CULTURE AS A BIOLOGICAL PRODUCT
This is the essence of the matter as I understand it: culture is ultimately a biological product. As biology progresses as a science, it is sure to alter our understanding of social behavior and institutions. A large part of the variance in personality and cognition, in many cases half or more, is hereditary in origin. Even then the total amount due to heredity and environment combined is only a minute fraction of the amount conceivable, because cognitive development is severely constrained by genetically prescribed rules common to human beings. It has been said that there are no genes for building airplanes. That of course is true. But people build airplanes to conduct the primitive operations of human beings, including war, tribal reunions, and bartering, which conform transparently to their biological heritage. Culture conforms to an important principle of evolutionary biology: most change occurs to maintain the organism in its steady state.

The principal driving force of genetic evolution of all organisms studied to date is natural selection, the differential contribution to the next generation by various
genetic types belonging to the same population. This is the process often called Darwinism, to distinguish it from mutation pressure, orthogenesis (straight-line evolution), and other conceivable driving forces. A great deal of evolution at the level of molecular structure appears to be due to genetic drift, the random substitution of alleles affecting amino acid substitutions in proteins. Nevertheless, the main features of anatomy, physiology, and behavior are ultimately ascribable to natural selection.

A differential contribution to the next generation can be achieved by the interplay of two advantages gained: longer life and greater reproduction. Individuals can put more of their genes into the future by reproducing as fast as possible, counting on at least a few surviving to maturity. This is the $r$ strategy of reproduction. Or they can get the same result by producing only a small number of high-quality offspring and nurturing them carefully to be sure that most or all reach maturity in good condition. This is the $K$ strategy of reproduction. Which of the two strategies works best depends on the environment. When resources are unpredictable, with a good chance of extinction from one place or time to another, the $r$ strategy works best. When resources are dependable and fixed, so that land tenure is important, the $K$ strategy is more likely to succeed. Biologists often place species and genetic strains along an $r-K$ continuum, relating their reproductive strategies to the environment in which the species and strains have evolved. It is also possible to have geno-
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types that program switches from one strategy to the next as conditions change. Human beings occupy a small segment of the r–K continuum near the K extreme.

Gene-Culture Coevolution

Human evolution is a unique dual-track system compounded of genetic change and cultural change. On the one hand genetic change brought about an extremely rapid growth of the human brain, with a 3.2-fold increase in the volume of the cerebral cortex alone from the time of *Homo habilis* 2 million years ago to the appearance of early *Homo sapiens* about 500,000 years ago, accompanied by profound architectural innovations in the larynx and speech centers of the brain. Cultural change is much faster, but it is limited and directed by the restricting properties of the brain and sensory apparatus.

Most of the difficulty in human sociobiology arises not from the differences in procedure and language between biologists and social scientists, although these are real enough, but from the fact that the subject of common interest, the interaction of biological and cultural evolution, remains largely unexplored. We all know that human social behavior is transmitted through learning and culture. We also know that the distinctive properties of cognition, ranging from a sensory perception to
memory and decision making, have a powerful effect on culture. Culture is determined ultimately by the mental development of individual human beings. The properties of this development can be characterized by epigenetic rules, which are defined as any regularities that bias behavior in a particular direction. To give a quick example, human beings are highly audiovisual and depend very little on smell and taste in comparison with the great majority of animal species. This biological property redounds to a much richer vocabulary describing hearing and vision than is the case for smell and taste. In various languages around the world, about two-thirds to three-fourths of all the words applying to the senses describe hearing and vision, while one-tenth or fewer describe smell and taste.

Genetic evolution thus affects cultural evolution. Conversely, cultural evolution affects biological evolution, by creating the environment in which the genes (the ones prescribing epigenetic rules) are tested through natural selection. Genes and culture are in fact inseverably linked. Changes in one inevitably force changes in the other, resulting in what has come to be called gene-culture coevolution. The process is believed to occur as follows:

- The genes prescribe the rules of development (the epigenetic rules) by which the individual mind is assembled.
- The mind grows by absorbing parts of the culture already in existence.
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- The culture is created anew in each generation by the summed decisions and innovations of all members of the society.
- Some individuals possess epigenetic rules enabling them to survive and reproduce better in the contemporary culture than other individuals. This genetic fitness can be enhanced either by direct selection, the furthering of direct descendants, or by kin selection, the furthering of collateral kin in addition to direct descendants.
- The more successful epigenetic rules spread through the population, along with the genes that encode them. Put another way, the population evolves genetically with reference to the epigenetic rules.

