degree, not of kind. It becomes a matter that can be settled and agreed upon empirically, should the adversaries agree to take an objective approach.

Nurturists have also traditionally thought that the heritability of intelligence and personality traits is low, while hereditarians have considered it to be high. That disagreement has been largely resolved. In contemporary Caucasians of Europe and the United States at least, heritability is usually in mid-range, with its exact value varying from one trait to another.

Nurturists think that culture is held on a very long genetic leash, if held at all, so that the cultures of different societies can diverge from one another indefinitely. Hereditarians believe the leash is short, causing cultures to evolve major features in common. This problem is technically less tractable than the first two, but it is also empirical in nature, and in principle can be solved. I will take it up again shortly, and give several examples that illustrate how a resolution can in fact be reached.

There is already at least some common ground to build upon. Nurturists and hereditarians generally agree that almost all the differences between cultures are likely to be the product of history and environment. While individuals *within* a particular society vary greatly in behavioral genes, the differences mostly wash out statistically *between* societies. The culture of the Kalahari hunter-gatherers is very distinct from that of Parisians, but the differences between them are primarily a result of divergence in history and environment, and are not genetic in origin.

THE CLARIFICATION OF norms of reaction and heritability, while admittedly a bit technical and dry, is the crucial first step toward unbraiding the roles of heredity and environment in human behavior, and hence important for the attainment of consilience of biology with the social sciences. The logical next step is the location of the genes that affect behavior. Once genes have been mapped on chromosomes and their pathways of expression identified, their interaction with the environment can be more precisely traced. When many such interactions have been defined, the whole can be braided back again to attempt a more complete picture of mental development.

The state of the art in human behavioral genetics, including its still formidable difficulties in gene mapping, is illustrated by the study of schizophrenia. This most common of psychoses afflicts just under 1 percent of people in populations around the world. The symptoms of schizophrenia are highly variable from person to person. But they share one diagnostic trait: mental activity that consistently breaks with reality. In some cases the patient believes he is a great personage (the Messiah is a popular choice) or the target of a clever and pervasive conspiracy. In others, he hallucinates voices or visions, often bizarre, as in a dream while fully awake.

In 1995 independent groups of scientists achieved three breakthroughs while probing the physical origins of schizophrenia. Neurobiologists at the University of California in Irvine discovered that during fetal development some nerve cells in the prefrontal cortex of future schizophrenics fail to communicate with other cells required for normal exchanges with the rest of the brain. In particular, the cells are unable to manufacture messenger RNA molecules that guide synthesis of the neurotransmitter GABA, or gamma aminobutyric acid. With GABA missing, the nerve cells cannot function, even though they look normal. In some manner still unknown, the impairment promotes internal mental constructions with no connection to external stimuli or ordinary rational thought. The brain creates a world of its own, as though closed off in sleep.

In the same year a second team from Cornell University and two medical research centers in England reported the first direct observation of brain activity in hallucinating schizophrenic patients. Using positron emission tomography (PET) imaging, the investigators monitored active sites in the cortex and limbic systems of patients during periods of both normal and psychotic activity. In one case, they watched a male patient's brain light up while (according to his testimony) disembodied heads rolled through his mind barking orders. The region

responsible for the most abnormal events is the anterior cingulate cortex, a region thought to regulate other portions of the cerebral cortex. Its malfunction evidently diminishes the integration of external information and provokes erratic, dreamlike confabulation by the wakened brain.

What is the ultimate cause of schizophrenia? For years data from twin and family-history studies have suggested that the malfunction has at least a partially genetic origin. Early attempts to locate the responsible genes misfired; particular chromosomes were tentatively identified as sites of schizophrenia genes, but then further studies failed to duplicate the results. In 1995, four independent research groups, using advanced chromosome mapping techniques on large samples of subjects, placed at least one gene responsible for schizophrenia on the short arm of chromosome 6. (Humans have 22 pairs of chromosomes in addition to the sex chromosomes X and Y; each of the pairs of chromosomes is arbitrarily assigned a different number for easy reference.) Two other groups failed to confirm the result, but as I write two years later the weight of evidence from the four combined positive tests has led to wide acceptance of their conclusion as to the probable placement of at least one of the schizophrenia genes.

These recent advances and others have cleared the way toward an eventual understanding, not merely of one of the most important mental diseases but of a complex piece of human behavior. Although the behavior can in no way be called normal, it affects the evolution of culture. From the delusions and visions of madmen have come some of the world's despotisms, religious cults, and great works of art. The codified responses of societies to extreme strangeness have furthermore been part of the culture of the many societies that regard schizophrenics as either blessed by gods or inhabited by demons.

But surely, you may respond, culture is still based mainly on normal responses, not insanity. Why has so little progress been made on love, altruism, competitiveness, and other elements of everyday social behavior? The answer lies in the pragmatic bias of genetic research. Geneticists who study inheritance and development first look for big effects caused by single mutations, those easy to detect and analyze. In the classical period of Mendelian genetics, for example, they began with instantly recognizable traits, such as vestigial wings in drosophila fruit flies and wrinkled seed coats in garden peas. It so happens that big mutations are also harmful mutations, for the same reason that large random changes in an automobile engine are more likely to stall it than small random changes. Big mutations almost always reduce survival rates and reproductive capacity. Much of pioneering human genetics has therefore been medical genetics, as exemplified by the studies of schizophrenia.

