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Commentary on Charles J. Lumsden and Edward O. Wilson (1982) *Précis of Genes, Mind, and Culture*. BBS 5:1–37.

Abstract of the original article: Despite its importance, the linkage between genetic and cultural evolution has until now been little explored. An understanding of this linkage is needed to extend evolutionary theory so that it can deal for the first time with the phenomena of mind and human social history. We characterize the process of gene-culture coevolution, in which culture is shaped by biological imperatives while biological traits are simultaneously altered by genetic evolution in response to cultural history. A case is made from both theory and evidence that genetic and cultural evolution are inseparable, and that the human mind has tended to evolve so as to bias individuals toward certain patterns of cognition and choice rather than others. With the aid of mathematical models we trace the coevolutionary circuit: The genes prescribe structure in developmental pathways that lay down endocrine and neural systems, imposing regularities in the development of cognition and behavior; these regularities (loosely labeled “epigenetic rules”) translate upward into holistic patterns of culture, which can be predicted in the form of probability density distributions (ethnographic curves); natural selection acts within human history to favor certain epigenetic rules over others; and the selection alters the frequencies of the underlying genes. The effects of genetic and cultural changes reverberate throughout the circuit and are consequently tested with the passage of each life cycle. In addition to modeling gene-culture coevolution, we apply methods from island biogeography and information theory to examine the cultural capacity of the genes, the factors determining the magnitude of cultural diversity, and the possible reasons for the uniqueness of the human achievement.

Genetic and Cultural Evolution: The Gap, the Bridge, . . . and Beyond

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In their appetite for interpreting nature, scientists, especially in the Western tradition, constantly violate nature’s most sacred property – its unity. Through a “pocket and funneling approach,” nature is divided into “parts” which are then analyzed to the last detail. Despite the methodological convenience and even the necessity of this analytic approach, it sometimes leads to formidable, artificial, and apparently unbridgeable gaps between large realms of knowledge. Of these, the most enduring (and tragic, for it reflects a divorce of man from nature) is the gap between genetic and cultural evolution, between the biological and social sciences.

Sociobiology is a new, multidisciplinary field which is attempting a synthesis of biology and the social sciences. Gene-culture coevolution – the subject of Lumsden & Wilson’s (L & W) (1981; *Genes*) – book is sociobiology’s most recent, general, and unified theme, a revolutionary step in the direction of synthesis. In fact, gene-culture coevolution represents the first substantial attempt to bridge the old, enormous, and complex gap between biology and the social sciences, through a theory (gene-culture coevolutionary theory, or simply gene-culture theory, GCT) built with the scientific rigor and elegance of mathematical modeling. GCT builds a definite link between genetic and cultural evolution, tracing “development all the way from genes through the mind to culture” (Lumsden & Wilson 1981).

When Harvard biologist Edward O. Wilson wrote “The Prospect for a Unified Sociobiology” – the last chapter of his magnificent book *The Insect Societies* (1971) – he was not making a gratuitous proposal. On the contrary: Four years later, in 1975, he produced *Sociobiology – The New Synthesis*, a thorough, scholarly treatment of this new discipline. In this book, again in the last chapter, Wilson boldly proposed that the social sciences and humanities (even ethics!) be biologized

through evolutionary theory. Such a difficult, polemical task was candidly and insightfully followed by Wilson in his *On Human Nature*, in 1978. But this book was just a sociobiological interlude. Wilson – as if following a “last chapter rule” – closed it with “Hope,” a chapter in which he solemnly declared that “by a judicious extension of the methods and ideas of neurobiology, ethology, and sociobiology a proper foundation can be laid for the social sciences, and the discontinuity still separating the natural sciences on the one side and the social sciences and humanities on the other might be erased.” And such a discreet, but revolutionary suggestion was boldly and vigorously followed by Wilson in *Genes*, after teaming up with Lumsden, a physicist, in 1978.

Thus, L & W’s book emerges not only as a mature, natural product of a sociobiological tetralogy, but as a crucial step toward a major theoretical synthesis of modern science, perhaps only comparable to the intellectual revolutions brought about by the fundamental works of Copernicus, Darwin, and Einstein.

These remarks are necessary, for I firmly believe that *Genes*, should be judged by the scientific community in a context of history and philosophy of science. Otherwise, the emotional and narrow reactions to sociobiology, still fresh in the minds of many, might quickly be spread to GCT. Such an attitude would only delay the rational recognition of the theoretical and philosophical potentials of gene-culture coevolution.

