RECESSIVE HEREDITARY DEAFNESS, ASSORTIVE MATING, AND PERSISTENCE OF A SIGN LANGUAGE

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Introduction

Sign languages and spoken languages are systems of human communication that depend on a knowledge of rules and conventions. Persistence of *any* language would seem to require the presence of a number of individuals with the opportunity and motivation to learn it. In the case of sign language, these individuals are usually the deaf, who are a minority of the population. Indeed, the term sign language, as used here, refers to the naturally occurring form of communication among people who do not hear (Kyle and Woll, 1985).

There are hereditary and acquired forms of deafness. This paper focuses on the effect that genetic segregation may have on persistence of a sign language. According to Frazer (1976), the incidence of profound childhood deafness in the British Isles is 1/1000, the contribution of autosomal recessive forms being 1/3. Comparable estimates have been obtained in a study of Japanese school children (Furusho and Yasuda, 1973). Most hereditary deafness is believed to be caused by recessive genes at many loci (Chung et al., 1959). Here we consider the problem of one recessive locus.

When deafness is recessive, an affected child may be born to normal heterozygous parents. (By contrast, when it is dominant, an affected child has at least one affected parent.) In addition, when more than one recessive gene is segregating, a problem that is not treated in this paper, the parents may be affected homozygotes at different loci, in which case all children are expected to have normal hearing. In both examples of recessive inheritance, the transmission of a particular sign language across generations may be interrupted if it is not learned by hearing individuals. Such considerations suggest it may be difficult to prevent its loss. (See also Kyle and Woll, 1985)

The frequency of an allele causing deafness would usually be considered to be determined by the balance between negative selection and recurrent mutation. Hence, it is low. Nevertheless, it may be substantially higher in an isolated population (Groce, 1985). In this paper, we assume the gene frequency to be a parameter and do not explicitly consider how it is maintained. We do, however, take into account the change in equilibrium genotype frequencies due to assortative mating. There is strong assortment for deafness (Kyle and Woll, 1985), which cannot be ignored. An alternative possibility that we also

investigate is assortment for sign language.

We are interested in obtaining the conditions under which sign language users will not disappear from the population. The major part of the analysis is based on mathematical models that assume recessive hereditary deafness and cultural transmission of sign language from parents to their children (vertical transmission, Cavalli-Sforza and Feldman, 1981, pp. 77-129). But we also look at the effects of dominant hereditary deafness, acquired deafness, and alternative forms of cultural transmission.

Notation

We adhere to the following notation. There are two alleles A and a at a genetic locus affecting hearing, with A completely dominant to a. Unless otherwise stated, aa individuals are deaf from birth. The frequencies of the three genotypes AA, Aa, aa are D, $2H$, R. Signers (users of sign language) of genotypes AA, Aa, aa are present at frequencies u_1, $2u_2$, u_3. Set $p = D + H$, $q = H + R$, $x_1 = u_1 + u_2$, $x_2 = u_2 + u_3$, $K = u_1 + 2u_2 + u_3$. In our mathematical models, the gene frequencies p and q are constants and can be treated as parameters.

There are five other parameters that need to be defined here. The fraction of assortative matings is m. For example, in one assortment-by-deafness model (Crow and Kimura 1970), both hearing and deaf individuals mate assortatively at this same rate. When both parents are signers whether deaf or not, sign language is acquired by a fraction b of their hearing children and a fraction c of their deaf children. Since deaf children are more motivated to learn or their parents more eager to teach sign language, $b \leq c$. When only one parent signs, these probabilities are multiplied by the factor ℓ. Finally, an individual who is genetically normal may become deaf with probability e due to disease and other environmental causes.

Other parameters to be defined later include the oblique transmission parmeters, f and g, and the horizontal transmission parameters, h and i.

Assortment by deafness

Consider the basic model of recessive hereditary deafness (genotypes AA and Aa are hearing, genotype aa is deaf), and vertical (parents to children) transmission of sign language. When both hearing and deaf individuals mate assortatively at the same rate m, the equilibrium frequency of genotype aa is

$$R = \{1 + q^2 - mp^2 - [(1 + q^2 - mp^2)^2 - 4q^2]^{\frac{1}{2}}\}/2, \tag{1a}$$

(Crow and Kimura, 1970, pp. 144-148). The equilibrium frequency of genotype AA and half that of Aa are then given by

$$D = p - q + R, \tag{1b}$$

$$H = q - R. \tag{1c}$$

We assume equilibrium in what follows.