The practical value of the approach is beyond question. The use of large effects has been parlayed many times into important advances in medical research. Over 1,200 physical and psychological disorders have been tied to single genes. They range (alphabetically) from Aarskog-Scott syndrome to Zellweger syndrome. The result is the OGOD principle: One Gene, One Disease. So successful is the OGOD approach that researchers joke about the Disease of the Month reported in scientific journals and mainstream media. Consider this diverse set of examples: color blindness, cystic fibrosis, hemophilia, Huntington's chorea, hypercholesterolemia, Lesch-Nyhan syndrome, retinoblastoma, sickle-cell anemia. And so pervasive is the evidence of the origin of pathologies in single and multiple gene deviations—even cigarette smoking has a discernible heritability—that biomedical scientists like to quote the maxim that "all disease is genetic."

Researchers and practicing physicians are especially pleased with the OGOD discoveries, because a single gene mutation invariably has a biochemical signature that can be used to simplify diagnosis. Because the signature is a defect somewhere in the sequence of molecular events entrained by transcription off the affected gene, it can often be disclosed with a simple biochemical test. Hope also rises that genetic disease can be corrected with magic-bullet therapy, by which one elegant and noninvasive procedure corrects the biochemical defect and erases the symptoms of the disease.

For all its early success, however, the OGOD principle can be profoundly misleading when applied to human behavior. While it is true that a mutation in a single gene often causes a significant change in a trait, it does not at all follow that the gene *determines* the organ or process affected. Typically, many genes contribute to the prescription of each complex biological phenomenon. How many? For that kind of information it is necessary to turn from human beings to the house mouse, which, being a prime laboratory animal with a short life span, is genetically the best known of all the mammals. Even here knowledge is sketchy. In the mouse, genes contributing to the texture of the hairs and skin are known from no fewer than seventy-two chromosome

sites. At least forty-one other genes have variants that cause defects in the organ of balance in the inner ear, resulting in abnormal head shaking and circling behavior.

The complexity of mouse heredity is a clue to the difficulties still facing human genetics. Whole organs and processes, as well as narrowly defined features within them, are commonly prescribed by ensembles of genes, each of which occupies a different array of positions on the chromosomes. The difference in skin pigmentation between people of African and European ancestry is believed to be determined by three to six such "polygenes." The estimates for this and other such systems may be on the low side. In addition to the more potent genes, which are easier to detect, there can be many others that contribute small portions of the variation observed and thus remain undiscovered.

It follows that a mutation in any one of the polygenes might produce a large, overriding OGOD effect, or it may prescribe a much smaller quantitative deviation from the average. The common occurrence of mutations of the second type is one reason that genes predisposing the development of chronic depression, manic-depressive syndrome, and other disorders have proven so elusive. Clinical depression in Ireland, for example, may have at least a partially different gene-based predisposition from clinical depression in Denmark. In such a case, careful research in one laboratory that locates a gene site on one chromosome will fail to find confirmation by equally careful research conducted in a second laboratory.

Subtle differences in environment can also distort the classic patterns of Mendelian inheritance. One common effect is the condition called incomplete penetrance. The trait appears in one person but not another, even though both possess the same enabling genes. When one identical twin develops schizophrenia, for example, the chance that the other twin will follow suit is only 50 percent, despite the fact that exactly the same genes are found in both. Another consequence is variable expressivity. Those who develop schizophrenia have it in greatly varying form and intensity.

To summarize, human behavioral genetics provides one of the crucial links in the track from genes to culture. The discipline is still in its infancy, and hampered by formidable theoretical and technical difficulties. Its principal methods are classical twin studies and family-tree analysis, gene mapping, and, most recently, DNA sequence identification. These approaches have so far been but crudely joined. As their synthesis proceeds and is supplemented by studies of psychological development, a clearer picture of the foundations of human nature will emerge.

MEANWHILE, what we know or (to be completely forthright) what we *think* we know, about the hereditary basis of human nature can be expressed by linking together three determining levels of biological organization. I will present them from the top down, in a sequence that begins with the universals of culture, proceeds to epigenetic rules of social behavior, and ends in a second look at behavioral genetics.

In a classic 1945 compendium, the American anthropologist George P. Murdock listed the universals of culture, which he defined as the social behaviors and institutions recorded in the Human Relations Area Files for every one of the hundreds of societies studied to that time. There are sixty-seven universals in the list: age-grading, athletic sports, bodily adornment, calendar, cleanliness training, community organization, cooking, cooperative labor, cosmology, courtship, dancing, decorative art, divination, division of labor, dream interpretation, education, eschatology, ethics, ethno-botany, etiquette, faith healing, family feasting, fire-making, folklore, food taboos, funeral rites, games, gestures, gift-giving, government, greetings, hair styles, hospitality, housing, hygiene, incest taboos, inheritance rules, joking, kin groups, kinship nomenclature, language, law, luck superstitions, magic, marriage, mealtimes, medicine, obstetrics, penal sanctions, personal names, population policy, postnatal care, pregnancy usages, property rights, propitiation of supernatural beings, puberty customs, religious ritual, residence rules, sexual restrictions, soul concepts, status differentiation, surgery, tool-making, trade, visiting, weather control, and weaving.

