Gene–culture translation in the avoidance of sibling incest
(human sociobiology/social development/ethnography)

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ABSTRACT A preliminary analysis is made of the relation between the epigenetic rules of brother–sister incest avoidance, which operate during individual development, and the frequency of occurrence of this form of incest among cultures.

In an earlier article (1) we outlined a theory of gene–culture coevolution, in which genetic prescription determines the epigenetic rules of individual behavior and is in turn altered by natural selection through the epigenetically generated cultural patterns. Procedures were given by which it is possible to predict the influence on whole cultural patterns, defined by ethno-graphic probability distributions, imposed by bias in the behavioral development of individuals.

Epigenetic rules have been identified in a wide range of behavioral categories, and additional data permit the portrayal of a few ethnographic distributions (2–4). The method we have proposed has substantial power and can be applied to a wide range of cases both to predict the form of the ethnographic curves from developmental data and to infer the properties of the epigenetic rules from statistical ethnographic data. In applying translation analysis to real behavior, however, it is best to start with the simplest conceivable relationship, in which the epigenetic rules strongly bias individual development but not in a manner responsive to choices made by other members of the society. Although the evidence is still less than decisive, brother–sister incest avoidance apparently possesses properties that approximate these conditions and hence promises to serve as an early test case of gene–culture coevolutionary theory.

Many human societies tolerate and even encourage marriages between first cousins, but nearly all forbid it between siblings and half-siblings. A very few societies, including the Incas, Hawaiians, ancient Egyptians, Buganda, and Bunyoro, institutionalized brother–sister incest in the case of royalty or other groups of high status. Van den Berghe and Mesher (5) note that the incestuous males were in fact polygynous, behavior that resulted in outbreeding and a higher personal genetic fitness. Because of the general trend toward hypergamy, especially in such patrilineal societies, high-ranking women were less likely to marry downward in rank and hence were more susceptible to matches with their brothers.

Inbreeding at the level of siblings and half-siblings leads to a substantial increase in genetic defects among the offspring (6, 7). From a recent cross-cultural survey, Ember (8) concluded that the avoidance of these deleterious effects is the only explanation that fits the detailed patterns of same-generation incest aversion. It accounts not only for the inhibition of mating between brothers and sisters but also for the detailed patterns observed in the variable tolerance of cross-cousin marriages. The competing hypotheses that were tentatively discarded or assigned secondary explanatory power are the Freudian psychoanalytic model, the disruption of family bonds by incest, and the dependence upon exogamy as a bonding device among families.

The likelihood of sibling incest is automatically diminished by an epigenetic rule in the development of sexual behavior. From the study of sexual and marital preferences in Israeli kibbutzim (9) and Taiwanese villages (10), it has become apparent that close domestic familiarity during early childhood (in the case of the Israeli data, during the first 6 years) neutralizes later sexual attraction. The effect is very strong on any children raised closely together, whether genetically related or unrelated. This general result appears to be supported by anecdotal accounts of other societies, including the Trobrianders, Tallensi of Ghana, and Tikopians, as recently reviewed by Fox (11).

There is a need to confirm and refine the ethnographic analysis, which is directed at the ultimate adaptive value of incest avoidance, and developmental studies, which consider the existence of epigenetic rules. On the basis of existing information, we nevertheless can characterize the epigenetic rule of sibling incest and employ the translation model developed earlier (1) to predict the form of the ethnographic curves.

METHODS

Two cul turgens (1) are recognized: outbreeding and brother–sister incest. Any one of several degrees of incest can be used to demarcate these alternatives. The incest can entail marriage or equivalent long-term bonding, full sexual activity, and the procreation of children; or it can be defined at any lower level of involvement down to and including the most transient and casual forms of sexual contact. The more extreme possibility will be considered here, in which full sexual intercourse is practiced with or without marriage-like bonding.

From the Israeli and Taiwanese examples we can tentatively assign a value of the decision bias u21 in favor of outbreeding (cul turgens c1) close to unity and u12 in favor of brother–sister incest (cul turgens c2) close to zero. The young people in the large Israeli sample never chose heterosexual intercourse or marriage with unrelated children with whom they had been raised, even though the adults were permissive and encouraged matches within the kibbutzim. In 19 Taiwanese families that adopted girls as small children for the purpose of marriage to the hosts’ sons, the young couples later refused to go ahead with the match in 15 of the cases, despite parental pressure and a general consensus in the community favoring the arrangements. In two cases, one member of the pair died in childhood; the two remaining couples married.

The circumstances in the two societies suggest the development of a strong sexual inhibition during close domestic association (10). In the Taiwanese case particularly, the pressures exerted in favor of the sibling-like marriage are a reasonably potent substitute for a surrounding culture in which sibling incest is generally practiced. Thus the epigenetic rule appears to be relatively insensitive to social context. The assimilation...
functions \( u_j(\xi) \), which relate the individual transition probabilities to the choices made by other members of the society, can be approximated as constants. The variable \( \xi \) is defined as \( n_2/N - n_1/N \), in which \( n_2 \) individuals possess culturgen \( c_2 \) and \( n_1 \) individuals possess culturgen \( c_1 \) in a population of \( N \) members. The translation model can then be applied according to the remaining procedures outlined in ref. 1.