We wish to obtain the conditions under which signers will not disappear from the population. The linearized recursions in the frequencies u_1, u_2, and u_3 of the signers, valid when these quantities are small, are

$$u_1' = 2\ell b(D/p)(u_1 + u_2), \tag{2a}$$

$$u_2' = \ell b[(H/p)u_1 + u_2 + (1-m)pu_3], \tag{2b}$$

$$u_3' = 2\ell c\{(H/p)u_2 + [(1-m)q + m]u_3\}. \tag{2c}$$

(We use half the frequency of signers in the case of genotype Aa to avoid intrusive factors of 2.) We assume $0 < p$, $q < 1$, $0 \leq m < 1$, $0 \leq b \leq c \leq 1$, and $0 < \ell \leq 1$.

Derivation is illustrated for (2c). The factor ℓ enters because linearization in u_1, u_2 and u_3 implies that only one parent can be a signer, while c enters because individuals of genotype aa are deaf. Signer children of genotype aa are produced from the matings $Aa \times Aa$, $Aa \times aa$, $aa \times Aa$, and $aa \times aa$, where in each case the left parent is a signer and the right parent a non-signer. Table 1 lists the relevant mating types and gives their frequencies. All frequencies are multiples of 2 because either the mother or the father can be a signer. Thus

$$\begin{aligned}u_3' &= 2\ell c\{(1-m)u_2 H + mu_2 H/(1-R) \\ &\quad + (1-m)u_2 R + (1-m)u_3 H \\ &\quad + (1-m)u_3 R + mu_3 R/R\} \\ &= 2\ell c\{[(1-m)q + mH/(1-R)]u_2 + [(1-m)q + m]u_3\}.\end{aligned}$$

Finally, substituting the equilibrium relation $H/p = (1-m)q + mH/(1-R)$ (Crow and Kimura, 1970) gives the desired result.

Table 1 here.

The characteristic polynomial of (2a)-(2c) is

$$\begin{aligned}\phi(\lambda) =&(2\ell bD/p - \lambda)(\ell b - \lambda)\{2\ell c[(1-m)q + m] - \lambda\} \\ &- (2\ell bD/p - \lambda)2\ell^2 cb(1-m)H \\ &- \{2\ell c[(1-m)q+m] - \lambda\}2(\ell b)^2 DH/p^2.\end{aligned} \tag{3}$$

The eigenvalues of the matrix in (2) are the roots of the cubic $\phi(\lambda) = 0$. Signers will not disappear from the population if the equilibrium $\hat{u}_1 = \hat{u}_2 = \hat{u}_3 = 0$ is unstable, and instability is assured if the maximal eigenvalue, $\lambda_{\max}$, is greater than one in absolute value. Since the coefficients of (2a)-(2c) form a nonnegative irreducible matrix, the maximal eigenvalue is real and positive.

If $0 < b < c$, then

$$2\ell b < \lambda_{\max} < 2\ell c. \tag{4a}$$

To see this, note that $\phi(0) \geq 0$, $\phi(\ell b) < 0$, $\phi(2\ell b) > 0$, and $\phi(2\ell c) < 0$. Since $c \leq 1$, this result implies that $\lambda_{\max}$ can exceed one only if $\ell > 1/2$. In other words, one signer parent must be able to transmit sign language with greater than one-half the efficiency of two. If $0 = b < c$, then

$$\lambda_{\max} = 2\ell c[(1-m)q + m], \tag{4b}$$

which satisfies (4a). The latter result indicates that signers will not necessarily disappear, even if the hearing do not learn sign language ($b = 0$), provided that c is large enough. If $0 < b = c$, then $\phi(2\ell b) = 0$, and an argument similar to that used to prove (4a) shows

$$\lambda_{\max} = 2\ell b = 2\ell c, \tag{4c}$$

regardless of the value of m.

When mating is at random ($m = 0$), (3) factors into λ times a quadratic, and from the latter we have

$$2\ell[b(1-q^2)+cq^2] < \lambda_{\max} < 2\ell(bp+cq), \tag{4d}$$

if $0 \leq b < c$. In the limiting case $m = 1$, we obtain

$$\lambda_{\max} = 2\ell c. \tag{4e}$$

Comparison of (4d) and (4e) shows that, given $2\ell c > 1$, a sign language may disappear when mating is at random, whereas it will persist when mating is completely assortative. Furthermore, it suggests that the maximal eigenvalue, $\lambda_{\max}$, may increase monotonically as the rate of assortative mating, m, increases. This is manifestly true for $b = 0$ as can be seen from (4b), and for b near c (i.e., extreme values of b). Setting $\phi(\lambda) \equiv F(c, \lambda) = 0$ and applying the implicit function theorem gives

$$\left.\frac{d\lambda}{dc}\right|_{c=b,\,\lambda=2\ell b} = 2\ell R.$$

Hence for small $c - b$, we have

$$\lambda_{\max} = 2\ell b(1-R) + 2\ell cR. \tag{5}$$

Monotone increase of R as a function of m ensures the same for $\lambda_{\max}$.