It is tempting to dismiss these traits as not truly diagnostic for human beings, not really genetic, but inevitable in the evolution of *any* species that attains complex societies based on high intelligence and complex language, regardless of their hereditary predispositions. But that interpretation is easily refuted. Imagine a termite species that evolved a civilization from the social level of a living species. Take for the purpose the mound-building termites *Macrotermes bellicosus* of Africa, whose citylike nests beneath the soil each contain millions of

inhabitants. Elevate the basic qualities of their social organization in their present-day insectile condition to a culture that is guided, as in human culture, by heredity-based epigenetic rules. The "termite nature" at the foundation of this hexapod civilization would include celibacy and nonreproduction by the workers, the exchange of symbiotic bacteria by the eating of one another's feces, the use of chemical secretions (pheromones) to communicate, and the routine cannibalism of shed skins and dead or injured family members. I have composed the following state-of-the-colony speech for a termite leader to deliver to the multitude, in her attempt to reinforce the supertermite ethical code:

Ever since our ancestors, the macrotermitine termites, achieved ten-kilogram weight and larger brains during their rapid evolution through the late Tertiary Period, and learned to write with pheromonal script, termitic scholarship has elevated and refined ethical philosophy. It is now possible to express the imperatives of moral behavior with precision. These imperatives are self-evident and universal. They are the very essence of termitity. They include the love of darkness and of the deep, saprophytic, basidiomycetic penetralia of the soil; the centrality of colony life amidst the richness of war and trade with other colonies; the sanctity of the physiological caste system; the evil of personal rights (the colony is ALL!); our deep love for the royal siblings allowed to reproduce; the joy of chemical song; the aesthetic pleasure and deep social satisfaction of eating feces from nestmates' anuses after the shedding of our skins; and the ecstasy of cannibalism and surrender of our own bodies when we are sick or injured (it is more blessed to be eaten than to eat).

FURTHER EVIDENCE of human cultural universals is the dual origin of civilization in the Old and New Worlds, evolved in mutual isolation yet remarkably convergent in broad detail. The second part of "the grand experiment" began twelve thousand or more years ago, when the New World was invaded by nomadic tribes from Siberia. The colonists were at that time Paleolithic hunter-gatherers who most likely lived in groups of a hundred or fewer. In the centuries to follow they spread south through the length of the New World, from the Arctic tundra to the icy forests of Tierra del Fuego ten thousand miles distant, splitting as they went into local tribes that adapted to each of the land environments they encountered. Along the way, here and there, some of the societies evolved into chiefdoms and imperial states remarkably similar in their basic structure to those in the Old World.

In 1940 the American archaeologist Alfred V. Kidder, a pioneer student of early North American settlements and Mayan cities, summarized the independent histories of civilization in the Old and New Worlds to make the case for a hereditary human nature. In both hemispheres, he said, people started from the same base as stone-age primitives. First they brought wild plants under cultivation, allowing their populations to increase and form villages. While this was happening they elaborated social groupings and evolved sophisticated arts and religions, with priests and rulers receiving special powers from the gods. They invented pottery, and wove plant fibers and wool into cloth. They domesticated local wild animals for food and transport. They worked metal into tools and ornaments, first gold and copper, then bronze, the harder alloy of copper and tin. They invented writing and used it to record their myths, wars, and noble lineages. They created hereditary classes for their nobles, priests, warriors, craftsmen, and peasants. And, Kidder pointed out, "In the New World as well as in the Old, priesthoods grew and, allying themselves with temporal powers, or becoming rulers in their own right, reared to their gods vast temples adorned with painting and sculpture. The priests and chiefs provided for themselves elaborate tombs richly stocked for the future life. In political history it is the same. In both hemispheres group joined group to form tribes; coalitions and conquests brought preeminence; empires grew and assumed the paraphernalia of glory."

IMPRESSIVE AS the universals may be, it is still risky to use them as evidence of the linkage between genes and culture. While the categories listed occur too consistently to be due to chance alone, their finer details differ widely among societies within and between the hemispheres. The hallmarks of civilization are moreover too scattered and recent in origin to have been genetically evolved and somehow carried around the world by hunter-gatherers. It would be absurd to speak of particular genes that prescribe agriculture, writing, the priesthood, and monumental tombs.

In my own writings, from *On Human Nature* in 1978 forward, I have argued that the etiology of culture wends its way tortuously from the genes through the brain and senses to learning and social behavior. What we inherit are neurobiological traits that cause us to see the world in a particular way and to learn certain behaviors in preference to other behaviors. The genetically inherited traits are not memes, not units of culture, but rather the propensity to invent and transmit certain kinds of these elements of memory in preference to others.

As early as 1972 Martin Seligman and other psychologists had defined the bias in development precisely. They called it "prepared learning." By this concept they meant that animals and humans are innately prepared to learn certain behaviors, while being counterprepared against—that is, predisposed to avoid—others. The many documented examples of prepared learning form a subclass of *epigenetic rules*. As recognized in biology, epigenetic rules comprise the full range of inherited regularities of development in anatomy, physiology, cognition, and behavior. They are the algorithms of growth and differentiation that create a fully functioning organism.

A second productive insight, contributed by sociobiology, is that prepared learning of social behavior, like all other classes of epigenesis, is usually adaptive: It confers Darwinian fitness on organisms by improving their survival and reproduction. The adaptiveness of the epigenetic rules of human behavior is not the exclusive result of either biology or culture. It arises from subtle manifestations of both. One of the most efficient ways to study the epigenetic rules of human social behavior is by methods of conventional psychology, informed by the principles of evolutionary process. For this reason the scientists concentrating on the subject often call themselves evolutionary psychologists. Theirs is a hybrid discipline, drawn from both sociobiology—the systematic study of the biological basis of social behavior in all kinds of organisms, including humans—and psychology, the systematic study of the basis of human behavior. Given our growing understanding of gene-culture coevolution, however, and in the interest of simplicity, clarity, and—on occasion—intellectual courage in the face of ideological hostility, evolutionary psychology is best regarded as identical to human sociobiology.