But the gap is old, enormous, and complex; and the bridge, too new to be completed. In fact, there are some fundamental aspects of GCT which call for clarification and further refinement. In a recent work (Almeida 1981), I reconsidered certain topics of human adaptability in the light of GCT. On the basis of that work, I would like to illustrate briefly some of the points that may deserve L & W’s attention in further developments of their theory.

Since GCT draws on many different disciplines, its terminology should be as neutral as possible, free from any ambiguity. Apart from the central term of the theory – culturgen – a neutral and useful neologism, L & W are not always very clear about the linkage between meaning and phenomenon for important terms (e.g. learning, social contagion, teaching) in the context of different disciplines. For example, they recognize the importance and usefulness of distinguishing socialization and en-

culturation (and even cite Margaret Mead in support of this point), but decide to use these two terms interchangeably, although sometimes making a distinction between them. They provide the reader with a good glossary, but the complexity and multidisciplinary nature of GCT would have justified the inclusions of a terminological taxonomy.

L & W do not clearly recognize that behavioral plasticity is the major biocultural factor behind rapid, drastic changes of behavior, often between two opposite, conflicting culturgen.

Accordingly, they do not incorporate into their theory the phenomenon of manipulation and countermanipulation of behavior, perhaps the most adaptive trait from acultural to eucultural species, thus of extreme importance in a phylogeny of gene-culture coevolution.

Behavior shifting between continuous and discontinuous processes of decision making is not properly treated in L & W's modeling effort. (Otherwise, they could have used catastrophe theory to model this important behavioral aspect). Therefore, their theory cannot deal adequately with some deep cognitive phenomena such as dialogic behavior and value judgment, which are critically important for the theory and praxis of gene-culture coevolution. (Strangely, they do not even mention Pugh's, 1977, basic contribution to the biology of human values.)

In considering gene-culture translation, L & W do not formally appreciate the social influence of certain important components of the socialization-enculturation spectrum – for example, education – as the lifelong, intended mediation of learning and communication processes toward certain goals.

Interestingly, the “leash principle” – “the genes hold culture on a leash” – may work the other way around. Had the authors thought of gene manipulation, they might have reached this conclusion. And that would be a clear and beautiful way of showing gene-culture coevolution.

If the “last chapter rule” holds for *Genes*, one may easily conclude that this book will be followed by a thorough and radical reinterpretation of human biology, the social sciences, and the humanities. Moreover, I believe that L & W's theory may pave the way for the completion of an overall evolutionary synthesis: that giant intellectual leap toward a unified theory of cosmic and biocultural evolution. With *Genes*, we are now at least equipped with the boldness and insight to begin dealing with this idea. The theoretical, epistemological, and practical implications of such an intellectual venture are now beyond imagination. Surely, it will affect man's view of the cosmos and of himself in novel ways. After all, in Wald's (1963, p. 133) words, “We living things are a late outgrowth of the metabolism of our Galaxy. The carbon that enters so importantly into our composition was cooked in the remote past in a dying star.”

Mathematical models for gene-culture coevolution

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One of the central tenets of *Genes, Mind, and Culture* (henceforth *Genes*) is that any successful theory of the coevolution of genes and culture must be based on an appropriate mathematical model. In view of the importance that Lumsden and Wilson (L&W) themselves place on the role of their models (1982a, p. 34), an analysis of them is essential for an evaluation of their theory. A key step in their theory is the model for the translation from the activity of individual minds to social and cultural patterns. An examination of this model reveals that, first, it depends on several unjustifiable assumptions; second, it depends on a confusion between probabilities for being in a particular state and probabilities for making a transition from

one state to another; and third, the sensitivity of the predictions of the theory to its assumptions, rather than signifying the power of the theory to reveal the extreme sensitivity of culture to genetic factors as L&W argue, actually undermines it. In this commentary we focus on the model as presented in Lumsden and Wilson (1980b) because that treatment is presumably the most rigorous presentation of the theory. A more extensive and detailed critique of both Lumsden and Wilson (1980a) and (1980b) is given in Alper and Lange (1981).

The central assumption of the L&W theory is that there are genes that code for the rules that determine the probability of changing from one alternative form of a cultural trait (culturgen) to another. There is absolutely no evidence that any genes of this type exist, and as is argued more fully below, L&W's claim to the contrary is invalid. The empirical evidence they cite refers to the observed probabilities that individuals prefer one alternative to another. Quite aside from whether these preferences are genetic, at least one can show that there are differences among individuals with regard to these preferences. No one has ever demonstrated that there are observable differences among people in the probabilities of their *switching* from one cultural trait to another, let alone that such differences might arise from differences in their genes.

