The Channeling of Social Behavior

Genes, Mind, and Culture. The Coevolutionary Process. CHARLES J. LUMSDEN and EDWARD O. WILSON. Harvard University Press, Cambridge, Mass., 1981. xiv, 428 pp., illus. $20.

Hereditarians have often been cautioned that cultural inheritance or social learning can simulate Mendelian transmission. Now sociobiologists Lumsden and Wilson describe a theoretical model in which genetic processes can simulate cultural transmission.

Their model is an ambitious attempt to specify the mechanisms underlying the interaction between genes and the environment during the cognitive development and socialization of individuals and in the coevolution of genes and culture. In this model they describe a causal circuit that dynamically connects genes to the development of the nervous system and cognition and then connects cognition to social interaction and enculturation. Their creative contribution is the synthesis and integration of relevant theory and data from such diverse sciences as cognitive and developmental psychology, neurobiology, behavioral and population genetics, sociology, anthropology, and ecology. It is admirable that they have emphasized underlying mechanism and dynamics rather than superficial mathematical description. However, much of the theory is speculative and poorly documented. Arbitrary assumptions are made that bias the conclusions in a way that is easily predicted from the preconceptions described by Wilson in his earlier writings. Firm and sweeping generalizations are made from incomplete data about special cases. Such speculations and assumptions may be of heuristic value if they lead to explicit testable hypotheses. However, careful examination of the more controversial assumptions of this theory reveals that they are formulated so that they are either untestable or, at best, subject to weak, indirect tests.

Culture is broadly defined as the sum of all the individual artifacts, behaviors, and mental concepts transmitted among the members of society by learning. The individual units that make up culture are called "culturgens." Choices among alternative culturgens require the cognitive processing of information, including steps of sensory filtering, perceptual discrimination, valuation, and decision-making. This processing is subject to neurobiological constraints that channel mental development in specific directions during the interaction between an individual's genotype and environment. This process of gene-environment interaction during development is known as epigenesis. Any regular constraints on cognitive development are called "epigenetic rules" and affect the probabilities for choosing among alternative culturgens.

The central tenet of human sociobiology is that social behaviors are shaped by natural selection. In order to link genetic and cultural evolution directly, Lumsden and Wilson must assume the existence of heritable genetic bias in the development of social behavior and other culturgens. They admit that in human beings culturgen choices are neither directly nor completely determined by genes. However, they assume that genes influence the probability and form of learned behavior by "biases" inherent in the epigenetic rules. They further admit that epigenetic rules are often flexible and context-dependent; in other words, the reaction range of a human genotype depends on the physical environment, on the habitat, and eventually on prior learning or cultural experience. However, they emphasize that even with a flexible rule, once the context is specified, the form of the response may be completely predictable. That is, behavior may be both flexible (varying according to context) and selective (invariant within a given context).

Consequently a crucial empirical question for this theory is the degree of flexibility and selectivity in the epigenetic rules. After introducing their main ideas in chapter 1, the authors describe cognitive and behavioral epigenesis in detail at different levels of developmental complexity.

Social behaviors are the product of a complex developmental sequence of events. Each element in this sequence may be associated with an epigenetic rule. Thus, the epigenetic rules are equivalent to phenotypes that vary in their own developmental complexity or remoteness from the primary gene products. The authors consider epigenetic rules at two levels of complexity: the primary rules of mental development lead from sensory filtering to perception whereas the secondary rules include the evaluation of these primary percepts through the processes of storage in memory, feature evaluation, emotional response, and decision-making. Examples of constraints in the primary rules include congenital preference for sweet tastes and facilitation of human classification of color into four modal colors even though color is a continuous dimension. Examples of constraints in the secondary rules include fear of strangers in infants and prepared learning of phobias for selective types of dangers (for example, heights and water in contrast to guns or electric sockets). The primary rules are supposed to be more completely genetically determined than the secondary rules. The primary rules are more automatic processes that are highly inflexible and selective whereas the secondary rules are supposed generally to have intermediate flexibility and low selectivity. In other words, decision-making often depends on the environmental context and extensive nonheritable variation. Nevertheless there is supposed to be a high likelihood of at least a small degree of genetically determined bias in the choice among culturgens.