IN THE 1970S, as I stressed in my early syntheses, altruism was the central problem of sociobiology in both animals and humans. That challenge has now been largely met by successful theory and empirical research. In the 1990s attention is beginning to shift in human sociobiology to gene-culture coevolution. In this new phase of research, the definition of epigenetic rules is the best means to make important advances in the understanding of human nature. Such an emphasis seems logically inescapable. The linkage between genes and culture is to be found in the sense organs and programs of the brain. Until this process is better known and taken into account, mathematical models of genetic evolution and cultural evolution will have very limited value.

The epigenetic rules, I believe, operate, like emotion, at two levels. Primary epigenetic rules are the automatic processes that extend from the filtering and coding of stimuli in the sense organs all the way to perception of the stimuli by the brain. The entire sequence is influenced by previous experience only to a minor degree, if at all. Secondary epigenetic rules are regularities in the integration of large amounts of information. Drawing from selected fragments of perception, memory, and emotional coloring, secondary epigenetic rules lead the mind to predisposed decisions through the choice of certain memes and overt responses over others. The division between the two classes of epigenetic rules is subjective, made for convenience only. Intermediate levels of complexity exist, because more complex primary rules grade into simpler secondary rules.

All of the senses impose primary epigenetic rules. Among the most basic properties of such rules is the breaking of otherwise continuous sensations into discrete units. From birth, for example, the cones of the retina and the neurons of the lateral geniculate nuclei of the thalamus classify visible light of differing wavelengths into four basic colors. In similar manner, the hearing apparatus of both children and adults automatically divides continuous speech sounds into phonemes. Series of sounds that run smoothly from *ba* to *ga* are not heard as a continuum but either as *ba* or *ga*; the same is true of the transition from *v* to *s*.

An infant begins life with other built-in acoustic responses that shape later communication and social existence. The newborn can distinguish innately between noise and tone. By four months the infant prefers harmonious tones, sometimes reacting to out-of-tune notes with a facial expression of disgust, the same, it turns out, as elicited by a drop of lemon juice on the tongue. The newborn's response to a loud sound is the Moro reflex: If on its back, the infant first extends its arms forward, brings them slowly together as though in embrace, emits a cry, and then gradually relaxes. In four to six weeks the Moro reflex is replaced by the startle response, which, as I described earlier, is the most complex of the reflexes and lasts for the remainder of life. Within a fraction of a second after an unexpected loud noise is heard, the eyes close, the mouth opens, the head drops, the shoulders and arms sag, the knees buckle slightly. Altogether, the body is positioned as though to absorb a coming blow.

Some preferences in chemical taste also begin at or shortly after birth. Newborns prefer sugar solutions over plain water and in the following fixed order: sucrose, fructose, lactose, glucose. They reject substances that are acid, salty, or bitter, responding to each with the distinctive facial expressions they will use for the rest of their lives.

The primary epigenetic rules gear the human sensory system to process mostly audiovisual information. The predilection is in contrast to that of the vast majority of animal species, which depend mostly on smell and taste. The human audiovisual bias is reflected by the disproportionate weighting of vocabulary. In languages around the world, from English and Japanese to Zulu and Teton Lakota, two-thirds to three-fourths of all the words describing sensory impressions refer to hearing and vision. The remaining minority of words are divided among the other senses, including smell, taste, and touch, as well as sensitivity to temperature, humidity, and electrical fields.

Audiovisual bias also marks the primary epigenetic rules that establish social bonds in infancy and early childhood. Experiments have shown that within ten minutes after birth, infants fixate more on normal facial designs drawn on posters than on abnormal designs. After two days, they prefer to gaze at their mother rather than other, unknown women. Other experiments have revealed an equally remarkable ability to distinguish their mother's voice from voices of other women. For their part, mothers need only a brief contact to distinguish the cry of their newborns, as well as their personal body odor.

The face is the chief arena of visual nonlinguistic communication and the secondary epigenetic rules that bias their psychological development. A few facial expressions have invariant meaning throughout the human species, even though they are modified in different cultures to express particular nuances. In a classic experiment to test the universality of the phenomenon, Paul Ekman of the University of

California at San Francisco photographed Americans as they acted out fear, loathing, anger, surprise, and happiness. He also photographed New Guinea highland tribesmen from recently contacted villages as they told stories in which similar feelings were evoked. When individuals were then shown the portraits from the other culture, they interpreted the facial expressions with an accuracy greater than 80 percent.

Within the face the mouth is the principal instrument of visual communication. The smile in particular is a rich site of secondary epigenetic rules. Psychologists and anthropologists have discovered substantial degrees of similar programmed development in the uses of smiling across cultures. The expression is first displayed by infants between the ages of two and four months. It invariably attracts an abundance of affection from attending adults. Environment has little influence on the maturation of smiling. The infants of the !Kung, a hunter-gatherer people of South Africa's Kalahari desert, are nurtured under very different conditions from those in America and Europe. They are delivered by their mothers without assistance or anesthetic, kept in almost constant physical contact with adults, nursed several times an hour, and trained rigorously at the earliest possible age to sit, stand, and walk. Yet their smile is identical in form to that of American and European infants, appears at the same time, and serves the same social function. Smiling also appears on schedule in deaf-blind children and even in thalidomide-deformed children who are not only deaf and blind but also crippled so badly they cannot touch their own faces.