L&W then assume that “enculturation is conducted not just by the nuclear family, a common feature of some industrialized Western societies, but by a much broader array of relatives and parent surrogates” (1980b, p. 4382). Wilson, in his textbook on sociobiology, presented a contrasting view: “The building block of nearly all human societies is the nuclear family” (1975, p. 553). The assumption chosen by L&W, positing a much larger number of “enculturators,” is the one needed to guarantee the sensitivity of culture to genetic factors. No hard evidence has been provided to support either the assumption of L&W or the one held previously by Wilson.

L&W state that in many cases decision making is adequately described by a Markov process; that is, the decision made at any given time to retain or to switch cultural patterns depends only on the state of that individual and on the state of all the surrounding individuals at that time. The previous history of the population can be ignored completely. For example, the possibility that the environment was different the previous time a behavioral transition occurred and that this could affect the current transition probability is not considered. L&W justify their assumption of the applicability of Markov processes by referring to a textbook in mathematical sociology by Coleman (1964). Surprisingly enough (in view of their citation), Coleman in fact sees little merit in the use of the Markov approximation for modeling group behavior (pp. 38, 460, and 528).

The Markov approximation is justified only if we possess *complete* relevant knowledge of the state of the system. L&W assume that the state of the population of N individuals is completely determined by the specification of the number of individuals n_1 and $n_2 = N - n_1$ in each of the alternative culturgen. The probability of an individual switching from culturgen 1 to culturgen 2 is given by a function $u_{12}(n_1, n_2)$. This probability function depends on n_1 and n_2 only and does not depend on time (historical circumstances). L&W assume that such a function, which they call an assimilation function, exists and is a genetically determined expression of the epigenetic rules of decision making. They further assume that the functional form of u_{12} and the parameters specifying it can be deduced from empirical data.

To support their contention that the u_{ij} 's can be determined from empirical data, L&W summarize in Table 1 (1980b) approximate values of the relative assimilation probabilities for such traits as sugar preference and color classification, which they estimate from experimental data. This table, however, is labeled “Estimate of innate preference,” and the footnote to it states that “[t]he preferred culturgen is arbitrarily designated as c_2 and the estimated probability of the choice of this culturgen as

opposed to c_1 , is denoted u_{12} ." This definition of u_{12} is inconsistent with the definition of u_{12} given in the body of the paper, where u_{12} is defined as the probability of making a switch from c_1 to c_2 . For example, although 80% of the individuals may prefer c_2 and so according to Table 1, $u_{12} - u_{21} = 0.08 - 0.2 = 0.6$, it may be the case that each individual is satisfied with his choice and so the probabilities of a switch from c_1 to c_2 or from c_2 to c_1 are both zero. This ambiguity in the meaning of the epigenetic rules appears throughout the paper and also appears in *Genes* and in the BBS Précis (1982b).

To make contact with the empirical data, the definition of epigenetic rule as it appears in Table 1 is needed, because, as L&W point out, cultural "responses have not been investigated with reference to their dependence on the behavior of the rest of society" (1980b, p. 4385) as would be required in evaluating u_{12} (n_1, n_2) defined as a transition probability function. The L&W theory cannot be related to the empirical data, at least at present, because the transition probability function which is needed as an input to the mathematical model is a totally unknown quantity (assuming such a quantity exists at all) and cannot be estimated from the empirical data of Table 1.

Making use of all these assumptions (including, in addition, an unstated one that the frequency of decision points is governed by a first-order rate law), L&W are then able to write down and solve a differential equation relating the time rate of change of the probability that at any given time n_1 and n_2 individuals will possess culturgen 1 and 2 respectively to the assimilation functions u_{ij} .

The major conclusion L&W draw from their model is that "even small differences in the epigenetic rules, reflected in the assimilation functions are magnified during social interaction into the dependent ethnographic patterns" (1980b, p. 4384). In other words, imperceptible genetic differences can lead to widely varying social behavior. For the particular choice of the u_{ij} 's made by L&W, as well as for many other choices of the u_{ij} 's, the solution of the differential equation contains a term in which one of the genetically determined parameters characterizing a u_{ij} is multiplied by N , the population size. Because this product appears as an exponent and because N is large, the sensitivity of the results to small changes in the parameter is guaranteed. L&W maintain that this sensitivity is a strength of the theory because it shows how small changes in the genetic rules, the u_{ij} 's, can result in large changes in the cultural patterns. We regard this sensitivity as arising from the extreme sensitivity of the model to its fundamental assumptions. The magnification property arises because each individual is affected to an equal extent by every other member of the population and because the population is quite large.