To summarize to this point, culture is created and shaped by biological processes while the biological processes are simultaneously altered in response to cultural change. This process is not difficult to envisage, but the rates at which the two forms of evolution occur and the tightness of the linkages between them remain largely unsolved problems.

The Units of Culture

The principal theoretical difficulties of the social sciences are two in number. First, in the study of culture there are
no "natural kinds," basic atomic units equivalent to genes, cells, and organisms that can form the base of permutational operations in analysis. The lack of natural kinds guarantees the second difficulty, "nomic isolation." Each major discipline—anthropology, sociology, political science, and so forth—has been required to develop its own conceptual base and language.

The discovery of natural kinds in culture would represent a key theoretical advance in the social sciences. Most scholars appear to believe that such units either do not exist or, if they do exist, cannot be derived by any means currently available. However, there is some reason to believe that natural units do exist and are built on the natural units of semantic memory. Semantic memory comprises words and symbolic manipulation, as opposed to episodic memory, which entails running sequences of visual and other sensory experience. It tends to organize impressions into discrete clusters. Experimental studies have revealed that the cuts are made around objects or abstractions that have the most attributes in common. Hence although categories such as "tree," "dog," and "house" do not exist in the real world, they are collections of objects that share a relatively large number of stimuli most easily processed by the brain. Children move easily into this mode of memory formation, performing equally well on objects or collections of objects. They organize certain identifying stimuli into ensembles (such as "cookies" versus "cakes" and "chairs" versus "stools") that are almost as sharply demarcated as the separate objects themselves.
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The brain speeds processing still further by compounding the clusters hierarchically into larger assemblages that possess a discrete, interchangeable form. The units of semantic memory, which are experienced as objects or abstractions, are appropriately called nodes, thus aligning the description to the nodes and the links between nodes envisioned in spreading-activation models of memory storage and recall. There are at least three levels of nodes. Concepts, the most elementary clusters, are signaled by words or phrases (such as “dogs” and “hunt”). Propositions are signaled by phrases, clauses, or sentences expressing objects and relationships (“dogs hunt”). Finally, schemata are signaled by sentences and larger units of text (the “technique of hunting with dogs”). Node-link structures were originally proposed by psychologists as theoretical representations, but they have gained considerable substance through methods that detect their organization. Node-link structures steadily enlarge in size and complexity in the growing child, and the main steps in the growth correspond at least roughly to the Piagetian stages of mental development. The stages are not mere accidents of personal growth but general processes that show some regularity across cultures. Hence, in a manner important for the entire relation of biology to culture, the semantic mechanisms of culture formation are more robust and consistent than the final products they generate.

For each concept the brain tends to select a prototype that constitutes the standard, such as a particular wavelength and intensity to form the idealized color red or a
particular body shape and size to form the typical "dog." Given an array of similar variants, the mind can deduce a standard near the average of the variants and use it as the prototype even without having perceived any example of it directly. The most important result for gene-culture coevolution is that the divisions are created and labeled, even when the stimuli being processed vary continuously. In short, the mind automatically imposes a semidiscrete, hierarchical order upon the world.

Most of the concepts that make up the basic units of semantic memory are subject to purely phenotypic variation arising from the particularities of cultural history. Nevertheless there is a tendency for those belonging to at least a few categories to occur consistently across cultures. As Eleanor Rosch has shown, such categories include elementary geometric forms (square, circle, equilateral triangle), the facial expressions of six basic emotions (happiness, sadness, anger, fear, surprise, disgust), and the basic colors (red, yellow, green, blue).