In applications of practical interest, the frequency, q, of the allele causing deafness is low. For m not too close to 1, $D \approx 1 - 2q$, $H \approx q$, and $R \approx 0$ to first order in q. Thus the value of the characteristic polynomial at $\lambda = 1$ is approximated by

$$\phi(1) \approx (2\ell b - 1)\{2\ell c[\ell b - 1 - (2\ell b - 1)q]m - [\ell b - 1 + 2\ell(c-b)q]\}. \tag{6}$$

We know already that $\lambda_{\max} < 1$ if $2\ell c \leq 1$ and $\lambda_{\max} > 1$ if $2\ell b \geq 1$. When $2\ell b < 1 < 2\ell c$, a consideration of the cubic (3) shows that stability is determined by the sign of $\phi(1)$: if $\phi(1) > 0$ then $\lambda_{\max} > 1$, and if $\phi(1) < 0$ then $\lambda_{\max} < 1$. Thus, from (6), signers will not disappear if

$$2\ell cm > 1 - (2\ell c - 1)q/(1 - \ell b). \tag{7}$$

Inequality (7) is an explicit condition involving all parameters of the model. The condition is more easily satisfied the larger are the values of q, m, b, c, and ℓ.

Recessive and dominant hereditary deafness

The mode of inheritance of deafness may alter the chances of survival of a sign language. By making a few simplifying assumptions, we can show that λ_{max} is smaller with recessive deafness than in the dominant case except when m is close to one. These assumptions are (i) that the hearing do not learn sign language ($b = 0$) and (ii) that the frequency of the allele causing deafness (q for a recessive and p for a dominant) is low.

In the recessive case, λ_{max} is given by (4b). This formula is exact, but we assume that q is small. In the dominant case, the genotypes AA and Aa are deaf whereas aa hears. Exchanging b and c in (3) and setting $b = 0$ gives

$$\lambda_{max} = \ell c\{2(D/p) + 1 + [1 + 4(D/p) - 4(D/p)^2]^{\frac{1}{2}}\}/2. \qquad (8)$$

$D \approx (1 - \sqrt{1-m})p$ to first order in p. Substituting into (8) gives

$$\lambda_{max} \approx \ell c\{3 - 2\sqrt{1-m} + [1 + 4\sqrt{1-m} - 4(1-m)]^{\frac{1}{2}}\}/2.$$

Comparison of the above with (4b) shows that λ_{max} is smaller with recessive deafness if

$$\sqrt{1-m} > (1 - \sqrt{1-2q})/2(1-q). \qquad (9)$$

The right hand side of (9) reduces to $q/2$ when we ignore higher order terms, indicating that λ_{max} is indeed smaller with recessive deafness except when m is close to one.

Further insight can be obtained by expanding (8) in powers of $\sqrt{1-m}$. When terms of order $(1-m)\sqrt{1-m}$ are retained,

$$\lambda_{max} \approx 2\ell c\{1 - (1-p)(1-m) + (2-p)\sqrt{1-p}(1-m)\sqrt{1-m}\}.$$

Comparison with (4b) rewritten as $\lambda_{max} = 2\ell c[1 - (1-q)(1-m)]$ suggests that λ_{max} is always smaller with recessive deafness if the frequency of the recessive allele causing deafness does not exceed that of the dominant, i.e., if $q \leq p$.

Oblique and horizontal transmission with recessive deafness

A child may learn sign language from an individual other than his or her parents. When that individual is a random member of the parental generation, oblique transmission is said to have occurred. Similarly, when that individual is a random member of the same generation as the child, horizontal transmission is said to have occurred (Cavalli-Sforza and Feldman 1981). We assume that all learning takes place before reproductive age.

Let the oblique transmission parameters be f for the hearing children (genotype AA and Aa) and g for the deaf ones (genotype aa). Then the linearized recursions with oblique transmission occuring after vertical are

$$u_1' = 2\ell b(D/p)(u_1 + u_2) + fDK, \tag{10a}$$

$$u_2' = \ell b[(H/p)u_1 + u_2 + (1-m)pu_3] + fHK, \tag{10b}$$

$$u_3' = 2\ell c\{(H/p)u_2 + [(1-m)q + m]u_3\} + gRK, \tag{10c}$$

where $K = u_1 + 2u_2 + u_3$.