L&W constructed their theory in an attempt to overcome the current limitations of sociobiology. However, because the assumptions of their theory are so severe and because the environmental parameters included are limited to a single one (the number of individuals in a particular cultural state), the L&W theory does not appear to offer any new understanding of the coevolution of genes and culture.

Gene-culture theory and inherited individual differences in personality

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We believe Lumsden and Wilson's (L & W's) *Genes, Mind, and Culture* (1981; henceforth *Genes*) to be a landmark book. L & W's basic thesis, that there is a positive feedback loop such that genes → neural and chemical substrates → mind → behavior → culturgen assimilation → genes, with the environment exerting

influence at each link, seems substantially true (i.e. congruent with most of what we know). More important, gene-culture theory suggests novel programs of research that may lead to a synthesis of the biological and social sciences. We suggest that progress in this endeavor will be facilitated by the explicit addition of the nomothetic study of individual differences (i.e. the psychology of personality).

The nomothetic study of personality consists of a search for general laws having wide applicability to people in which consistent patterns of individual differences in behavior, sometimes called traits, play a central role. Basic assumptions of this approach include substantial consistencies of people's behavior when reliably assessed, and considerable predictive power of measures of traits in accounting for behavior (Rushton, Jackson & Paunonen 1981). Numerous dimensions of personality have been investigated over the last few decades, and assessment techniques have been created for their measurement (Anastasi 1982). Moreover, there is a growing literature demonstrating that individual differences on many of these traits are inherited, including: activity level (Willerman 1973), aggression (Owen & Sines 1970), altruism (Rushton, Fulker, Neale, Blizard & Eysenck, 1984), anxiety (Floderus-Myrhed, Pedersen & Rasmuson 1980), criminality (Ellis 1982), dominance (Carey, Goldsmith, Tellegan & Gottesman 1978), intelligence (Bouchard & McGue 1981), locus of control (Miller & Rose 1982), political attitudes (Eaves & Eysenck 1974), sexuality (Eysenck 1976), sociability (Floderus-Myrhed et al. 1980), tough-mindedness (Eysenck & Eysenck 1976), and values and vocational interest (Loehlin & Nichols 1976). The cited studies found that approximately 50% of the phenotypic variance was associated with additive genetic influences. We suggest, therefore, a redrawing of the schematic presentation of L & W's reciprocal process between genes and culture to make the individual-difference component explicit. Thus: Individual differences in genes → individual differences in neural and chemical substrates → individual differences in minds → individual differences in behavior → individual differences in culturgen assimilation → individual differences in genes.

It seems strange to us that an explicit focus on inherited individual differences is such a rare occurrence in writings on human sociobiology for, clearly, theories in evolutionary biology *require* that individuals differ genetically one from the other. Yet most sociobiological writings focus on either interspecies differences (rather than intraspecies) or on presumed universals in human behavior. *Genes* is only partly an exception to this. Although at the outset L & W posit that, for their theory to be correct, "genetic variance in epigenetic rules must exist within human populations" (p. 10), they subsequently place little emphasis on such genetic variance in their discussion of either the epigenetic rules themselves (Chapters 2 and 3) or how the genes do translate into culture (Chapter 4). This is unfortunate, for a focus on individual differences might have highlighted interesting facts. Consider, for example L & W's discussion of the hypothesized epigenetic rules underlying fear of strangers among infants. Their discussion proceeds as though such fears were (a) universal, and (b) limited to a particular point in ontogeny. A focus on individual differences, however, might have led to the prediction that those infants who were the most fearful of strangers would grow into the most socially anxious adults, an expectation borne out by data (Block 1981; Kagan & Moss 1962). Thus, from an individual-difference perspective, anxiety is a deep-rooted personality disposition, partly inherited, demonstrating longitudinal stability, and manifesting itself at a very early age. From a gene-culture coevolutionary perspective, it might also be expected that high and low anxiety people will have different life-styles and social environments (culturgens) and subsequently demonstrate differential genetic fitness.

