Translation of epigenetic rules of individual behavior into ethnographic patterns

(human sociobiology/social development/gene–culture coevolution)

CHARLES J. LUMSDEN AND EDWARD O. WILSON

Museum of Comparative Zoology Laboratories, Harvard University, Cambridge, Massachusetts 02138

ABSTRACT   The pivotal process in gene–culture coevolution is envisaged to be the evolution of behavioral epigenesis. From premises based on the known properties of enculturation and usage diffusion within societies, a probabilistic model is constructed to estimate the degree to which rules governing individual development canalize ethnographic curves (the probability density distributions of societies engaged in varying patterns of usage). The results indicate that under most conceivable conditions the translation from individual epigenesis to social pattern is amplified, to an extent that differences in bias too faint to be detected in ordinary developmental studies can generate conspicuous variation in the ethnographic curves. Examples are cited of sufficiently biased epigenesis in human behavior.

During socialization in a cultural species, individuals transmit an array of behaviors and artifacts, which for convenience will be termed "culturgens" [L. *cultur(a)*, culture + L. *gen(o)*, produce]. This unit can be consistently delineated by applying the set-theoretic definition of artifact employed in quantitative archeological studies (1): A relatively homogeneous set of artifacts or behaviors that either share without exception one or a selected set of important attribute states or at least share a consistently recurrent range of attribute states within a given polythetic set. Enculturation can theoretically consist of one or the other of three forms (Fig. 1): (*i*) Pure genetic transmission, in which all members are genetically constrained to learn one culturgen within a given category of alternative culturgens (thus it is possible to have a purely genetic culture); (*ii*) pure cultural transmission, in which no innate predisposition exists favoring one culturgen over another; or (*iii*) gene-culture transmission, in which one culturgen is favored because of innate bias in the teaching or acquisition processes.

Transmission is subject to a sequence of epigenetic rules, which are the genetically determined peripheral sensory filters, interneuron coding processes, and more centrally located procedures of biased learning that affect the probability of acquiring one culturgen as opposed to another. Epigenetic rules that produce the gene–culture form of transmission are widespread, if not general, in human behavior. They have been demonstrated in newborn taste preferences (2, 3), discretization of hue perception (4), phoneme production (5), preferred level of visual pattern complexity (6), preferred visual design (7), general facial recognition (8), basic facial expressions (9), mother–infant bonding (10), infant carrying (11), fear of strangers and other generalized fears and phobias (9, 12), brother–sister incest avoidance (13), and others.
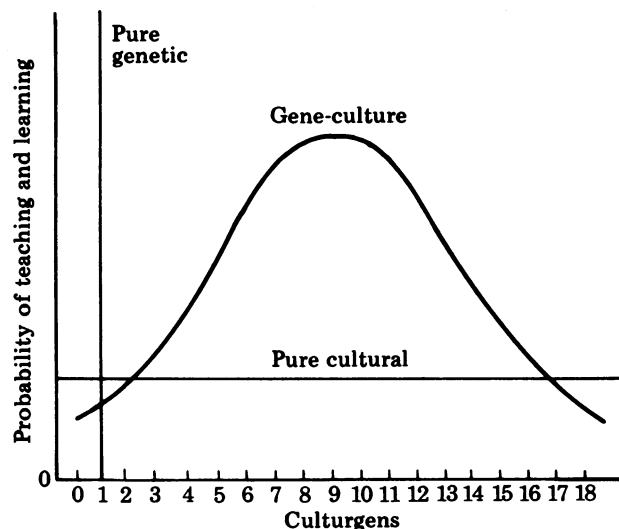
FIG. 1.   Three conceivable classes of programs of informational transmission in a social species.