The level of the node of semantic memory, whether concept (the most elementary recognizable unit), proposition, or schema, determines the complexity of the generated behavior or artifact maintained in the culture. For example, the differentiation of letters or ideographs is at the level of the concept, the initial verbal reaction to a stranger is a proposition, and the expression of an incest taboo is a schema. If this model of semantic memory holds, new discoveries refining the hierarchy of memory nodes can be expected to advance the identification of
culture units, or "culturgens," in the same manner that advances in cellular chemistry have improved our comprehension of the gene and studies of population structure have refined our understanding of biological species.

Although a direct correspondence between nodes and generative units of culture appears feasible at lower levels of organization, there is no reason to expect the more complex constructions of culture to be mapped onto semantic nodes in a one-to-one fashion. Marriage ceremonies and temple architecture, for example, are the outcomes of numerous interlocking behaviors that result from cognitive activity with multiple culturgens. These in turn vary according to the particularities of local history. Nevertheless, each can be realistically interpreted as the outcome of cognitive development, which is attained principally through the assembly of node-link networks. Cultural evolution is the shifting of the outer phenotypes of behavior and artifacts through the insertion and combination of their basic generative structures in semantic memory. The compound structures of culture arise from the semantic nodes.

**Epigenetic Rules**

The epigenetic rules of cognitive development determine the manner in which the nodes are created and combined to form the semantic networks—and hence, culture.
These physiological processes impose a strict filtering of stimuli from the environment and alter each step of cognition thereafter, from short-term memory and storage in long-term memory to recall, feeling, reveries, and decision making.

The most fully analyzed example of the biological channeling of culture by the processes of filtering and biasing arises in the vocabulary of vision. Light intensity is perceived as a continuum; if the light in a room is raised or lowered gradually with a dimmer switch, the conscious brain perceives the change as a continuous progression along a more or less even gradient. There are no steps or benchmarks, and consequently languages contain relatively few words to describe the variation of light intensity. In contrast, normally sighted individuals see variation in wavelength not as a continuously varying property of light (which it is) but as the four basic colors of blue, green, yellow, and red, along with various blends in the intermediate zones. If a room is flooded with monochrome light of short wavelength (blue), and the wavelength is then gradually increased, the change is seen as a series of steps from one basic color to another. The physiological basis of this illusion is partially known. The innate human color classification starts from the differentiation of the retinal cones into three types, whose maximal sensitivities correspond to blue, green, and red. The light-sensitive pigments in the cones are membrane proteins, with retinal, a pigment molecule, attached in each
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case to an apoprotein. When the retinal is altered by a photon of light to pass from the *cis* to the *trans* state, the apoprotein is induced into a configurational change which in turn depolarizes an afferent nerve cell. The red and green pigments have recently been identified, and the genes specifying them located and sequenced. The Mendelian genetics of color blindness has also been partially worked out. Further encoding of color occurs in four classes of interneurons in the lateral geniculate nuclei of the thalamus that lead to the processing centers of the visual cortex.

How do such facts bear on culture? The epigenetic constraints in color perception are reflected in languages of all cultures thus far examined. In a classic study by Brent Berlin and Paul Kay, native speakers of twenty languages around the world (including Arabic, Bulgarian, Cantonese, Catalan, Hebrew, Ibibio, Japanese, Thai, Tzeltal, Urdu, and others) were shown arrays of chips classified by color and brightness in the Munsell system. They were asked to place each of the principal color terms of their language within this two-dimensional array. The results show clearly that the languages have evolved in a way that conforms closely to the epigenetic rules of color discrimination. The words fall into largely discrete clusters that correspond, at least approximately, to the principal colors that are innately distinguished.

The intensity of learning bias was further revealed by another experiment conducted by Eleanor Rosch. 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 addressed the following question: if Dani adults set out to learn a color vocabulary, would they do so more readily if the color terms corresponded 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 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 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 given a choice.

In a parallel experiment on "psychoaesthetics," Gerda Smets measured the degree of physiological arousal in adults caused by geometric designs of varying degrees of complexity. The measure she used was alpha wave blockage, generally interpreted to be an index of arousal even when unaccompanied by conscious awareness. A sharp peak of maximum response was obtained with computer-generated figures at 20 percent redundancy, the
amount found, for example, in a maze with between 10 and 20 angles. Less redundancy and more redundancy were far less stimulating. It does not seem coincidental that 20 percent is approximately the amount of complexity in logotypes, ideographs, frieze design, grille work, and other designs chosen for instant recognition and aesthetic pleasure. In other words, the development of art and written language may be strongly influenced by an innate constraint in cognition.