A synthesis of the psychology of personality, behavior genetics, and the theory of coevolution allows for a range of intermedi-

ate tests of gene-culture theory and leads to interesting lines of inquiry. Thus it follows that variance in (partly inherited) measurable personality traits will be correlated with (a) variance in the physiological systems underlying those traits, (b) variance in the culturgens produced and assimilated, and (c) variance in genetic fitness. Preliminary evidence can be gathered in support of each of these predictions. In regard to (a), that is the physiological systems underlying traits, Gray (1982) has described the cytoarchitecture of the "brain inhibition system" and linked activity in these fiber tracts to personality differences in anxiety level. [See also *BBS* multiple book review of Gray's *The Neuropsychology of Anxiety*, *BBS* 5(3) 1982.] The work on the evoked potential and other physiological correlates of IQ (Hendrickson & Hendrickson 1981) constitutes another prime example of matching individual differences in behavior with those in neurophysiological systems. In regard to (b), that is different personality types producing or assimilating different culturgens, consider the studies examining the role that personality plays in scientific creativity. Many studies have found successful scientists to be more socially introverted than average (e.g. Cattell 1962; Terman 1955); other studies have also found them to be more intellectually curious, needing of cognitive structure, dominant, and independent (Rushton, Murray & Paunonen 1983). Thus individual differences in scientific creativity are in part inherited (see also Karlsson 1978). In regard to (c), that is differential genetic fitness, epidemiological and demographic studies of abnormal personality suggest that those who suffer from extreme anxiety, depression, and low IQ have fewer children than those with more moderate scores (Rosenthal 1970).

The synthesis of gene-culture coevolution with behavior genetics and personality psychology has only just begun. The implications, however, may be far-reaching. One might conjecture, for example, that some personality types will thrive more in some cultures than others. To take some speculative examples, (a) genetically similar personality types may seek each other out in order to provide mutually supportive cultures (there is, for example, assortative mating for personality traits; Vandenberg 1972); (b) genetically similar individuals may form natural antipathies toward those who have genetically dissimilar personalities; (c) cross-cultural and group differences in behavior may be partly genetic in origin (Osborne, Noble & Weyl 1978); and (d) religious, political, and other ideological battles may become as heated as they do partly because they have implications for genetic fitness; in other words, genotypes will thrive more in some ideological cultures than others (recall that political attitudes are partly inherited; Eaves & Eysenck 1974).

Irrespective of the above, we are proposing that genetically based individual differences become a crucible for theory construction in gene-culture theory so that the formulation of hypotheses should lead to an immediate individual-difference test. If this were done, not only would predictions become more honed, but some hypotheses would be considered less useful even at the outset. For example, in Chapter 8, L & W suggest that knowledge of the deep structure of epigenetic rules might help humans to find and agree on universal goals. From the perspective of individual differences, however, one might ask: How could there ever be universal agreement on goals if there will always be individual differences in goal preferences?

Natural selection and unnatural selection of data

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I have now had the benefit of reading reviewers' comments on Lumsden & Wilson (1982b) (L & W) and the authors' reply

(Lumsden & Wilson 1982a). In view of the confusion which exists even among geneticists about the basic concepts of genetics, I am not much surprised at the favourable and, at times, admiring comments L & W receive from some of the non-geneticists. The second sentence of L & W's response is that "the reviewers do not deny that biological and cultural evolution are somehow coupled." To me this epitomises the basic misunderstanding among those who are loosely called "social biologists." The relationship between biological and cultural evolution is evident in phrases like natural selection by adaptation and the survival of the fittest. Needless to say, what a species found better for its survival, it incorporated into its "culture." It is true that some selectionists created controversy by attempting to explain the development of every feature of an organism by natural selection, but the relationship between the biological imperatives of a species and its "culture" has to my knowledge not been in dispute for some time. The problem arises when this simple and obvious hypothesis is applied to an organism that can control and alter its environment and culture.

I may be forgiven if I feel uninterested in the exotic debate concerning the definition of culturgens. I simply think that the word was an unfortunate choice. Neither have I any interest in the models of cultural transmission that involve no selection. L & W state epigenetic rules which, they say, are genetically determined procedures. They are determined to show that social behaviour is shaped by natural selection, and they give specific examples of gene-culture translation. Along the way they throw caution and scientific objectivity to the winds. They also show a remarkable unawareness of the major problem in establishing the evolution of any trait by natural selection.

L & W discuss three examples of gene-culture translation where genetically determined epigenetic rules apply. The first and most important is brother-sister incest avoidance. They say that "the epigenetic rule appears well established: a deep sexual inhibition develops between people who live in close domestic contact during the first six years of life" (1981, pp. 147-48). In support of this assertion they cite Wolf's (1966; 1968; 1970) data and also Kaffman (1977). Their description of Wolf's data, if accurate, would require an objective reader to grant the possibility and, indeed, the likelihood of the existence of their epigenetic rule. Unfortunately, omissions make it unreliable. Moreover, they fail to evaluate Wolf's research objectively.