When q is small, $2\ell b + f$ is an eigenvalue of the problem, though it is not necessarily the maximal one. Thus

$$2\ell b + f > 1 \tag{11}$$

is a sufficient condition for persistence of a sign language. In particular, if $b = 0$ then $\lambda_{\max}$ is given by (4b) for $f < 2\ell cm$ and $\lambda_{\max} \approx f$ for $f > 2\ell cm$.

Next, if the horizontal transmission parameters are h for the hearing and i for the deaf, the linearized recursions are

$$u_1' = 2\ell b(D/p)(u_1 + u_2) + hDL, \tag{12a}$$

$$u_2' = \ell b[(H/p)u_1 + u_2 + (1-m)pu_3] + hHL, \tag{12b}$$

$$u_3' = 2\ell c\{(H/p)u_2 + [(1-m)q + m]u_3\} + iRL, \tag{12c}$$

where

$$\begin{aligned} L = {} & 2\ell b(D/p)(u_1 + u_2) \\ & + 2\ell b[(H/p)u_1 + u_2 + (1-m)pu_3] \\ & + 2\ell c\{(H/p)u_2 + [(1-m)q + m]u_3\}. \end{aligned} \tag{12d}$$

Assuming again that q is small, we find that $2\ell b(1+h)$ is an eigenvalue. Thus

$$2\ell b(1+h) > 1 \tag{13}$$

is a sufficient condition for persistence. In this case, the maximal eigenvalue is given by (4b) if $b = 0$. Conditions similar to (11) and (13) with vertical transmission together with either oblique or horizontal transmissions can be found in Cavalli-Sforza and Feldman (1981, pp. 130-153).

The oblique and horizontal transmission parameters are products of contact rates and transmission probabilities, and hence are not necessarily bounded. Inequalities (11) and (13) indicate that the chances for the persistence of a sign language may be improved when these forms of cultural transmission also occur. However, it is important to note that g and i — the oblique and horizontal transmission parameters for the deaf — do not appear in the respective characteristic polynomials. Hence, opportunities for the deaf to acquire sign language from randomly encountered individuals outside the family do not seem to add to the chances that sign language will persist.

Acquired deafness

We have so far considered only hereditary deafness. In this section we introduce the possibility of acquired deafness.

The recessive homozygote, aa, is genetically deaf, and a proportion, e, of the normal genotypes, AA and Aa, becomes deaf due to environmental causes at or soon after birth. Then the hearing and deaf are present in the proportions $(1-R)(1-e)$ and $R+(1-R)e$. Among the hearing the frequency of allele a is $H/(1-R)$, and among the deaf it is $(He+R)/[R+(1-R)e]$. We assume a degree of assortment, m, for deafness regardless of causation, and the same degree of assortment for hearing.

The recursions in the genotype frequencies can be obtained by an extension of the argument used by Crow and Kimura (1970). In what follows we require only the recursion in R, which is

$$R' = (1-m)q^2 + m(1-R)(1-e)[H/(1-R)]^2 \\ + m[R+(1-R)e]\{(He+R)/[R+(1-R)e]\}^2.$$

Substituting $H = q - R$ yields

$$\begin{aligned} R' &= (1-m)q^2 \\ &\quad + m\{q^2[R(1-2e)+e] + R^2(1-e)(1-2q)\}/(1-R)[R(1-e)+e] \\ &\equiv F(R), \end{aligned} \tag{14}$$

say. There are two positive roots of the equation $R = F(R)$, which occur in the interval $q^2 < R < 1$. Since the transformation (14) is monotone for $0 < R < 1$, and $F(0) > 0$, the smaller root is the stable equilibrium. Subsequently, we assume that this equilibrium has been reached.

Next, we assume that sign language is transmitted vertically and that only the deaf learn it ($b = 0$). The linearized recursions in u_1, u_2, and u_3 are

$$u_1' = 2e\ell c M_e(u_1 + u_2), \tag{15a}$$

$$u_2' = e\ell c[(N_e u_1 + M_e u_3) + u_2] \tag{15b}$$

$$u_3' = 2\ell c N_e(u_2 + u_3) \tag{15c}$$

where

$$M_e = p\{1 - m + me/[R + (1 - R)e]\}, \tag{16}$$

$$N_e = (1 - m)q + m(He + R)/[R + (1 - R)e], \tag{17}$$

and dependence on e is indicated by the subscript. Note $M_e + N_e = 1$.

