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Two Problems in the Interaction between Genes and Culture

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The interaction between genes and culture is believed to have played an important role in the emergence of the human. In the present report, I briefly consider two problems that display some of the interesting features of this interaction.

Adult Lactose Absorption and Milk Use

Some adult humans can digest and absorb the sugar lactose. This ability is believed to be inherited as a simple dominant trait. High frequencies of lactose absorbers are observed in some populations that have a long history of drinking animal milk. This association may be the evolutionary consequence of a positive selection pressure induced by the culturally determined milk use. It is possible to relate the time required for gene frequency change to the parameters of cultural transmission and natural selection.

The treatment of time properties is facilitated by using a continuous time model. A discrete generations model was formulated and its continuous time approximation derived.

The reproductive adults mate at random and survive to enculturate the weaned children. The latter may or may not acquire the habit of drinking animal milk, depending on cultural and genetical factors. There are two phases of cultural transmission, oblique (between generations) and horizontal (within generations). After oblique transmission, the frequency of milk drinkers in the new generation is the same as in the adults of the previous generation. In particular, the oblique transmission rate is 1 for both lactose absorbers and malabsorbers. During horizontal transmission, differences in the preferences of absorbers and malabsorbers may be expressed. The horizontal transmission rates are a and b, respectively. There are four phenotypes, and their fitnesses are summarized in Table 1.

Table 1

	lactose absorber	lactose malabsorber
drinker	$1+s$	$1+s'$
nondrinker	1	1

Assuming weak selection, we define a new time scale, t, in which $s-s'$ units correspond to one generation in the old time scale, n. We assume $s > s'$. The continuous time approximation yields the following pair of ordinary differential equations in the frequency of drinkers, y, and of the dominant allele, p,

$$dy/dt = yz\left[(1+A)(1-q^2) + Bq^2\right], \qquad (1a)$$

$$dp/dt = pq^2y, \qquad (1b)$$

where $z=1-y$, $q=1-p$, $A=(a+s')/(s-s')$, $B=(b+s')/(s-s')$. Dividing (1a) by (1b) leads to a separable equation that can be integrated to give

$$y(p) = 1 - Cp^{-B}q^{1+A}\exp\left[-(1+A)/q\right]. \qquad (2a)$$

Here, C is a constant that depends on the initial values of the variables which are indicated by the subscript 0, i.e.,

$$C = z_0 p_0^B q_0^{-(1+A)} \exp(1+A)/q_0. \qquad (2b)$$

Hence, from (1b), (2a) and (2b), the time required for the allele frequency to increase from p_0 to p_t is

$$t = \int_{p_0}^{p_t} [pq^2 y(p)]^{-1} dp. \qquad (3)$$

Table 2 gives some values of t obtained by numerical integration of (3). I assumed $y_0 = p_0 = 0.5$, $p_t = 0.70$. The initial and final values of the gene frequency assumed here are conservative estimates for the ancestral and modern European populations in that the difference is probably greater.

Table 2

A \ B	-0.2	0.0	0.2	1.0
-0.2	219.5	21.8	15.0	9.2
0.0	56.0	19.7	14.2	9.1
0.2	38.4	18.1	13.6	9.0
1.0	20.9	14.5	12.0	8.7

Comparison of the coevolutionary model presented here with the standard genetic one is facilitated by setting $s' = 0$. With complete genetic determination, i.e., all absorbers are drinkers and all malabsorbers are nondrinkers, the time is 6.07 units. Table 2 shows that the time required for gene frequency change may be substantially longer when there is some cultural determination of phenotype.

The effect of s′ is interesting. The time reconverted to the original scale appears to be minimized at small positive values as shown in Table 3. Here, s=0.05, a=0.01, b=-0.01, $y_0 = p_0 = 0.5$, $p_t = 0.70$.

Table 3

s′	n
0.00	768
0.01	410
→ 0.02	367
0.03	424
0.04	711

Archaeological evidence indicates that some 5000 years or 200 generations have elapsed since animal milk was first consumed in quantity. The coevolutionary model predicts the need for much stronger selection than the standard genetic one if the gene frequency is to increase in the time available.

Recessive Deafness and Persistence of a Sign Language

Sign languages are the naturally occurring forms of linguistic communication among people who do not hear. Since most cases of profound childhood deafness are hereditary, in particular inherited as simple recessives, the social distribution and learning of a sign language are subject to strong, if indirect, genetic constraints. The possible consequences of this interaction between genetic and cultural transmission for the persistence of a sign language are interesting.

Assuming monogenic recessive inheritance of deafness, and cultural transmission of a sign language from deaf parents to their deaf children, the condition for signers not to disappear is

$$2f\,[(1-m)q+m] > 1. \qquad (4)$$

Here, q is the frequency of the recessive allele causing deafness, m is the fraction of matings that are assortative for deafness or for hearing, and f is the probability that a deaf child acquires the sign language when only one parent signs. If matings occur mostly at random so that m is small, the inequality (4) cannot be satisfied. However, estimates of the rate of assortative mating in England and the United States are greater than 80%. Hence, strong assortative mating for deafness may be one of the major factors contributing to the persistence of a sign language.

Two other results are worth mentioning. First, it is conceivable that assortment occurs for signing rather than for deafness, but our prediction in that case is that, paradoxically, a sign language may be more easily lost. Second, the incorporation of oblique and horizontal transmission of sign language has negligible effects.

Since recessive hereditary deafness can "jump a generaton", it is of interest to allow for cultural transmission from grandparents to their grandchildren. Suppose that a deaf child always acquires the sign language from the parents when at least one of them signs. When neither parent signs, he or she still may learn from signing maternal grandparents with probability g. Then, the condition for persistence is

$$2\,[(1-m)q+m] + gH(1-m) > 1. \qquad (5)$$

Here, H is half the frequency of heterozygotes at equilibrium under assortative mating, and since it is small, grandparental transmission has little effect in this case.

References

The theoretical results reported here are based on the 5 papers listed below. References to background information can also be found in these papers.

1. Aoki, K. (1986) A stochastic model of gene-culture coevolution suggested by the "culture historical hypothesis" for the evolution of adult lactose absorption in humans. Proc. Natl. Acad. Sci. USA 83, 2929-2933.
2. Feldman, M.W. and Cavalli-Sforza, L.L. (1989) On the theory of evolution under genetic and cultural transmission with application to the lactose absorption problem. In: Mathematical Evolutionary Theory (Feldman, M.W., Ed.) pp.145-173, Princeton Univ. Press.
3. Aoki, K. (no date) Time required for gene frequency change in a deterministic model of gene-culture coevolution, with special reference to the lactose absorption problem. Theor. Popul. Biol., submitted.
4. Aoki, K. and Feldman, M.W. (1990) Recessive hereditary deafness, assortative mating, and persistence of a sign language. Theor. Popul. Biol., in press.
5. Feldman, M.W. and Aoki, K. (no date) Assortative mating and grandparental transmission facilitate the persistence of a sign language. In preparation.