Lumsden and Wilson repeatedly make the provocative statement that epigenetic rules are ultimately genetically determined. This is misleading because in their theory it is equally true that epigenetic rules are ultimately environmentally determined. Both aspects of the process of nonadditive gene-environment interaction are necessarily involved. The only question of relevance to the potential for coevolutionary change is the extent to which genetic and environmental differences determine differences in culturgen usage.

Unfortunately, no strong evidence of heritable genetic variance in the secondary epigenetic rules is ever presented. Lumsden and Wilson do not even describe the kinds of empirical studies that are needed to test their assumptions about the heritability of epigenetic rules. The criterion they do use to evaluate genetic bias in their examples is inadequate. According to them, transmission is purely genetic when the same culturgen is always selected in a population. In contrast, when all culturgens are equally likely to be used transmission is purely cultural. The intermediate case, called gene-culture transmission, occurs when alternative culturgens are not equally likely to be chosen. As examples, every household in a certain society may have a television, and music by the Beatles may be more popular than classical renditions of Bach. It is naïve to conclude from these statements that ownership of a television is completely controlled genetically and that musical preference is partially genetically determined.

What kinds of empirical data would be required to evaluate gene-environment interaction? Studies at three population levels are relevant to gene-cultural coevolution: comparisons between different "eucultural" species, between societies within species, and within societies. The etiology of traits that are common to all members of a species (that is, the Lumsden-Wilson case of pure genetic transmission) can be studied only by comparisons of two eucultural species because, as they note, inferences can be made only about nonuniform epigenetic rules. However, they also conclude that only human beings have developed euculture, that is, a culture with extensive reliance on symbolization and prolonged purposive teaching of children. Therefore the possibility of pure genetic transmission is an article of sociobiological faith that is not testable. In addition, cultural evolution must be evaluated by comparisons between and within human societies, and, unfortunately, different social groups will differ in both their genotypic and their culturgenic distributions. As a result, inferences about causation will usually be ambiguous when nonadditive interaction is possible.

Analysis of data about intact families or extended pedigrees using such methods as segregation analysis, linkage analysis, and path analysis can provide much useful information. However, when there may be interaction of genetic and environmental factors, inferences about causation from pedigree data alone are highly model-dependent and open to question because of unconfirmed assumptions of the models. Nevertheless, gene-environment interaction may be evaluated, in principle, in a model-free way by observations on the range of reaction of genotypes in cross-fostering data about adoptees and data about monozygotic twins reared apart. Then both pedigree and separation data may be evaluated together to test alternative transmission models. For example, such evidence for both congenital and postnatal influences on use and abuse of ethyl alcohol has recently been obtained. However, such data are available about few traits. Generalizations to all social behavior from individual traits is unjustified.

Lumsden and Wilson also seem to suggest that any regularity in developmental sequence must be due to genetic bias. They use longitudinal developmental data to support their assumptions about genetic determination of secondary epigenetic rules about facial recognition in chapter 3. This follows from another major, but arbitrary, assumption: the only consistent directional influence on epigenesis (and hence on evolution) is genetic and not cultural. This assumption is never made explicit but is necessary to ensure that genetic biases are amplified in their model rather than being overcome by purposive teaching and thereby lost in the process of gene-cultural translation. Actually this assumption is inconsistent with other parts of the theory. Culturgens are assumed to act via relational networks in long-term memory that should facilitate their interacting in a functional manner. Expectancy and prior learning may influence subsequent information-processing. In other words, teaching may involve purposive indoctrination, and, despite the authors' assertions, this may alter both the rate and direction of gene-culture coevolution.