Throughout life smiling is used primarily to signal friendliness and approval, and beyond that to indicate a general sense of pleasure. Each culture molds its meaning into nuances determined by the exact form and the context in which it is displayed. Smiling can be turned into irony and light mockery, or to conceal embarrassment. But even in such cases its messages span only a tiny fraction of those transmitted by all facial expressions taken together.

At the highest levels of mental activity complex secondary epigenetic rules are followed in the process called reification: the telescoping of ideas and complex phenomena into simpler concepts, which are then compared with familiar objects and activities. The Dusun of Borneo—to take one of countless examples from the archives of anthropology—reify each house into a "body" possessing arms, a head, a belly, legs, and other parts. It is believed to "stand" properly only if

aligned in a certain direction; it is thought to be "upside down" if built on the slope of a hill. In other dimensions the house is classified as fat or skinny, young or old and worn-out. All its interior details are invested with intense meaning. Every room and piece of furniture is connected to calendric rituals and magical and social beliefs.

Reification is the quick and easy mental algorithm that creates order in a world otherwise overwhelming in flux and detail. One of its manifestations is the dyadic instinct, the proneness to use two-part classifications in treating socially important arrays. Societies everywhere break people into in-group versus out-group, child versus adult, kin versus nonkin, married versus single, and activities into sacred and profane, good and evil. They fortify the boundaries of each division with taboo and ritual. To change from one division to the other requires initiation ceremonies, weddings, blessings, ordinations, and other rites of passage that mark every culture.

The French anthropologist Claude Lévi-Strauss and other writers of the "structuralist" school he helped found have suggested that the binary instinct is governed by the interaction of inborn rules. They posit oppositions such as man:woman, endogamy:exogamy, and earth:heaven as contradictions in the mind that must be met and resolved, often by mythic narrative. Thus the concept of life necessitates the concept of death, which is resolved by the myth of death serving as the gateway to eternal life. Binary oppositions, in the full-dress structuralist version, are linked still further into complex combinations by which cultures are assembled into integrated wholes.

The structuralist approach is potentially consistent with the picture of mind and culture emerging from natural sciences and biological anthropology, but it has been weakened by disagreements within the ranks of the structuralists themselves concerning the best methods of analysis. Their problem is not the basic conception, insofar as I have been able to understand the massive and diffuse literature, but its lack of a realistic connection to biology and cognitive psychology. That may yet be achieved, with potentially fruitful results.

NOW TO THE next step in the search for human nature, the genetic basis of the epigenetic rules. What is that basis, and how much variation is there in the prescribing genes? As a cautionary prelude to an answer, let me again stress the limitations of the genetics of human behavior as a whole. Human behavior genetics is an infant field of study and still vulnerable to ideologues who would be unkind to it in pursuit of their personal agendas. In only one level of analysis, the estimation of heritability, can it be said to be an advanced scientific discipline. With sophisticated statistical techniques, geneticists have calculated the proportionate contributions of genes across a large array of traits in sensory physiology, brain function, personality, and intelligence. They have arrived at this important conclusion: Variation in virtually every aspect of human behavior is heritable to some degree, and thus in some manner influenced by differences in genes among people. The finding should come as no surprise. It is equally true of behavior in all animal species that have been studied to date.

But the measurement of heritability does not identify *particular* genes. Nor does it provide us with a hint of the intricate pathways of physiological development leading from the genes to the epigenetic rules. The principal weakness of contemporary human behavioral genetics and human sociobiology is that only a small number of the relevant genes and epigenetic rules have been identified. This is not to deny that many others exist—quite the contrary—only that they have not yet been identified and pinpointed in genetic maps. The reason is that human behavioral genetics is technically very difficult at this level.

The paucity of examples has another, heightened consequence. Because both the genes affecting epigenetic rules and the rules themselves are usually searched out independently by different teams of researchers, matches between genes and epigenetic rules are even rarer. They come to light mostly by sheer luck. Suppose, at a guess, that 1 percent of the relevant genes and 10 percent of the epigenetic rules have been discovered up to the present time. The number of matches would be as few as the multiple of the two percentages, in this case one tenth of 1 percent. The scarcity of matches is less a failing, however, than an opportunity for scientific discovery waiting to be seized. It is precisely in this domain, on the frontier between biology and the social sciences, that some of the most significant progress in studies of human behavior can be expected to occur.

Among the known gene mutations affecting complex behavior is one that causes dyslexia, a reading disorder produced by impairment of the ability to interpret spatial relationships. Another reduces performance on three psychological tests of spatial ability but not on three other tests that measure verbal skill, speed at perception, and memory. Genes affecting personality have also been discovered. A mutation inducing outbursts of aggressive behavior, still known only in a single Dutch family, has been located on the X chromosome. It evidently causes a deficiency in the enzyme monoamine oxidase, needed to break down neurotransmitters that regulate the fight-or-flight response. Because the neurotransmitters accumulate as a result of this deviation, the brain remains keyed up, prepared to respond violently to low levels of stress. A more normal variant of personality is brought about by a "novelty-seeking gene," which alters the brain's response to the neurotransmitter dopamine. Persons possessing the gene when given standard tests are found to be more impulsive, curiosity-prone, and fickle. The molecules of the gene and the protein receptor it helps prescribe are longer in molecular length than the unmutated forms. They are also widespread, having been detected in different ethnic groups both in Israel and in the United States (but not in a Finnish group). A variety of other gene variants have been discovered that change the metabolism and activity of neurotransmitters, but their effects on behavior await investigation.