L & W write that in "the nineteen families analyzed by Wolf's 1966 report, for example, the young couples refused to go ahead with the match in fifteen cases. In two cases one member of the pair died in childhood, while the two remaining couples married" (1981, p. 149). Actually, in his 1966 report Wolf discussed two different samples. Members of the sample L & W discuss were born between 1910 and 1930. Members of the other sample were born before 1910. In that sample the position was almost exactly the opposite. This may be the reason L & W ignore it. Of the 22 young couples in that sample, one member of the pair died in four cases, in one case the parents decided not to go ahead with the arrangement, and in one case they were dissuaded from going ahead. The remaining 16 couples married. This hardly provides evidence for L & W's "well-established" epigenetic rule. Anyone reading Wolf's papers objectively cannot disagree with his assertion (Wolf 1966) that "while these data [the 1910-30 sample] indicate that young people were not always happy with the alternate form of marriage, this is not necessarily a result of their having grown up in intimate association."

L & W are entitled to say that they dispute Wolf's interpretation of his data, but they are not entitled to do so if they indulge in selection from his data. Moreover, by selecting data they free themselves from a consideration of the reason for the cultural change indicated by the two sets of data. Did this change occur because of some epigenetic rule? The answer is no.

The families Wolf studied brought up the daughters of other families as "little brides" in their own homes. These brides were

called *sim-pua*. The main advantages of the system were: (1) the son was assured of a wife, (2) the family did not have to pay the customary expensive "dowry" to the bride's family and did not have to buy expensive presents for the bride, (3) the marriage ceremony itself was cheap because no outside guests needed to be invited. In short, as Wolf (1970, p. 513) says, "The desire to economise is one reason for choosing to raise a son's wife." Needless to say, the practice was *not* universal in the town studied by him.

A *sim-pua* was very badly treated by the adopted family. She was more a servant than an honoured member of the family. This is hardly a setting in which love and romance flourish. The young men from these families could not rebel against the system because of their absolute economic dependence on their families. In 1923 the railroad created new industries and new jobs. The youth became more independent. They could afford to pay dowry to their bride's family, could buy her expensive presents, and could afford to invite their friends to their wedding. In short, they could emulate their better-off brethren in the town. The conditions that gave rise to the institution of *sim-pua* ceased to exist, and the youth in the 1910–30 sample refused to uphold it. There is no need to invoke an epigenetic rule.

L & W discuss Wolf's (1970) data giving various percentages. How reliable are those data? Wolf says that "the data reported in this paper were compiled for me by clerks in the household registration office. I spent my own time conducting a general ethnographic survey" (1970, p. 507–8). Concerning the accuracy of these records he says, "Although I have since had occasion to doubt the wisdom of my choice, I decided to rely on the information available in the household registration records¹¹ (p. 506).

The household registration office did not keep information on adultery, so Wolf recruited an assistant whom he described as "a petty racketeer and confidence man." They chose two men in the town to provide supplementary information. They would invite them for dinner and after drinks tell them that prostitution and adultery were rife in the United States and Western Europe. In these circumstances the two men retailed stories of adultery. Wolf's percentages, on which L & W rely, include this supplementary information.

For their second and third example, fission in Yanomamó villages and fashion in women's dress, L & W say that the basic epigenetic rules are not known. I feel relieved, but I am surprised that they were looking for them in women's fashion! In any case, I cannot take seriously a hypothesis concerning the determination of a behavioural trait if it has to rely on measurements taken "from European and American paintings and fashion magazines from 1605" (p. 170).

My main objection is that in attempting to show that social behaviour is shaped by natural selection, L & W fail to see the major theoretical problem. Natural selection can affect a trait only if it is correlated with fitness. Such a trait may spread in a population under the influence of natural selection. A trait not correlated with fitness will not be affected by natural selection. Genetically determined rules for a behavioural trait will exist only if it is correlated with fitness.

Unfortunately, even a positive correlation of a behavioural trait with natural selection cannot ensure that it will become the accepted mode. A prerequisite for a change in the frequency of the behavioural trait is the availability of additive variance in fitness population. Additive variance in fitness may not be available in all populations. Falconer (1966, p. 229) says that "a population subject to natural selection over a long period of time under constant environmental conditions will come to genetic equilibrium in which fitness is maximal . . . The heritability of fitness is then zero." In a natural population where social considerations do not affect fitness, the heritability of fitness will be very small.