It is apparent from the data of cross-cultural studies that many epigenetic rules find expression in the ultimate patterns of social behavior. Examples especially noted by previous investigators include features of verbal color classification (14) and brother–sister incest avoidance (15, 16). We propose a general theoretical construction that focuses on behavioral epigenesis as the product of genetic prescription, which in turn is altered by natural selection acting through the epigenetically determined cultural patterns. The key questions of gene–culture coevolution then become the degree to which epigenesis impacts cultural evolution and the degree to which natural selection acting on culture affects the genes committed to behavioral epigenesis. The first step, which we explore in this article, is to identify the cognitive epigenetic rules, which hitherto have been the concern of psychology, and to link them to the ethnographic patterns, which have been the concern of cultural anthropology. Such a procedure, if successful, could render ethnographic patterns predictable from first principles and allow a more precise evaluation of the flexibility of human social behavior.

METHODS

The new coevolutionary schema that we propose is faithful to the known principles of culturgen transmission within societies. In 80% or more of societies, 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

Model	Qualitative choice structures $u_{ij}(\zeta)$		Analytic description
Threshold response			$u_{12} = \begin{cases} a_1, \zeta \leq \zeta_1 \\ a_2, \zeta > \zeta_1 \end{cases}$ $u_{21} = \begin{cases} b_1, \zeta \leq \zeta_0 \\ b_2, \zeta > \zeta_0 \end{cases}$
Saturatable "trend watching"			$u_{12} = a_1 + a_2 \tanh \zeta$ $u_{21} = b_1 - b_2 \tanh \zeta$
Nonsaturatable "trend watching"			$u_{12} = a_1 e^{a_2 \zeta}$ $u_{21} = a_3 e^{-a_2 \zeta}$
Preference for partial but not total consensus			$u_{12} = a_1 + a_2 \sin(\pi \zeta)$ $u_{21} = b_1 + b_2 \sin[\pi(1+\zeta)]$
High sensitivity to minority opinion			$u_{12} = a_0 + a_1 [1 - e^{-a_2(1+\zeta)}]$ $u_{21} = b_0 + b_1 [1 - e^{-b_2(1-\zeta)}]$

FIG. 2. The conceivable choice structures $u_{ij}(\xi)$ selected for analysis.

parent-surrogates. This circumstance insures a relatively uniform exposure to culturgens and transmission of dominant values (17). The spreading patterns of about 20 kinds of successful culturgens that have been studied by social scientists are well described by logistic and Gompertz equations. In the latter case, which provides the closer fit, the general form of the equation can be derived from elementary assumptions concerning imitation, evaluation, and culturgen substitution as functions of the levels of general usage in the society (18).

Consider a system in which two alternative culturgens, c_1 and c_2, are the options of interest. This is a common circumstance in ethnography and modern decision making, and even complex arrays of alternative culturgens often can be clustered into binary sets for purposes of analysis (1, 19, 20). Individual members of the society choose between c_1 and c_2 at decision points; they can decide to retain their active culturgen ($1 \rightarrow 1$ or $2 \rightarrow 2$) or to change ($1 \rightarrow 2$ or $2 \rightarrow 1$). In many cases of practical intent, such decision and learning processes are adequately described by a Markov process as a first approximation, as noted by others who have modeled group behavior (21). We suggest that a similar approach is a useful starting point in the analysis of epigenesis–ethnography translation. In particular, the epigenetic rules can be expressed in abstract form as the transition probabilities u_{ij} from culturgen i to culturgen j at each decision point.

The mean lifetime between sequential decision points is τ_1 for a c_1-user and τ_2 for a c_2-user, and the rate constants are $r_1 = 1/\tau_1$ and $r_2 = 1/\tau_2$. The parameters τ_1 and τ_2 are then the

means of exponential probability densities:

$$D_1(t) = \frac{1}{\tau_1} e^{-t/\tau_1}, \quad t \geq 0 \qquad [1a]$$

$$D_2(t) = \frac{1}{\tau_2} e^{-t/\tau_2}, \quad t \geq 0. \qquad [1b]$$

The transition rates of the decision process are v_{ij}, where $v_{ij} = r_i u_{ij}$, $i \neq j$.