We assume $0 < p$, $q < 1$, $0 \leq m < 1$, $0 < c \leq 1$, $0 < \ell \leq 1$, $0 \leq e < 1$. The derivation is illustrated for (15a). Signer children of genotype AA occur only among a proportion, e, of all children who are deaf due to environmental causes. They are produced from the matings $AA \times AA$, $AA \times Aa$, $Aa \times AA$, and $Aa \times Aa$, where in each case the left parent is a signer and the right parent is a non-signer. Table 2 lists the relevant mating types and gives their frequencies. Thus

$$\begin{aligned} u_1' &= 2e\ell c\{(1-m)u_1 D + mu_1 De/[R + (1-R)e] \\ &\quad + (1-m)u_1 H + mu_1 He/[R + (1-R)e] \\ &\quad + (1-m)u_2 D + mu_2 De/[R + (1-R)e] \\ &\quad + (1-m)u_2 H + mu_2 He/[R + (1-R)e]\} \\ &= 2e\ell c(D + H)\{1 - m + me/[R + (1-R)e]\}(u_1 + u_2). \end{aligned}$$

The characteristic polynomial of (15a)–(15c) is

$$\begin{aligned} \phi(\lambda) = -\lambda\{\lambda^2 - \ell c[2 + e - 2M_e(1-e)]\lambda \\ + 2(\ell c)^2 e[1 - M_e^2(1-e)]\}. \end{aligned} \tag{18}$$

If $e = 0$, then $\lambda_{\max} = 2\ell c N_0$ which is equivalent to (4b). In this case $\lambda_{\max} > 1$ if and only if $2\ell c N_0 > 1$. In general it can be shown that a sufficient condition for $\lambda_{\max} > 1$ is

$$2\ell c N_e > 1. \tag{19}$$

In applications of practical interest, the incidence of acquired deafness is expected to be low. Setting $\phi(\lambda) \equiv F(e, \lambda) = 0$, and using the implicit function theorem,

$$\left.\frac{d\lambda}{de}\right|_{e=0,\,\lambda=2\ell c N_0} = \ell c p[R_0(1-m) - 2m]/R_0, \tag{20}$$

where R_0 is the equilibrium frequency of genotype aa when $e = 0$ (see(1a)). From (20) it can be seen that $\lambda_{\max}$ may increase or decrease as the incidence of acquired deafness increases from zero to some low level. In particular, (20) is positive if $m = 0$ and negative if $m = 1$.

Assortment by signing

Cavalli-Sforza and Feldman (1981) have developed the evolutionary dynamics of a dichotomous phenotype with cultural transmission where assortative mating occurs among the phenotypes. The phenotypic dichotomy in the present case is between signers and nonsigners. In addition, we now have genetic variation for deafness and hearing.

We suppose that the population initially has nonsigners of genotypes AA, Aa and aa, respectively, in frequencies $D, 2H$ and R. We seek conditions under which the frequencies of signers of these genotypes, introduced at small frequencies $u_1, 2u_2$ and u_3, respectively, will initially increase. The vertical transmission parameters are as in the previous sections. With assortative mating by signing status, the mating frequencies differ from those in Table 1. Table 3 presents the relevant mating frequencies and transmission rules when $u_1, 2u_2$ and u_3 are small with $D, 2H$ and R correspondingly close to fixed initial values.

Table 3 here.

The linearized recursions near $(D, 2H, R)$ analogous to (2) above are

$$u_1' = 2\ell b(1-m)(u_1+u_2)p + bm(u_1+u_2)^2/K \tag{21a}$$

$$u_2' = \ell b(1-m)[(u_1+u_2)q + (u_3+u_2)p] + bm(u_1+u_2)(u_3+u_2)/K \tag{21b}$$

$$u_3' = 2\ell c(1-m)(u_3+u_2)q + cm(u_3+u_2)^2/K, \tag{21c}$$

where $K = u_1+2u_2+u_3$ is the frequency of signers in the population and $p = D+H = 1-q$. In writing this system, quadratic terms in u_1, u_2 and u_3 have been neglected but the terms with coefficients bm or cm may not be neglected since the denominator K is of linear order. Thus, ratios such as $(u_1+u_2)^2/K$ are of linear order and must be included. Write $x_1 = u_1+u_2$, $x_2 = u_3+u_2$. Then from (21) we have

$$x_1' = [\ell b(1-m)(1+p) + bm]x_1 + \ell b(1-m)px_2 \tag{22a}$$

$$x_2' = \ell b(1-m)qx_1 + [2\ell c(1-m)q + \ell b(1-m)p]x_2 + x_2 m(cx_2+bx_1)/K \tag{22b}$$

Clearly the local recursion (22) is nonlinear in x_2 unless $b=0$ or $b=c$. In the latter case the largest eigenvalue of the resulting transformation is

$$\lambda_{\max} = 2\ell b(1-m) + bm, \tag{23}$$

while in the former it is $\lambda_{\max} = 2\ell c(1-m)q + cm$ which is increasing in m if q is small.