The innate bias in learning, described by psychologists as “prepared” (bias toward) and “counterprepared” (bias against), is perhaps most strikingly illustrated by phobias. These are extreme, irrational fears associated with nausea, cold sweat, and other reactions of the central nervous system. It is notable that the phobias are most easily evoked by many of the greatest dangers of mankind’s ancient environment, including tight spaces, heights, thunderstorms, running water, snakes, and spiders, but are rarely evoked by the greatest dangers of modern technological society, including guns, knives, automobiles, explosives, and electric sockets.

The Translation from Genes to Culture

In order to picture gene-culture coevolution more clearly, imagine two alien civilizations on distant planets. Both
The patterns of nature have about the same level of cultural sophistication as human beings, and both transmit virtually all of their cultures by means of learning. However, in one of the civilizations only a single version of each category of learning can be transmitted: one language, one love song, one marriage ceremony, one mode of warfare, and so forth. In this extreme form, a "pure genetic transmission" of the culture, the genes restrict the learning process—even though the culture is taught in classrooms, recorded in books, and so forth. The conception is not too far-fetched. Individuals of this species are like the white-crowned sparrows of California, which must hear the song of their own species in order to learn it but are impervious to all other songs.

The second alien species outwardly resembles the first, but it possesses a totally blank-state mind. All cultural possibilities are open to the inhabitants. They can be taught any language, any song, any martial tactic with approximately equal ease. In this "pure cultural transmission" scenario, the genes direct the construction of the body and brain but not the behavior. The mind is entirely a product of the accidents of history, including the place the aliens live in, the foods they encounter, and the stray inventions of words and gestures.

Human beings are of course in between these extremes. Our social behavior is based on gene-culture transmission: an immense array of possibilities can be learned, innovation occurs frequently, but biological
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Properties in the sense organs and brain make it more likely that certain choices will be preferred or at least more easily learned than others. In some categories, such as incest avoidance, the choices are narrowly constrained. In others, such as the semantic content of particular languages (but not the deep grammatical properties), the choices are very broad and more nearly equipotent.

This conception of mental development brings us to the question of variation in the choice of culturgens among members of a given society and among entire societies. The evolution of culture displays some striking parallels with genetic evolution. Innovations appear in the population in the manner of mutations, spread like genes, and are favored or abandoned by processes resembling natural selection and random drift. The interaction of these biologically based entities with the environment is at least as complex and analytically formidable as that controlling conventional genetic evolution. Among the variables that must eventually be taken into account are the particular environment in which the society lives, the degree of its contact with surrounding cultures, the accidents of history, and the genetic variation among its members.

Using a separate language, social scientists and humanists have already explored these matters in considerable depth. But although their accounts of cultural variation are rich and illuminating, they do not penetrate to the biological underpinnings of mental life. Ordinary inductive
descriptions of behavior and culture can in fact never achieve this end; it is just not enough, as Darwin said, to attack the citadel itself. The more promising approach is less direct. It reconstitutes cultural variation along with central tendencies in a combined analytic-synthetic fashion, from the bottom up, using the facts of biology and cognitive psychology to work into more complex social phenomena.

It is logical to begin such an analysis with the simple case of a human population that is genetically uniform with reference to the processes of cognition. In studies conducted in 1980–1982 and described in our 1984 book, *Promethean Fire*, Charles Lumsden and I chose as a goal the transition from individual learning and decision making to cultural diversity in the absence of genetic variation and in a relatively uniform environment. We set out to find which patterns of cultural diversity can be expected to result from different forms and degrees of bias in cognitive development, and we asked whether the observed patterns of cultural diversity were consistent with what is understood about this development.