In the two-culturgen case, where n_1 members possess c_1 and n_2 members possess c_2, the probability $P(n_1, n_2, t)$ that a steady-state society of N members possesses a particular combination of $n_1 + n_2 = N$ culturgens changes at the rate

$$\begin{aligned}
\partial_t P(n_1, n_2, t) \\
= (n_1 + 1) \cdot v_{12}(n_1 + 1, n_2 - 1) \cdot P(n_1 + 1, n_2 - 1, t) \\
+ (n_2 + 1) \cdot v_{21}(n_1 - 1, n_2 + 1) \cdot P(n_1 - 1, n_2 + 1, t) \\
- [n_1 \cdot v_{12}(n_1, n_2) + n_2 v_{21}(n_1, n_2)] P(n_1, n_2, t) \qquad [2]
\end{aligned}$$

for $0 < n_1 < N$. The probability density distribution of culturgen frequencies at any given time can be called the *ethnographic curve* of the population.

It is more efficient to write the culturgen proportions as a single variable

$$\xi \triangleq (n_2 - n_1)/N \qquad [3]$$

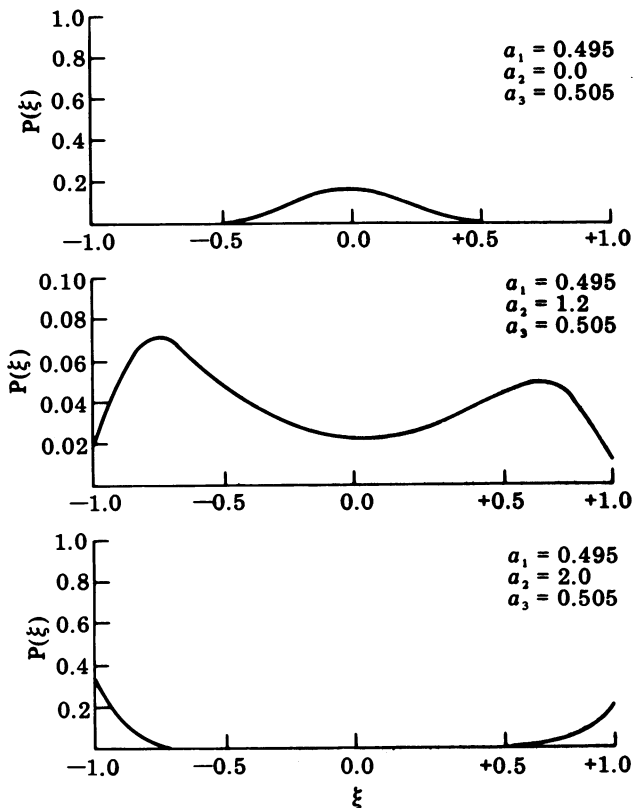which ranges from -1 to $+1$ as n_2 ranges from 0 to N. The

FIG. 3. Amplifying effect of the epigenetic rules on their dependent ethnographic distributions. Ethnographic curves were calculated from Eq. 5 for a group of 25 individuals. The assimilation functions are of the nonsaturatable "trend-watcher" form, specifically $u_{12} = a_1 e^{+a_2 \xi}$ and $u_{21} = a_3 e^{-a_2 \xi}$ respectively, with $\tau_1 = \tau_2$. Above $a_2 \approx 1.0$, the ethnographic curve $P(\xi)$ has two distinct modes for values of a_1 and a_3 with $|a_1/a_3| \approx \mathcal{O}$ (1). The $P(\xi)$ series shows the response to a slight difference in intrinsic bias $|a_1 - a_3|$ and increasing sensitivity to cultural choices made by other members of the society.

steady-state ethnographic curve, which is the attractor state for the motion (Eq. 2), is

$$P(\xi) = P(n_1, N - n_1)|_{\xi = 1 - 2n_1/N}$$

$$= P(0,N) \cdot \binom{N}{n_1} \cdot \prod_{i=1}^{n_1} \frac{v_{21}(i - 1, N - i + 1)}{v_{12}(i, N - i)}. \qquad [4]$$

The dependence of culturgen transition rates in many categories of behavior on the proportion of individuals possessing one culturgen as opposed to another is a general phenomenon and has been measured by social scientists (17, 22). It can be specified in the present translation model as the *assimilation function* $v_{ij}(\xi)$.