When $c > b > 0$ the analysis is carried out in two steps. First we show that the ratio $w = x_1/x_2$, near $(D, 2H, R)$, converges to a limit ξ. Then this limit is included in (22) to produce a linear recursion. To see this note from (22) that

$$\begin{aligned} w' &= [(\alpha + bm)w^2 + (\alpha + \beta + bm)w + \beta]/[\gamma w^2 + (\gamma + \delta + bm)w + \delta + cm] \\ &\equiv F(w), \end{aligned} \tag{24}$$

say, where

$$\begin{aligned} \alpha &= \ell b(1-m)(1+p), & \beta &= \ell b(1-m)p, \\ \gamma &= \ell b(1-m)q, & \delta &= 2\ell c(1-m)q + \ell b(1-m)p. \end{aligned} \tag{25}$$

It can be shown that the transformation $F(w)$ is monotone increasing and that $F(0) = \beta/(\delta + cm) > 0$. Moreover, there is exactly one positive equilibrium of (24) except when

$$[\ell(1-m)(1+p) + m]/[2\ell(1-m)q + m] < c/b < p/2q, \tag{26}$$

in which case there may be three (a possible double root is counted as two). The lower bound in (26) must exceed 1 if this inequality is to be satisfied since $c/b > 1$. In fact, for c/b close to 1 there is a unique positive equilibrium whose value is close to the value p/q, valid when $b = c$. It follows that over time the recursion (24) converges to a positive limit ξ, although the equilibrium approached may depend on the ratio of the initial values of x_1 and x_2.

Although the exact value of ξ is too cumbersome to use explicitly, ξ may be substituted into (22) to produce a linear recursion in x_1 and x_2, the matrix of which is strictly positive. For small $(c - b)$, use of the implicit function theorem shows that the leading eigenvalue of this matrix is approximately

$$\lambda_{\max} = [2\ell b(1-m) + bm](1-q^2) + [2\ell c(1-m) + cm]q^2. \tag{27}$$

From (23), and more generally from (27), $\lambda_{\max}$ can exceed one only if $\ell > 1/2$. But when $\ell > 1/2$, $\lambda_{\max}$ is monotone decreasing in m. Thus assortment for signing, unlike that for deafness, is apparently an unfavorable circumstance for the persistence of sign language. However, even if signing among hearing individuals might not have spread in the population, it may do so as a consequence of more efficient transmission (i.e., $c > b > 0$) to deaf offspring.

To see that the transmission parameters interact with gene frequencies in determining initial increase of signing, consider first the case $m = 0$ and $b = c$. Then signing increases initially if $2\ell b > 1$. If $2\ell b < 1$ and $m = 0$, then from the local stability quadratic for (22) signing increases initially if

$$2\ell cq > [1 - \ell b(1 + 2\beta) + 2\ell^2 b^2 p^2]/[1 - \ell b(1 + p)], \tag{28}$$

which requires $c > b$, since the right side of (28) is greater than $2\ell bq$. If q is very small, however, (28) cannot be satisfied. If (28) holds for some value of q, say q_0, then, for the same values of c and b, it holds for all $q > q_0$. If the opposite inequality to (28) holds, then signing cannot increase when rare.

To conclude this section, consider the case $b = c$ and compare the two kinds of assortment, that based on hearing-deaf dichotomy and that based on signing-nonsigning differences. Table 4 below shows the comparison and illustrates clearly the dependence of initial increase, under the latter type of assortment, on the extent of assorting. In particular, a sign language is more likely to persist under the former type of assortment.

Table 4 here.

Discussion

It is only recently that the various sign languages used by deaf communities have come to be recognized as natural languages. Presumably, each sign language has a history, but unfortunately this is not well documented. In this paper we derive the conditions under which a particular sign language may persist over many generations, based on simple models of hereditary and environmental deafness. These conditions are difficult to satisfy, possibly suggesting a fairly recent origin for the extant sign languages. By contrast, the spoken languages are probably much older. A time depth of at least 5000 years is generally accepted for the Indo-European family (Crystal, 1987), and all spoken languages are believed by some linguists to be traceable to a unique ancestral language (e.g., Ruhlen, 1990).