I do not mean to suggest by citing these examples that it is only necessary to discover and list genes one by one in order to establish the genetic basis of human behavior. The mapping of genes is just the beginning. Most traits, including even the simplest elements of intelligence and cognition, are influenced by polygenes, which are multiple genes spread across different chromosome sites and acting in concert. In some cases polygenes simply add their effects, so that more genes of a certain array means more of the product—more of a transmitter, say, or a higher concentration of skin pigment. Such additive inheritance, as it is called, typically produces a bell-shaped curve in the distribution of the trait in the population as a whole. Other polygenes add up until they reach a certain threshold number, at which point the trait emerges for the first time. Diabetes and some mental disorders appear to belong to this class. Finally, polygenes can interact epistatically: The presence of a gene at one chromosome site suppresses the action of a gene at another chromosome site. Brain wave patterns as revealed in electroencephalograms (EEGs) are an example of a neurological phenomenon inherited in this manner.

Finally, to complicate matters further, there is pleiotropy, the prescription of multiple effects by a single gene. A classic human example of pleiotropy is provided by the mutant gene that causes phenylketonuria, the symptoms of which include an excess of the amino acid phenylalanine, a deficiency of tyrosine, abnormal metabolic products of phenylalanine, darkening of the urine, lightening of hair color, toxic damage to the central nervous system, and—mental retardation.

The pathways from the genes to the traits they prescribe may seem overwhelmingly convoluted. Still, they can be deciphered. A large part of future human biology will consist of tracing the development of body and mind they influence. In the first two decades of the coming century, if current research stays on track, we will see the complete sequencing of the human genome and a mapping of most of the genes. Furthermore, the modes of inheritance are scientifically manageable. The number of polygenes controlling individual behavioral traits is finite, with those responsible for most of the variation often being fewer than ten. The multiple effects of single genes are also finite. They will be defined more fully as molecular biologists trace the cascades of chemical reactions entrained by groups of genes, and as neuroscientists map the patterns of brain activity that are among the final products of these reactions.

For the immediate future the genetics of human behavior will travel behind two spearheads. The first is research on the heredity of mental disorders, and the second is research on gender difference and sexual preference. Both classes are favored by strong public interest and have the further advantage of entailing processes that are well marked, hence relatively easily isolated and measured. They fit a cardinal principle in the conduct of scientific research: Find a paradigm for which you can raise money and attack with every method of analysis at your disposal.

Gender differences are an especially productive paradigm, even though politically controversial. They are already richly described in the psychological and anthropological literature. Their biological foundations are partly known, having been documented in the corpus callosum and other brain structures; in patterns of brain activity; in smell, taste, and other senses; in spatial and verbal ability; and in innate play behavior during childhood. The hormones that mediate the divergence of the sexes, resulting in statistical differences with overlap in these various traits, are relatively well understood. The major gene that triggers their ultimate manufacture during fetal and childhood development has been located on the Y chromosome. It is

called *Sry*, for sex-determining region of Y. In its absence, when the individual has two X chromosomes rather than an X and Y, the fetal gonads develop into ovaries, with all the consequences that follow in endocrine and psychophysiological development. These facts may not satisfy everyone's ideological yearning, but they illustrate in yet another way that, whether we like it or not, *Homo sapiens* is a biological species.

TO THIS POINT I have traced most of the steps of gene-culture coevolution, circling from genes to culture and back around to genes, as evidence allows. These steps can be summed up very briefly as follows:

Genes prescribe epigenetic rules, which are the regularities of sensory perception and mental development that animate and channel the acquisition of culture.

Culture helps to determine which of the prescribing genes survive and multiply from one generation to the next.

Successful new genes alter the epigenetic rules of populations.

The altered epigenetic rules change the direction and effectiveness of the channels of cultural acquisition.

The final step in this series is the most crucial and contentious. It is embodied in the problem of the genetic leash. Throughout prehistory, particularly up to a hundred thousand years ago, by which time the modern *Homo sapiens* brain had evolved, genetic and cultural evolution were closely coupled. With the advent of Neolithic societies, and especially the rise of civilizations, cultural evolution sprinted ahead at a pace that left genetic evolution standing still by comparison. So, in this last exponential phase, how far apart did the epigenetic rules allow different cultures to diverge? How tight was the genetic leash? That is the key question, and it is possible to give only a partial answer.

Cultural evolution vs. genetic evolution

In general, the epigenetic rules are strong enough to be visibly constraining. They have left an indelible stamp on the behavior of people in even the most sophisticated societies. But to a degree that may prove discomfiting to a diehard hereditarian, cultures have dispersed widely in their evolution under the epigenetic rules so far studied. Particular features of culture have sometimes emerged that reduce Darwinian fitness, at least for a time. Culture can indeed run wild for a while, and even destroy the individuals that foster it.

THE BEST WAY to express our still very imperfect knowledge of the transition from the epigenetic rules to cultural diversity is to describe real cases. I will offer two such examples, one relatively simple, the other complex.