In the case of groups no larger than hunter–gatherer bands, which have evidently contained 15–75 members throughout the history of the genus *Homo* (23), the steady state distribution is readily simulated by Eq. 4. However, more direct insight into the relation of ethnographic curves to the epigenetic rules can be obtained by a Fokker–Planck approximation that treats ξ as an effectively continuous variable. After transients decay, the ethnographic curve approaches a steady state that takes the form

$$P(\xi) = \frac{C}{Q(\xi)} \cdot \exp\left[2 \int_{-1}^{\xi} \frac{X(\xi')}{Q(\xi')} d\xi'\right] \qquad [5]$$

where C is a normalization constant and

$$X(\xi) = (1 - \xi) \cdot v_{12}(\xi) - (1 + \xi) \cdot v_{21}(\xi) \qquad [6a]$$

$$Q(\xi) = \frac{2}{N}(1 - \xi) \cdot v_{12}(\xi) + \frac{2}{N}(1 + \xi) \cdot v_{21}(\xi). \qquad [6b]$$

RESULTS

Structure of the Assimilation Functions. The categories of assimilation that we have evaluated are summarized in Fig. 2. Few data exist that can be used to derive real curves. The most elementary straight-line function (v_{ij} insensitive to ξ) and step functions will result in relatively uniform, easily predictable, species-specific traits. They are most likely to occur during early infancy, when the most robust epigenetic rules direct behavior to certain limited and virtually inevitable choices. Apparent examples include certain broad categories of taste preferences (2, 3), the major categories of color perception and vocabulary (4), and basic facial expressions (9). The monotonic, "trend-watching" cases are also likely to occur. The existence of curves of this general form are implied by substantial empirical data on intragroup cultural diffusion in Western industrial societies (18, 24) and data on small-group behavior (25, 26).

Amplification to the Ethnographic Patterns. When $dv_{ij}/d\xi = 0$ on (−1,1), in other words when each group member operates independently of the others, interior maxima or minima in the ethnographic curve $P(\xi)$ are determined by $e^{2V(\xi)}$, where $V(\xi)$ is the integral in Eq. 5, through the spectrum of zeroes in $X(\xi)$. $Q(\xi)$ is positive linear and plays no role. When $dv_{ij}/d\xi$ is nonzero on (−1,1), $Q(\xi)$ is not strictly monotonic. Nevertheless, $e^{2V(\xi)}$ varies exponentially with group size N while $Q(\xi)$ varies as N^{-1}, with the result that in many conceivable cases of practical interest, the factor $e^{2V(\xi)}$ dominates in the behavior of the ethnographic curves over much of the interval (−1,1) in ξ. Because of the dependence of $Q(\xi)$ and $V(\xi)$ on the $v_{ij}(\xi)$, the form of the ethnographic curve is sensitive to changes in the epigenetic rules. In other words, translation entails a cooperative process, magnifying the social effects of the constraints on individual development. Examples are provided in Figs. 3 and 4. Our studies over a wide range of parameters and assimilation functions have revealed a substantial robustness in the qualitative result.

DISCUSSION

Two findings of potentially broad significance have emerged from the translation models. The first is that even small differences in the epigenetic rules, reflected in the assimilation function, are magnified during social interactions into the dependent ethnographic patterns. Differences in intrinsic learning bias toward competing culturgens as low as 0.02—probably below the detectable level in standard studies of behavioral development (7)—generate differences 1.5 times or greater in the corresponding modes of the ethnographic curves. The second finding is a corollary of the first: Even when the underlying epigenetic rules and assimilation functions are rigidly constrained, they can generate wide cultural diversity. Fine tuning in the innate parameters of these processes can create large shifts in the social patterns.