There are two basic premises of this paper. First, the deaf are more motivated to learn sign language than the hearing who, if their parents are signers, learn with positive probability. Second, a vertically transmitted sign language, unlike recessive hereditary deafness, cannot "jump a generation" to be expressed among grandchildren. Since an estimated two-thirds of hereditary deafness is recessive, and acquired deafness occurs sporadically, transmission of a particular sign language across generations is expected to be interrupted unless hearing individuals also participate in its use.

In this paper, we consider the effects of assortative mating for deafness or for signing, mode of inheritance, acquired deafness, and different forms of cultural transmission. Some of the results are fairly general, but others are obtained on restrictive assumptions such as no sign language acquisition by the hearing or a low frequency of the allele causing deafness.

It is interesting that assortment according to whether an individual is deaf or not facilitates persistence of a sign language, but assortment according to whether an individual can sign or not has the opposite effect. Paradoxically, this is because assortment for signing leads to the inclusion of terms in the linearized recursions (21) deriving from matings between two signer parents; and since persistence requires that one signer parent be able to transmit sign language with greater than one-half the efficiency of two, the maximal eigenvalue will be reduced due to the inclusion of these terms.

When the two common modes of inheritance of deafness (dominant and recessive autosomal) are compared (Chung et al., 1959), the former is found to be more favorable to the persistance of sign language. The reason for this would appear to be clear, since a deaf child has at least one deaf parent when deafness is dominant. However, with almost complete assortment for deafness, the effect may unexpectedly be reversed depending on the frequencies of the dominant and recessive alleles for deafness.

When deafness may be caused by environmental as well as hereditary factors, the results are difficult to interpret. We note that the maximal eigenvalue can increase or decrease with the incidence of acquired deafness, depending on the degree of assortment for deafness. Numerical work not attempted here should help in elucidating the problem further.

Assortative mating as well as oblique and horizontal transmission are density dependent phenomena. The persistence of sign language is facilitated by increased levels of assorting for deafness and of oblique/horizontal transmission. Sparsely distributed populations would, therefore, appear to be unlikely candidates for successful establishment of sign language. We might speculate that under conditions such that $\lambda_{max} < 1$, there might be short periods of primitive sign language. With high levels of oblique or horizontal communication $\lambda_{max} > 1$ and more complex sign language has a chance to evolve.

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References

Cavalli-Sforza, L.L. and Feldman, M.W. (1981) *Cultural Transmission and Evolution.* Princeton, N.J.: Princeton University Press.

Chung, C.S., Robinson, O.W. and Morton, N.E. (1959) A note on deaf mutism. *Ann. Hum. Genet.* **23**, 357-366.

Crow, J.F. and Kimura, M. (1970) *An Introduction to Population Genetics Theory.* New York: Harper and Row.

Crystal, D. (1987) *The Cambridge Encyclopedia of Language.* Cambridge: Cambridge University Press.

Frazer, G.R. (1976) *The Causes of Profound Deafness in Childhood.* Baltimore: Johns Hopkins University Press.

Furusho, T. and Yasuda, N. (1973) Genetic studies on inbreeding in some Japanese populations. XIII. A genetic study of congenital deafness. *Jpn. J. Hum. Genet.* **18**: 47-65.

Groce, N.E. (1985) *Everyone Here Spoke Sign Language.* Cambridge, Mass.: Harvard University Press.

Kyle, J.G. and Woll, B. (1985) *Sign Language.* Cambridge: Cambridge University Press.

Ruhlen, M. (1990) The origin of language: retrospective and prospective. *Proceedings of a Conference on Language Change and Biological Evolution*, Torino, Italy, May 23-26, 1988.

Table 1

Mating types relevant to derivation of linear recursions (2a)-(2c) for assortment by deafness model. Frequencies of mating types are given to first order in u_1, u_2 and u_3.