**RESULTS**

The average number of outbreeders in an array of societies each composed of \( N \) members is expected to be

\[
\bar{n}_1 = Nv_{21}(v_{12} + v_{21})^{-1} \tag{1a}
\]

\[
= N(1 + \tau_2u_{12}/\tau_1u_{21})^{-1}, \tag{1b}
\]

in which \( u_j \) are the individual transition probabilities at each decision point, and \( \tau_1 \) and \( \tau_2 \) are the mean lifetimes between decision points for outbreeders and inbreeders, respectively. Changes in the values of \( u_j \) are mapped through the ethnographic curve \( P(\xi) \) into shifts of the mean toward \( \xi = \pm 1 \). In the reverse direction, observation of \( \bar{n}_1 \) in arrays of societies provides estimates of the epigenetic parameters from ethnographic data.

The simple and robust form of the epigenetic rules of sibling incest generate a correspondingly simple structure for the ethnographic curves \( P(\xi) \), in which by definition \( \xi = 1 - 2n_1/N \). The exact steady-state solution \( P(n_1, N - n_1) \) of the master equation for culturgen dynamics (see equation 4 of ref. 1) is the binomial density

\[
P(n_1, N - n_1) = \binom{N}{n_1} \rho^{n_1}(1 - \rho)^{N - n_1}, \tag{2}
\]

in which

\[
\rho = (1 + \tau_2u_{12}/\tau_1u_{21})^{-1}. \tag{3}
\]

When the assimilation functions \( v_{ij} \) are such that \( v_{21} > Nv_{12} \), the most probable ethnographic state is pancultural avoidance of brother–sister incest. In the limit of large \( N \), the variable \( \xi \) is effectively continuous and for \( v_{12} \ll v_{21} \) Eq. 2 is conveniently approximated by the Fokker–Planck density (see equation 5 of ref. 1)

\[
P(\xi) = C(\beta - \phi\xi)^{N\Lambda} e^{N\beta\xi/\phi}, \tag{4}
\]

in which \( C \) is a normalization constant given by

\[
C^{-1} = \frac{e^{N\beta^2/\phi^2}}{|\phi|} \left[ \frac{\phi^2}{N\beta} \right]^{N\Lambda} \left[ \gamma\left( N\Lambda, \frac{N\beta(\beta - \phi)}{\phi^2} \right) - \gamma\left( N\Lambda, \frac{N\beta(\beta + \phi)}{\phi^2} \right) \right] \tag{5}
\]

such that

\[
\phi = v_{12} - v_{21}
\]

\[
\beta = v_{12} + v_{21}
\]

\[
\Lambda = (\beta^2 - \phi^2)/\phi^2
\]
\[
\epsilon = \begin{cases} 
1 & \text{if } v_{12} < v_{21} \\
-1 & \text{if } v_{12} > v_{21}
\end{cases},
\]
and the \(\gamma(\cdot, \cdot)\) are incomplete gamma functions of the first kind. Fig. 1 presents a series of ethnographic curves based on Eq. 2. In this case we have taken the transition values to be independent of the culture possessed by the individual; in other words, \(\tau_1 = \tau_2, u_{12} = u_{22}, \) and \(u_{21} = u_{11}\). The mean number of outbreeders is then just
\[
n_1 = u_{21}N. \quad [6]
\]
The strong aversion to the incestuous relationship when the social arrangements are such as to make it all but a fait accompli suggests that this special case is a useful approximation to the real epigenetic rules.

**DISCUSSION**

Although few exact ethnographic data are available (8, 11–13), anecdotal accounts of sexual practice in a wide range of societies (3–5, 9–12) indicate that the true curve is closer to that generated by \(u_{21} = 0.99\) than to the others displayed in Fig. 1. This is the qualitative result to be expected from the strength of the epigenetic rule of incest avoidance revealed by developmental studies (9, 10), although the Taiwanese data allow a value of \(u_{21}\) as low as 0.90. The epigenetic rules can be expected to be more permissive toward casual forms of sexual contact than those designated in the present study, resulting in epigenetic curves that span segments of the \(\xi\) scale further to the right.

We have treated the \(u_i\) values as constants, but this condition can be relaxed somewhat with little effect on the qualitative results. The Israeli and Taiwanese data suggest that, if there is variation in the values, it most likely consists of a slight monotonic trend upward in \(u_{12}\) and downward in \(u_{21}\) as \(\xi\) increases. In translation models accurate to first-order in such a case, the \(u_i(\xi)\) are given by truncated Taylor series \(u_i(\xi) = a_{ij} + b_{ij}\xi,\) where the intercepts \(a_{ij}\) are given by \(u_i(0)\) and the slopes \(b_{ij}\) by \(du_i(0)/d\xi.\) For brother–sister incest, \(|b_{ij}/a_{ij}| \ll 1\) and the ethnographic curves are closely approximated by Eq. 2.

The incest case appears to provide one of the simplest conceivable cases of gene–culture translation. Our model of the translation yields a correspondingly clear and unsurprising relation between the degree of bias in the epigenetic rules and the mode of the ethnographic curve. But it also illustrates the very general principle that even fixed epigenetic rules, provided they do not favor one culture absolutely, can be expected to yield substantial cultural diversity as measured by the variance of the ethnographic distributions. Put another way, the existence of a great deal of variation among societies in a particular behavioral category does not imply the absence of genetically prescribed bias in the epigenetic rules. Only closer studies of cognitive development at the individual level, linked to ethnographic data through appropriate translation models, can reveal the relation between genes and culture.

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