Are the human epigenetic rules sufficiently specific to create such constraints on the cultural patterns? The answer is that they often are; in some cases, they exceed the marginal levels we have demonstrated by one or two orders of magnitude. In Table 1 we have summarized the cases known to us in which approximate values of relative assimilation probabilities can be estimated from experimental data. These examples are mostly limited to initial enculturation, because of the relative ease with which they could be measured; but it is reasonable to suppose that the innate biases they reveal carry over into the later, post-enculturation transition probabilities between the culturgens. This persistence of bias is, in fact, well marked in the case of sugar preference, color classification, and infant holding.
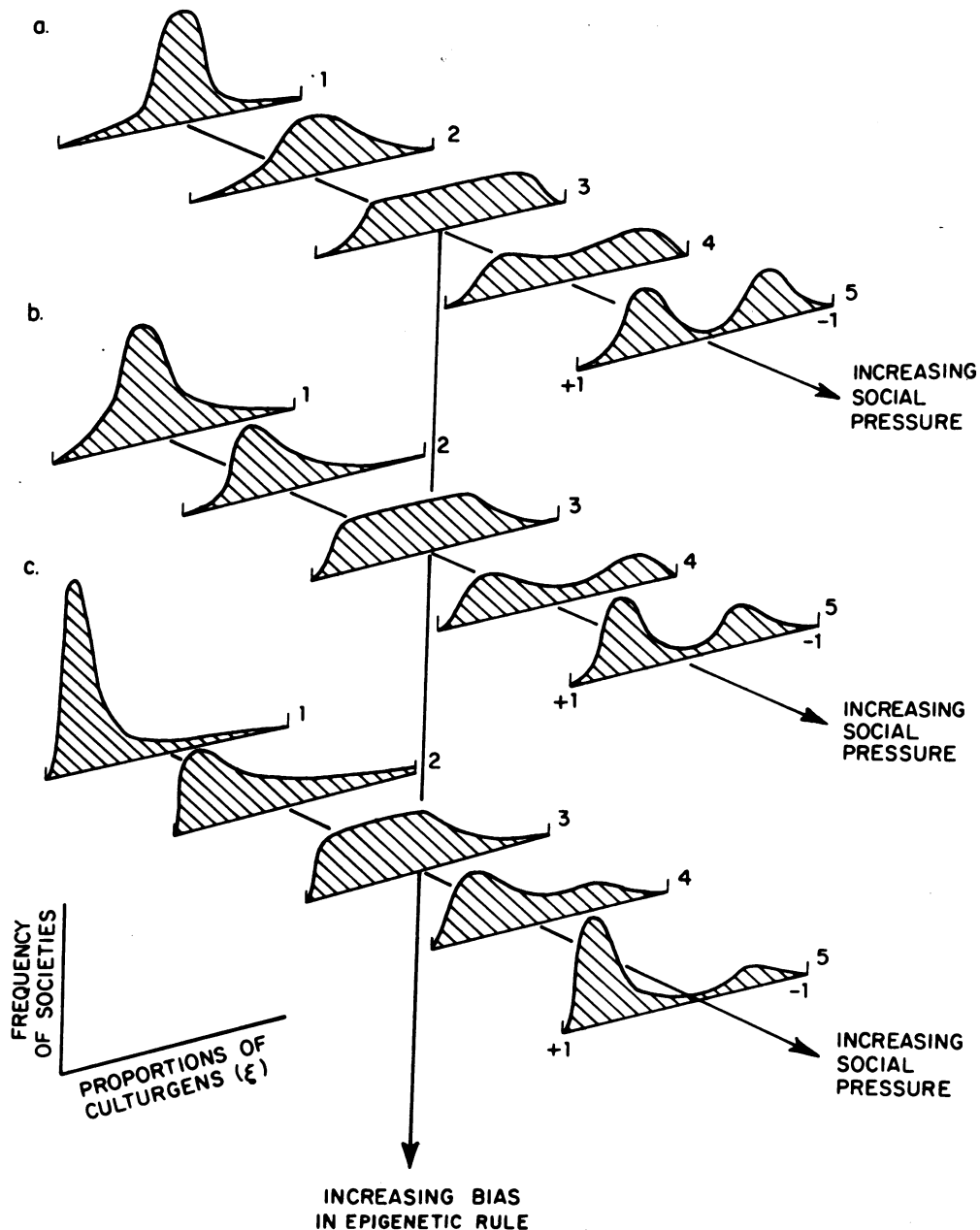
FIG. 4.   Ethnographic curves that give the frequencies of societies possessing various proportions of alternative culturgens are strongly affected by the innate epigenetic rules and patterns of response to the surrounding culture. Each of the 15 curves results from a different combination of learning rules and patterns of culturgen choice made by others. The assimilation function in this example is the nonsaturable "trend-watcher" form shown in Fig. 2. The range of behavior shown by the remaining models described in Fig. 2 is similar, with the number and locations of modes fixed by the zeroes of $X(\xi)$.