Given these basic assumptions and hypotheses, Lumsden and Wilson then proceed in chapter 4 to deduce the properties of gene-culture translation, that is, the consequences of the epigenetic rules for cultural structure and changes in social patterns within a single generation. They deduce two properties of their model that are their most important conclusions: first, biases in the epigenetic rules are amplified during gene-culture translation so that even small biases produce profound changes in the overlying cultural pattern; second, epigenetic rules can be highly heritable and yet generate rapid social change and wide cultural diversity. Gene-culture translation is modeled as a two-state Markov chain to reach these conclusions. Individual learning and decison-making are treated as a Markov process, that is, transition from one culturgen state to another depends only on the immediately antecedent state and not on any earlier history. The epigenetic rules set probabilities of transition from one culturgen to another rather than fixing usage patterns. The prereproductive period is assumed to be sufficiently long that each individual will make decisions so many times that the system reaches equilibrium within a single generation. This model does not consider gene frequencies or variation across generations. No genetics is actually involved, but, to the authors, the model is relevant to gene-culture transmission simply because two culturgen states are present in the population. The effects of epigenetic rules are evaluated by the distribution of probabilities that a society will possess each possible culturgen pattern given the transition probabilities. This distribution is called an ethnographic curve. The authors give three examples of this model: brother-sister incest avoidance (incest or outbreed), fission of Yanomamö villages (depart or remain), and fashion in women's dress (low or high waistlines). However, the connection of the Markov chain models and these examples to the interpretation of their gene-culture theory is specious. The mathematical model is just as relevant to cultural transmission of decision-making as it is to genetic transmission. The validity of the assumption of equilibrium is never discussed.

Essentially the authors have shown that a stochastic (probabilistic) process biased by either cultural or genetic determinants may be associated with wide cultural diversity. However, bias in the epigenetic rules underlying this diversity may be too small to be detected and may still be invoked to explain cultural variation according to this theory. In addition, any bias that is detected may not be heritable in terms of a significant parent-offspring correlation but nonadditive gene-environment interaction may be invoked to implicate genetic determination of directional effects. The predictions of the theory are ethnographic distributions that would be experimentally testable only if repeated observations could be made on a large array of culturally and genetically matched populations. Thus the theory is well buffered against the risk of falsification.

The authors' formal evaluation of changes across generations is initiated in chapters 5 and 6. They consider the effect of environmental heterogeneity on inflexible epigenetic rules in chapter 5 and more general coevolutionary dynamics with flexible epigenetic rules in chapter 6. They point out that epigenetic rules of mental development are likely to be influenced by multiple genetic loci. However, they suggest that research should initially be focused on those influenced by a single major locus and formally consider only a diallelic single locus with three genotypes that each have a different probability for using a certain culturgen. The epigenetic rules are affected by both parental and offspring culturgen frequencies. Thus, the culturgen frequencies for the offspring depend on both the epigenetic rule and gene frequencies in the parental generation. At the same time, the gene frequencies in the offspring depend on the gene frequency in the parental generation and on the differential fertility rates of the three genotypes. The gene-culture link is completed by assuming that the fertility rates are modified by genotype-dependent social behavior. Accordingly, if use of a culturgen is defined as a phenotype, the Lumsden-Wilson model is equivalent to a single-locus model with incomplete penetrance. In order to apply the model to real data the validity of the single-locus model has to be established for individual behavioral traits. Furthermore, the magnitude of the fertility differences associated with different social behaviors must be precisely estimated because the relative differences in reproductive fitness may be only a few percent of the population average. Unfortunately, much practical experience in population genetics shows that such efforts will be extremely difficult, especially for such behavioral traits as aversion to strangers and skirt length in women, notwithstanding the allure of the quest.

The authors note the analogy between gene-culture coevolution and island biogeography in chapter 7. This extension is a natural one because the innovation of culturgens and their persistence in a population is analogous to the introduction of a new species and its survival. The final chapter summarizes and discusses future directions for human sociobiology.

Lumsden and Wilson have succeeded in demonstrating the theoretical possibility that genetic bias in cognitive and behavioral development can simulate pure cultural transmission. They have synthesized an abundance of fascinating interdisciplinary data into a dynamic model that emphasizes underlying mechanism. The Lumsden-Wilson theory of gene-culture coevolution will reward all who carefully study it because the authors have given us an explicit blueprint of the machinery linking genes and social learning as well as reviewed relevant operating characteristics of cognitive development.