Falconer (1966) shows that the response, that is change in

mean value, of a trait evolving under natural selection will be equal to the additive genetic covariance between the trait and the fitness. If the additive genetic variance of fitness is zero, no trait can evolve under natural selection.

L & W recognize the rudimentary nature of their gene-culture coevolution hypothesis. I hope they will accept that they were unwise in relying upon and selecting from Wolf's data. They must also understand the nature of the questions they should ask if they wish to make progress with their hypothesis. They need to show that (1) additive variance of fitness in a population is significantly different from zero and (2) the behavioural trait under consideration is genetically correlated with fitness. I sincerely hope that they will now address themselves to these questions.

Author's Response

On incest and mathematical modeling

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Vetta is the one who selected the data to produce an unsupportable conclusion. The last article by Wolf that he cites was published in 1970. Had he consulted the book by Wolf and Huang (1980), the principal source for our conclusions in *Genes, Mind, and Culture*, (1981; henceforth *Genes*) he would have found his objections met. The contrast between the pre-1910 and post-1910 birth cohorts in the Taiwan minor marriage analysis was interpreted by Wolf and Huang as resulting from the weakening of parental domination in the 1930s, when the post-1910 cohort was maturing, permitting the deeper inhibitory effect to be expressed. The hypothesis raised by Vetta, that the minor marriages failed more frequently after 1930 because they conferred less status, is contravened (as noted by Wolf and Huang) by two circumstances. First, the reduction in consummation preceded the reduction in practice of *sim-pua* recruitment by the parents. Thus the rebellion against parental authority – made possible by improving economic conditions – preceded abandonment of the practice. Second, Wolf and Huang showed that couples brought together before the age of about six years had lower rates of consummation than couples joined after this age, a key result consistent with the critical-period age independently estimated in the Israeli kibbutzim studies. The pre-six group also had higher divorce rates, as noted by Wolf and Huang (as well as lowered fertility – Wolf, personal communication). Thus, while perceived social status may have played a role, as suggested by Vetta, the early-childhood inhibitory affect appears to be the more important.

Vetta seems eager to discredit the data on adultery by depicting Wolf as plying the informants with drink and leading questions. This is an unjustified affront to a professional anthropologist of unimpeachable integrity, who has taken care to present his methods and data in a cautious, open-minded fashion. And contrary to Vetta's claim, Wolf's interpretation is the same as our own; we attempted to reflect his main results. Moreover, from his

early writings on the subject to his summary book with Huang, Wolf has favored the inhibition hypothesis as we stated it in *Genes*.¹

Although Vetta cites Kaffman (1977), he does not mention the Israeli kibbutzim by name or our citation, in *Genes*, of the key work by Shepher (1971). A more recent and masterly summary, addressing the principal results in the Israeli studies, and their convergence with the Taiwanese data, has been provided by Shepher (1983). A second informative analysis has been provided by van den Berghe and commentators in *The Behavioral and Brain Sciences* (1983).

In short, Vetta's particular objections to the two major studies on the avoidance of brother-sister incest have no visible substance. Our use of the pre-six inhibition as an epigenetic rule may yet prove incorrect, but for the moment it seems to be reasonably well based on two independent studies of the effects of early propinquity.

Alper & Lange consider some of the mathematics we use in *Genes*. Their comments largely restate limitations and simplifications in the formalism already discussed by us in the book. These commentators criticize our use of Markov dynamics rather than transition models that incorporate longer-term memory effects and more complex dependence on the cultural surroundings. Their point is unwarranted. Markov models of the type we use incorporate memory and social context to an extent sufficient to fit real (but by no means all) sociological data (e.g. Coleman 1964). Thus one has an empirically motivated entrée to the difficult problem of societal modeling. When applications involving longer-term memory processes and other factors occur, the appropriate formalism can be set in place of the simpler idealizations in order to provide more realistic treatment (e.g. Coleman 1964; Fararo 1978; Simon 1979; and p. 266 ff. of *Genes*, where *contra* Alper and Lange the encoding of cultural information into long-term memory, with permanent effects on behavior, is unified by us with a Markov dynamic of later choice and decision).

Alper & Lange point out our use of infant preference data (transition probability data are reported much less often) and contrast it with our use of transition probabilities in the basic theory. But if, for example, the transition rates are v_{12} and v_{21} , respectively, in a two-choice experimental design (such as normal versus rear-ranged face patterns), then the proportion of infants preferring pattern 2 to pattern 1 is $v_{12} / (v_{12} + v_{21})$, and similarly with more complex designs. The preference patterns and transition rates for choice are closely related. So we fail to see a problem.