Relevant mating types signer × non-signer	Frequencies	Signers among children AA	Aa	aa
$AA \times AA$	$2(1-m)u_1 D + 2mu_1 D/(1-R)$	ℓb		
$\times Aa$	$4(1-m)u_1 H + 4mu_1 H/(1-R)$	$\ell b/2$	$\ell b/2$	
$\times aa$	$2(1-m)u_1 R$		ℓb	
$Aa \times AA$	$4(1-m)u_2 D + 4mu_2 D/(1-R)$	$\ell b/2$	$\ell b/2$	
$\times Aa$	$8(1-m)u_2 H + 8mu_2 H/(1-R)$	$\ell b/4$	$\ell b/2$	$\ell c/4$
$\times aa$	$4(1-m)u_2 R$		$\ell b/2$	$\ell c/2$
$aa \times AA$	$2(1-m)u_3 D$		$\ell b/2$	
$\times Aa$	$4(1-m)u_3 H$		$\ell b/2$	$\ell c/2$
$\times aa$	$2(1-m)u_3 R + 2mu_3 R/R$			ℓc

Table 2

Mating types relevant to derivation of linear recursions (15a)-(15c) for the acquired deafness model. Frequencies of mating types are given to first order in u_1, u_2 and u_3.

Relevant mating types signer × non-signer	Frequencies	Signers among children AA	Aa	aa
$AA \times AA$	$2(1-m)u_1D + 2mu_1De/[R+(1-R)e]$	$e\ell c$		
$\times\ Aa$	$4(1-m)u_1H + 4mu_1He/[R+(1-R)e]$	$e\ell c/2$	$e\ell c/2$	
$\times\ aa$	$2(1-m)u_1R + 2mu_1R/[R+(1-R)e]$		$e\ell c$	
$Aa \times AA$	$4(1-m)u_2D + 4mu_2De/[R+(1-R)e]$	$e\ell c/2$	$e\ell c/2$	
$\times\ Aa$	$8(1-m)u_2H + 8mu_2He/[R+(1-R)e]$	$e\ell c/4$	$e\ell c/2$	$e\ell c/4$
$\times\ aa$	$4(1-m)u_2R + 4mu_2R/[R+(1-R)e]$		$e\ell c/2$	$e\ell c/2$
$aa \times AA$	$2(1-m)u_3D + 2mu_3De/[R+(1-R)e]$		$e\ell c$	
$\times\ Aa$	$4(1-m)u_3H + 4mu_3He/[R+(1-R)e]$		$e\ell c/2$	$e\ell c/2$
$\times\ aa$	$2(1-m)u_3R + 2mu_3R/[R+(1-R)e]$			$e\ell c$

Table 3

Mating types relevant to deviation of linear recursions (10) for assortment by signing status. Frequencies of mating types are given to first order in u_1, u_2, u_3. Bar indicates a signer, $K = u_1 + 2u_2 + u_3$

Relevant mating types	Frequencies to first order	Signers among children		
		AA	Aa	aa
$\overline{AA} \times \overline{AA}$	mu_1^2/K	b	0	0
$\overline{AA} \times AA$	$2(1-m)u_1 D$	ℓb	0	0
$\overline{AA} \times \overline{Aa}$	$4mu_1u_2/K$	$b/2$	$b/2$	0
$\overline{AA} \times Aa$	$4(1-m)u_1 H$	$\ell b/2$	$\ell b/2$	0
$AA \times \overline{Aa}$	$4(1-m)u_2 D$	$\ell b/2$	$\ell b/2$	0
$\overline{AA} \times \overline{aa}$	$2u_1u_3m/K$	0	b	0
$\overline{AA} \times aa$	$2(1-m)u_1 R$	0	ℓb	0
$AA \times \overline{aa}$	$2(1-m)u_3 D$	0	ℓb	0
$\overline{Aa} \times \overline{Aa}$	$4mu_2^2/K$	$b/4$	$b/2$	$c/4$
$\overline{Aa} \times Aa$	$8(1-m)u_2 H$	$\ell b/4$	$\ell b/2$	$\ell c/4$
$\overline{Aa} \times \overline{aa}$	$4mu_2u_3/K$	0	$b/2$	$c/2$
$\overline{Aa} \times aa$	$4(1-m)u_2 R$	0	$\ell b/2$	$\ell c/2$
$Aa \times \overline{aa}$	$4(1-m)u_3 H$	0	$\ell b/2$	$\ell c/2$
$\overline{aa} \times \overline{aa}$	mu_3^2/K	0	0	c
$\overline{aa} \times aa$	$2(1-m)u_3 R$	0	0	ℓc

Table 4

Comparison of results with $b = c$ for assortment by hearing status ($\lambda_{\max}^{(d)}$) and by signing status ($\lambda_{\max}^{(s)}$).

Leading eigenvalue	$2\ell b < 1$	$2\ell b > 1$
$\lambda_{\max}^{(d)} = 2\ell b$	< 1	> 1
$\lambda_{\max}^{(s)} = 2\ell b(1 - m) + bm$	< 1	> 1 if $m < (2\ell b - 1)/(2\ell b - b)$