There have been relatively few such developmental studies, and the responses have not been investigated with reference to their dependence on the behavior of the rest of the society. However, the examples cited are not likely to be flexible in this regard, because they either entail fundamental sensory discrimination or else occur in socially invariant circumstances, such as early physical contact between mother and infant. In fact, the values that have been ascertained may prove to be among the highest that actually exist, for the reason that extremely specific epigenetic rules are also those most likely to catch the attention of experimental psychologists. Yet, as illustrated by the projections of Fig. 3, far less specific rules operating on the adult transition probabilities can still create powerful canalizing effects.

Finally, we suggest the existence of a feedback of ethno-graphic patterns on the evolution of epigenetic rules, resulting in a mode of gene–culture coevolution that can be explicitly analyzed within the framework of natural selection theory. The fitness of the genes affecting cultural behavior are determined by the patterns of social response, whose statistical properties are expressed in the ethnographic distributions. But the important mediating process, which has hitherto eluded traditional population genetics and sociobiology, is the epigenesis of social behavior, including especially cultural transmission. Although prescribed by genes, the epigenetic rules are the more appropriate "molecular units" by which biologically based postulational-deductive models of human social behavior can be developed. The manner in which natural selection works back through the epigenetic rules to alter gene ensembles will be the subject of future reports.

Table 1. Estimates of innate preferences

Alternative responses	Age at first response	$u_{12} - u_{21}$	Later social effects	Source
Preference for sugar (sucrose, fructose, glucose, lactose)	Newborn	0.2–0.5 according to sugar and at 0.2–0.3 M	Sugar preference extends at least into childhood and influences adult cuisine	2, 3
Discrete four-color classification over continuous or other discrete classifications	4 months	Approaches 1.0 in fully color-sighted persons	Linguistic color classifications across cultures can be mapped from 1:1 to 3:1 onto the four categories	4, 14, 27
Preference for schematic pattern of human face over similar designs	Newborn	$\geqslant 0.02$ to $\geqslant 0.20$ according to design	Long-term focusing on face, especially eyes; facilitation of parent–offspring bonding and perhaps later forms of interpersonal bonding	8
Preference for intermediate complexity in visual design: Approximately 10 turns in figures as opposed to 5 or 20 turns	Newborn	$\geqslant 0.1$	Followed by comparable degree of preference in school-age children; adults also prefer intermediate complexity, with a redundancy of about 20%	6, 28
Fear response to strangers	8 months	>0.5	Possibly contributes to early group distinctions and hostility to strangers and out-groups by children and adults	9, 29, 30
Infant holding: Women carry babies on left side; men carry them at random, to left or right	Adult; possibly traceable to sex differences in object-carrying behavior that extends back to preadolescence	0.2–0.6, according to age of infant	Proximity to heart beat soothes infant and possibly facilitates mother-infant bonding	11, 31

The preferred culturgen is arbitrarily designated as c_2, and the estimated probability of choice of this culturgen as opposed to c_1 is denoted as u_{12}.

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