Alper & Lange also discuss our amplification equations for the effects of genetic changes on the overlying cultural pattern (*Genes*, p. 137 ff., Eqs. (4-39)-(4-48)). Their feeling is that the results cannot be true, tied as they are to allegedly "simple" models. However, they offer no formal proof leading to more realistic amplification equations that contravene those derived by us. Their argument therefore seems of little interest. The amplification equations in *Genes* are first approximations, but they are derived for models of a type usefully related to sociological data (e.g. Coleman 1964, and associated references cited in *Genes*). We have also examined several of the complicating factors omitted from the initial amplification theorems, such as long-term semantic memory

effects, and suggested that these further properties of cognition may increase rather than decrease the magnitude of the gene-culture amplification (*Genes*, p. 144). The construction of amplification equations for improved models, combined with empirical investigation, will allow these proposals to be studied more fully (Lumsden, in preparation).

The Alper & Lange theses are, ultimately, generated by a tidy confusion of the notion of a scientific theory with that of a mathematical model. If the predictive and explanatory power of the theory of gene-culture coevolution were exhausted by the simple formalisms (already hard enough for the practitioner!) utilized in *Genes*, there would indeed be cause for gloom. But such is not the case. The mathematical models are initial cases, in idealized form, of general principles built into the theory. Findings derived from them are recorded in *Genes* as theoretical propositions amenable to empirical test. We showed how mathematical psychology, the cognitive sciences, and theoretical sociology are replete with formal tools for handling more subtle, complex representations of mental and anthropological phenomena than we could initially consider. The exciting task of unifying these fields with evolutionary biology has only begun. *Genes* is a step toward this goal, with the simplest cases first.

Of course, the formal treatment of biological and cultural history may ultimately prove to be intractable (we doubt it), but this will be discovered through the process of careful theoretical modeling and empirical testing in the mode of scientific inquiry, not through the mode of a priori assertions advocated and exemplified by the critique of Alper & Lange.

Finally, we agree largely with the comments by Almeida and by Rushton & Russell and do not feel that a response is needed at this time.

NOTES

1. We are grateful to Professor A. P. Wolf for discussing these matters with us and confirming our summary of his views as presented here.

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Commentary on Jeffrey A. Gray (1982) Précis of *The neuropsychology of anxiety: An enquiry into the functions of the septo-hippocampal system*. BBS 5:469–534

Abstract of the original article. A model of the neuropsychology of anxiety is proposed. The model is based in the first instance upon an analysis of the behavioural effects of the antianxiety drugs (benzodiazepines, barbiturates, and alcohol) in animals. From such psychopharmacological experiments the concept of a “behavioural inhibition system” (BIS) has been developed. This system responds to novel stimuli or to those associated with punishment or nonreward by inhibiting ongoing behaviour and increasing arousal and attention to the environment. It is activity in the BIS that constitutes anxiety and that is reduced by antianxiety drugs. The effects of the antianxiety drugs in the brain also suggest hypotheses concerning the neural substrate of anxiety. Although the benzodiazepines and barbiturates facilitate the effects of γ -aminobutyrate, this is insufficient to explain their highly specific behavioural effects. Because of similarities between the behavioural effects of certain lesions and those of the antianxiety drugs, it is proposed that these drugs reduce anxiety by impairing the functioning of a widespread neural system including the septo-hippocampal system (SHS), the Papez circuit, the prefrontal cortex, and ascending monoaminergic and cholinergic pathways which innervate these forebrain structures. Analysis of the functions of this system (based on anatomical, physiological, and behavioural data) suggests that it acts as a comparator: It compares predicted to actual sensory events and activates the outputs of the BIS when there is a mismatch or when the predicted event is aversive. Suggestions are made as to the functions of particular pathways within this overall brain system. The resulting theory is applied to the symptoms and treatment of anxiety in man, its relations to depression, and the personality of individuals who are susceptible to anxiety or depression.

The septo-hippocampal system and ego

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Interesting ideas have a way of appearing in widely different times and places and in differing guises. While reading Jeffrey

Gray's (1982a) *Neurobiology of Anxiety* and the BBS précis (Gray 1982b), I felt my recognition memory telling me that all in it was not novel. Some subsequent checking behavior confirmed that I had perceived a similar pattern in the writings of a behavioural scientist of a different age and discipline.

In his work *The Problem of Anxiety*, written late in his career, Freud (1936) reconsidered anxiety from an ego psychological