The simple first. If all verbal communication were stripped away, we would still be left with a rich paralanguage that communicates most of our basic needs: body odors, blushing and other telltale reflexes, facial expressions, postures, gesticulations, and nonverbal vocalizations, all of which, in various combinations and often without conscious intent, compose a veritable dictionary of mood and intention. They are our primate heritage, having likely persisted with little change since before the origin of language. Although the signals differ in detail from one culture to the next, they contain invariant elements that reveal their ancient genetic origin. For example:

- Anstrostenol is a male pheromone concentrated in perspiration and fresh urine. Perceived variously as musk or sandalwood, it changes sexual attraction and warmth of mood during social contacts.
- To touch another is a form of greeting regulated by the following innate rules: Touch strangers of the same sex on the arms only, spreading to other parts of the body as familiarity increases, the more so for intimates of the opposite sex.
- Dilation of the pupils is a positive response to others, and one especially prominent in women.
- Pushing the tongue out and spitting are aggressive displays of rejection; flicking the tongue around the lips is a social invitation, used most commonly during flirtation.
- Closing the eyes and wrinkling the nose is another universal sign of rejection.
- Opening the mouth while pulling down the corners of the mouth to expose the lower teeth is to threaten with contempt.

These and other nonverbal signals are ideal subjects for understanding the coevolution of genes and culture. A great deal is already known of their anatomy and physiology; and their genetic prescription

and controlling brain activity are likely to prove simple in comparison with verbal communication. The variation in meaning of each signal in turn caused by cultural evolution can be observed by its multiple uses across many societies. Each signal has its own amount of such variation, its own flexibility and resulting scatter of nuance across the cultures of the world. Put another way, each set of genes prescribing the basic structure of particular signals has its own norm of reaction.

The culture of nonverbal signals awaits study from this comparative viewpoint. An instinctive case of moderate dispersion is that of eyebrow flashing, one of many examples provided by the pioneering German ethologist Irenäus Eibl-Eibesfeldt. When a person's attention is caught, he opens his eyes widely to improve vision. When he is surprised, he opens his eyes very widely, while lifting the eyebrows conspicuously. Eyebrow lifting has been universally ritualized, presumably by genetic prescription, into eyebrow flashing, a signal that invites social contact. By ritualization is meant the evolution of a movement with a function in one context, in this case eye opening and eyebrow lifting, into a conspicuous, stereotyped form, in this case eyebrow flashing used for communication. That is the genetic part of the gene-culture coevolution. Eyebrow flashing has also been subjected to moderate dispersion of meaning across societies by the cultural part of gene-culture coevolution. In different societies and contexts it is combined with other forms of body language to signal greeting, flirtation, approval, request for confirmation, thanking, or emphasis of a verbal message. In Polynesia it is used as a factual "yes."

The second case of gene-culture coevolution I wish to present, because it is the most thoroughly researched of the more complex examples to date, is color vocabulary. Scientists have traced it all the way from the genes that prescribe color perception to the final expression of color perception in language.

Color does not exist in nature. At least, it does not exist in nature in the form we think we see. Visible light consists of continuously varying wavelength, with no intrinsic color in it. Color vision is imposed on this variation by the photosensitive cone cells of the retina and the connecting nerve cells of the brain. It begins when light energy is absorbed by three different pigments in the cone cells, which biologists have labeled blue, green, or red cells according to the photosensitive pigments they contain. The molecular reaction triggered by the light energy is transduced into electrical signals that are relayed to the retinal ganglion cells forming the optic nerve. Here the wavelength information is recombined to yield signals distributed along two axes. The brain later interprets one axis as green to red and the other as blue to yellow, with yellow defined as a mixture of green and red. A particular ganglion cell, for example, may be excited by input from red cones and inhibited by input from green cones. How strong an electric signal it then transmits tells the brain how much red or green the retina is receiving. Collective information of this kind from vast numbers of cones and mediating ganglion cells is passed back into the brain, across the optic chiasma to the lateral geniculate nuclei of the thalamus, which are masses of nerve cells composing a relay station near the center of the brain, and finally into arrays of cells in the primary visual cortex at the extreme rear of the brain.

Within milliseconds the visual information, now color-coded, spreads out to different parts of the brain. How the brain responds depends on the input of other kinds of information and the memories they summon. The patterns invoked by many such combinations, for example, may cause the person to think words denoting the patterns, such as: "This is the American flag; its colors are red, white, and blue." Keep the following comparison in mind when pondering the seeming obviousness of human nature: An insect flying by would perceive different wavelengths, and break them into different colors or none at all, depending on its species, and if somehow it could speak, its words would be hard to translate into our own. Its flag would be very different from our flag, thanks to its insect (as opposed to human) nature.

The chemistry of the three cone pigments—the amino acids of which they are composed and the shapes into which their chains are folded—is known. So is the chemistry of the DNA in the genes on the X chromosome that prescribe them, as well as the chemistry of the mutations in the genes that cause color blindness.

So, by inherited and reasonably well understood molecular processes the human sensory system and brain break the continuously varying wavelengths of visible light into the array of more or less discrete units we call the color spectrum. The array is arbitrary in an ultimately biological sense; it is only one of many arrays that might have evolved over the past millions of years. But it is not arbitrary in a cultural sense: Having evolved genetically, it cannot be altered by learning or fiat. All of human culture involving color is derived from this

unitary process. As a biological phenomenon color perception exists in contrast to the perception of light intensity, the other primary quality of visible light. When we vary the intensity of light gradually, say by moving a dimmer switch smoothly up or down, we perceive the change as the continuous process it truly is. But if we use monochromatic light—one wavelength only—and change that wavelength gradually, the continuity is not perceived. What we see, in going from the short-wavelength end to the long-wavelength end, is first a broad band of blue (at least one more or less perceived as that color), then green, then yellow, and finally red.