Sadly, their sophistic presentation seems to be motivated by unjustified hereditarian advocacy. This is surely counterproductive to their goal of uniting the social and biological sciences. Their main conclusions depend on arbitrary assumptions and mathematical analyses that are ambiguous. The validity and generality of their assumptions about the inheritance of social behavior must be tested empirically. They lack perspective on the practical limitations of both genetic epidemiology and evolutionary genetics and pay inadequate attention to existing theories of frequency-dependent selection. Most critically, their theory can have little heuristic value because it is open to only weak tests at best. It will primarily serve to widen the schism between social and biological sciences because of its provocative overstated rhetoric.

The book is not suitable for a general audience. It requires some knowledge of stochastic processes, especially theories of Markov processes. The relationship, or lack of it, between the theoretical interpretations and the mathematical results must be cautiously weighed. The serious flaws in this theory can be remedied only by greater emphasis on the design of empirical tests and collection of extensive human data. Until that is done, the Lumsden-Wilson theory, like the psychodynamic theories of Freud and his faithful disciples, will enjoy wide retrospective explanatory power but can make only limited testable predictions.

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Phytoplankton Dynamics

The Physiological Ecology of Phytoplankton. I. MORRIS, Ed. University of California Press, Berkeley, 1980. x, 626 pp., illus. $74.50. Studies in Ecology, vol. 7.

Our attempts to understand the behavior of phytoplankton have been stymied to a large degree by our inability to bridge the gaps in spatial and temporal scale between the real world of microbes and the simulated world we are forced to deal with. This inability is related far more to our limited analytical and experimental capabilities than it is to any lack of creative hypotheses about how small organisms cope with their environment. Morris, in his preface to this important book on phytoplankton ecology, forewarns us of this problem by stating that "understanding the interactions between natural populations of organisms and their environment is not easy." The 15 chapters that follow, written by an articulate and most competent group of phytoplankton ecologists and edited in an exemplary fashion by Morris, are, on the one hand, reassuring in clearly demonstrating the great progress we have made in the past decade in dealing conceptually with the relations between physical processes in the aquatic environment and the physiological and biochemical machinery of the phytoplankton. On the other hand, the book reveals many of the inadequacies in our bag of experimental tricks that, unless remedied, will keep us in the dark for a long time to come.

The book is divided into four sections: Algae and Methodology, Light, Carbon and Photosynthesis, Nutrient Dynamics, and Population Dynamics. The chapters are uniformly well written and documented, and there is good continuity between sections. The opening chapter by Taylor is a synoptic review of the basic biology of phytoplankton, reflecting the author's many years of painstaking observations on the taxonomic and physiological characteristics of the phytoplankton groups. His view that in placing major emphasis on rate processes we are in danger of ignoring systematics serves as a somewhat sober reminder that the tedious and unrewarding jobs of counting and enumerating species are, and always will be, integral components of ecological analysis regardless of how sophisticated the science becomes.

Phytoplankton rate processes are, however, a major integrating theme of the book, and the emphasis primarily is on the physiological response to environmental perturbations. The chapters by Harris on photosynthesis and light, McCarthy on nitrogen dynamics, Walsby and Reynolds on sinking and floating, Platt and Denhan on patchiness, and Malone on algal size point out the gross disparities between the actual temporal responses of phytoplankton in a highly dynamic and changing environment, controlled for the most part by mixing and turbulence, and the measurement of these responses on captured samples contained in small bottles.

Similarly, Huntsman and Sunda elucidate the tremendous difficulties facing the physiologist in trying to understand the role of trace metals in phytoplankton ecology, primarily because of analytical limitations in determining the ambient concentrations, degree of complexation, and chemical kinetics of these sparingly soluble constituents. The importance of organism–trace-metal interactions becomes increasingly clear, however, as analytical techniques continue to improve. As Sakshaug and McCarthy point out, limitations in both quantitative low-level analysis of ambient nutrients and determination of the chemical composition and total biomass of phytoplankton in the presence of other organic materials place severe restrictions on our ability to test many of the current hypotheses on the physiological response of phytoplankton to nutrient availability. In this regard Smayda painstakingly outlines what we know about phytoplankton spe-