We began with the simple observation that each individual comes to favor certain marital customs, modes of dress, ethical precepts, and so forth, from among those available. And every time individuals modify their memories or face decisions in everyday life, they enact intricate sequences of events in cognition that obey the peculiar, constraining properties of semantic memory. Not all the
culturgens being processed are treated equally; cognition has not evolved as a wholly neutral filter, and the mind incorporates and uses certain culturgens more readily than others. Furthermore, the biases often shift with age, creating patterns that change with the demographic properties of societies.

Because such usage biases are both discrete and episodic in operation, they can be approximated by transition probabilities, which can then be converted into rates of change treated as Markov processes. Experience from sociological studies has shown that such models can incorporate memory and social context to an extent sufficient to fit real (but by no means all) data on choices made by individuals. We have examined ways of incorporating experience and memory to make the needed jump to cultural variation still more realistic.

In particular, the transition rates from one alternative choice to another are affected by the choices already made by others, in other words the cultural context. Few quantitative studies have been made of this social influence, but enough is known to establish that it varies substantially from one behavioral category to another. For example, sibling incest is avoided by individuals throughout their lives regardless of the preferences of others, whereas the direction of attention of individuals in street crowds rises steadily in conformity with others as the percentage looking in one direction increases.

With the aid of these mathematical techniques, it is
possible to translate decision making and the effects of social networks into patterns of cultural diversity. Although this phase of the work is theoretical, it has yielded several general results that are interesting enough to merit closer attention. First, the procedure identifies the quantitative description of cultural diversity most readily aligned with studies of cognitive science. This is the *ethnographic distribution*, comprising the relative frequencies of societies in which different percentages of the members use or at least prefer to use each of the competing culturgens. A simple ethnographic distribution would be the following: in 52 percent of the societies all members prefer outbreeding to incest, in 46 percent of the societies 99 percent prefer outbreeding, and in 2 percent of the societies 98 percent prefer it.

A notable finding of the models is that very substantial cultural diversity can be expected even when all of the societies are genetically biased to a rather high degree with respect to that particular category of cognition and behavior. Even though all of humanity may be genetically very likely to choose outbreeding over incest, substantial variation will still arise among the societies in the percentages of members choosing avoidance over acceptance. Because the mind is probabilistic in operation, what emerges is not a fixed percentage of individuals making one choice across all societies but rather the pattern of diversity, in other words, the form of the ethnographic distribution. A distinct ethnographic curve will
arise from each different degree of bias toward one cul-
turgen and each different degree of sensitivity toward the
choice already made by others in the society. For each cat-
egory of cognition and behavior, human beings appear to
have a distinctive degree of developmental bias and sensi-
tivity. As a result the amount and pattern of cultural diver-
sity can be expected to differ among these categories.

It is often argued that the existence of cultural diversity
shows that there is no underlying genetic constraint. That
conclusion, which at first may seem common sense, is in-
correct: the mere occurrence of the diversity says nothing
one way or the other about constraints. On the other
hand, patterns of diversity can tell us a great deal. Another
common misconception is that the existence of biological
influence on diversity implies genetic differences between
the societies. But as Lumsden and I have shown, diversity
arises in distinctive patterns even in genetically uniform
populations.

The models lead to another substantive result of the
gene-to-culture theory. Quite small differences in bias
and sensitivity of the magnitude demonstrated among dif-
ferent categories of human cognition and behavior are
enough to generate strong differences among their pat-
terns of cultural diversity. Most strikingly, the distribu-
tions pass from a single mode to multiple modes (a mode
is a frequency higher than surrounding frequencies)
rather rapidly as sensitivity is altered. These differences
are great enough to be detected even with relatively crude
ethnographic or sociological data. They show how studies of cognitive and social psychology can be fed directly into the data of anthropology and sociology as part of a general quantitative theory of culture.

Culture is deeply rooted in biology. Its evolution is channeled by the epigenetic rules of mental development, which in turn are genetically prescribed. We can envisage the full chain of causation from genetic prescription to the formation of culture and back again through natural selection to changes in gene frequencies. Gene-culture coevolution, as the reciprocating process is known, has been documented through part of the cycle, and some of the key steps have been addressed with analytic models. Its further exploration seems very promising for the future study of culture.