The creation of color vocabularies worldwide is biased by this same biological constraint. In a famous experiment performed in the 1960s at the University of California at Berkeley, Brent Berlin and Paul Kay tested the constraint in native speakers of twenty languages, including Arabic, Bulgarian, Cantonese, Catalan, Hebrew, Ibibio, Thai, Tzeltal, and Urdu. The volunteers were asked to describe their color vocabulary in a direct and precise manner. They were shown a Munsell array, a spread of chips varying across the color spectrum from left to right, and in brightness from the bottom to the top, and asked to place each of the principal color terms of their language on the chips closest to the meaning of the words. Even though the terms vary strikingly from one language to the next in origin and sound, the speakers placed them into clusters on the array that correspond, at least approximately, to the principal colors blue, green, yellow, and red.

The intensity of the learning bias was strikingly revealed by an experiment conducted on color perception during the late 1960s by Eleanor Rosch, also of the University of California at Berkeley. In looking for "natural categories" of cognition, Rosch exploited the fact that the Dani people of New Guinea have no words to denote color; they speak only of *mili* (roughly, "dark") and *mola* ("light"). Rosch considered the following question: If Dani adults set out to learn a color vocabulary, would they do so more readily if the color terms correspond to the principal innate hues? In other words, would cultural innovation be channeled to some extent by the innate genetic constraints? Rosch divided 68 volunteer Dani men into two groups. She taught one a series of newly invented color terms placed on the principal hue categories of the array (blue, green, yellow, red), where most of the natural vocabularies of other cultures are located. She taught a second group of Dani men a series of new terms placed off center, away from the main clusters formed by other languages. The first group of volunteers, following the "natural" propensities of color perception, learned about twice as quickly as those given the competing, less natural color terms. They also selected these terms more readily when allowed a choice.

Now comes the question that must be answered to complete the transit from genes to culture. Given the genetic basis of color vision and its general effect on color vocabulary, how great has been the dispersion of the vocabularies among different cultures? We have at least a partial answer. A few societies are relatively unconcerned with color. They get along with a rudimentary classification. Others make many fine distinctions in hue and intensity within each of the basic colors. They have spaced their vocabularies out.

Has the spacing out been random? Evidently not. In later investigations, Berlin and Kay observed that each society uses from two to eleven basic color terms, which are focal points spread across the four elementary color blocks perceived in the Munsell array. The full complement (to use the English-language terminology) is black, white, red, yellow, green, blue, brown, purple, pink, orange, and gray. The Dani language, for example, uses only two of the terms, the English language all eleven. In passing from societies with simple classifications to those with complicated classifications, the combinations of basic color terms as a rule grow in a hierarchical fashion, as follows:

Languages with only two basic color terms use them to distinguish black and white.

Languages with only three terms have words for black, white, and red.

Languages with only four terms have words for black, white, red, and either green or yellow.

Languages with only five terms have words for black, white, red, green, and yellow.

Languages with only six terms have words for black, white, red, green, yellow, and blue.

Languages with only seven terms have words for black, white, red, green, yellow, blue, and brown.

No such precedence occurs among the remaining four basic colors, purple, pink, orange, and gray, when these have been added on top of the first seven.

If basic color terms were combined at random, which is clearly not the case, human color vocabularies would be drawn helter-skelter from among a mathematically possible 2,036 possibilities. The Berlin-Kay progression suggests that for the most part they are drawn from only twenty-two.

At one level, the twenty-two combinations of basic terms are the dispersion of memes, or cultural units, generated by the epigenetic rules of color vision and semantic memory. In simple language, our genes prescribe that we see different wavelengths of light a certain way. Our additional propensity to break the world into units and label them with words causes us to accumulate up to eleven basic color units in a particular order.

That, however, is not the end of the story. The human mind is much too subtle and productive to stop at eleven words that specify different wavelengths. As the British linguist John Lyons has pointed out, the recognition of a color in the brain does not necessarily lead to a term that denotes only the light wavelength. Color terms are often invented to include other qualities as well, particularly texture, luminosity, freshness, and indelibility. In Hanunóo, a Malayo-Polynesian language of the Philippines, *malatuy* means a brown, wet, shiny surface, the kind seen in freshly cut bamboo, while *marara* is a yellowish, hardened surface, as in aged bamboo. English-language speakers are prone to translate *malatuy* as "brown" and *marara* as "yellow," but they would capture only part of the meaning and perhaps the less important part. Similarly, *chloros* in ancient Greek is usually translated as simply "green" in English, but its original meaning was apparently the freshness or moistness of green foliage.

The brain constantly searches for meaning, for connections between objects and qualities that cross-cut the senses and provide information about external existence. We penetrate that world through the constraining portals of the epigenetic rules. As shown in the elementary cases of paralanguage and color vocabulary, culture has risen from the genes and forever bears their stamp. With the invention of metaphor and new meaning, it has at the same time acquired a life of its own. In order to grasp the human condition, both the genes and culture must be understood, not separately in the traditional manner of science and the humanities, but together, in recognition of the realities of human evolution.