

# Evolution of social learning: a mathematical analysis

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Received 1 April 2004

Available online 11 September 2004

## Abstract

Social learning is an important ability seen in a wide range of animals including humans. It has been argued that individual learning, social learning, and innate determination of behavior are favored by natural selection when environmental changes occur at short, intermediate, and long intervals, respectively. Only recently, however, has the hypothesis been examined by means of mathematical models. In this paper, we construct a simple model in which each organism uses one of three genetically determined strategies — it is an individual learner, a social learner or an “innate” — and the three types of organisms are in direct competition with each other. A reduced model, involving only the individual learners and innates, is effectively linear, and we show that by solving the eigenvalue problem of this reduced system we arrive at a good approximation to the global dynamics of the full model. We also study the effect of stochastic environmental changes and reversible mutations among the three strategies. Our results are consistent with the predictions of previous studies. In addition, we identify a critical level of environmental constancy below which only individual and social learners are present.

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*Keywords:* Social learning; Individual learning; Innate behavior; Environmental change

## 1. Introduction

The behavior of a biological organism is a complex process involving the expression of relevant information possessed by that organism. For example, as we write these words, we are presumably accessing learned knowledge stored in our brains that we believe applies to the problem we hope to solve. At the risk of oversimplification (Gould and Marler, 1987), it is possible to classify behaviors by the three distinct ways in which this information can be obtained (Cavalli-Sforza and Feldman, 1983a; Boyd and Richerson, 1985; Laland et al., 2000; Henrich and McElreath, 2003; Alvard, 2003). This trichotomous classification labels behavior as being either “innate,” “socially learned,” or “individually learned”.

A behavior is innate when it entails the direct expression of information encoded in the genes, which are inherited from the parents via the germ cells. Social learning entails the transfer of information between socially interacting individuals, as a result of which the behavior exhibited by a “model” is adopted by an “observer” (Galef, 1988; Whiten and Ham, 1992; Heyes, 1993). This rubric covers teaching, imitation (goal-directed copying of an action pattern), local enhancement (attention drawn to a particular object by the behavior of another, leading to independent discovery of that behavior), and various other psychological processes. Finally, individual learning refers to learning that occurs independently of any social influences. Examples are trial-and-error and insight.

Social learning is of special interest to anthropologists because it is the process that supports cultural inheritance (Cavalli-Sforza and Feldman, 1981; Durham, 1991). As noted above, social learning is a generic term describing many different processes, and it is exhibited

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by a wide variety of animals. Although much attention has been paid to social learning in humans, we consider here the evolution of social learning in general.

The utility of social learning (and cultural inheritance) was first studied quantitatively by Cavalli-Sforza and Feldman (1983a,b) and Boyd and Richerson (1985) (see also Feldman and Cavalli-Sforza, 1976). The key point is that social learners are equally receptive to both adaptive and maladaptive behaviors. The fitness of social learners depends on the individuals from whom they acquire information, and this complicates the evolutionary dynamics of social learning (Cavalli-Sforza and Feldman, 1983a,b; Aoki and Feldman, 1987, 1989; Aoki, 1990; Takahasi and Aoki, 1995).

Rogers (1988) proposed a simple model of competition between individual and social learners in a temporally variable environment. In this model, the environment may change between generations. There is an optimal behavior appropriate to each environmental state. Individual learners achieve this optimal behavior on their own, but suffer a fitness cost due to errors made in learning. Social learners “copy” an organism of the parental generation chosen at random (oblique transmission, Cavalli-Sforza and Feldman, 1981), at a direct cost that is smaller, but run the risk of copying an inappropriate behavior. Since only the individual learners are able to accurately track the changing environment — the social learners are parasitic on the individual learners — this risk increases as the frequency of individual learners decreases (or equivalently the frequency of social learners increases). Hence, we intuitively expect that the fitnesses of individual and social learners may be equal at some intermediate frequency, and that this should define a polymorphic equilibrium. Feldman et al. (1996) rigorously reformulate the Rogers (1988) model for both periodically and randomly changing environments. Their analysis confirms the prediction (Rogers 1988) that social learners will be eliminated if the environment changes too often. Social learners can be maintained in the population if the environment is sufficiently constant, and at higher frequency the greater is this stability.

Most previous studies have compared only two strategies. Recently, we extended the model of Feldman et al. (1996) to propose a new model in which all three strategies (innates, social learners and individual learners) compete at the same time (Aoki et al., submitted). Numerical analysis of this model confirms the consensus view that individual learning, social learning (from the parental generation), and innate determination of behavior are favored by natural selection when the interval, measured in generations, between environmental changes is short, intermediate and long, respectively. Moreover, we showed that there is a critical frequency of environmental change. When the environment changes at a frequency higher than this critical level,

the individual and social learners coexist while the innates go extinct. When this frequency is lower than the critical level, innates dominate while both individual and social learners are eliminated. These transitions seen in the numerical analysis are very sharp.

In this paper, we investigate further the model of Aoki et al. (submitted). First, we argue that the behavior of this model can, to a good level of approximation, be described in terms of the eigenvalue problem of the reduced evolutionary dynamics in which social learners are neglected. This assumption permits us to obtain an analytic expression for the critical frequency of environmental change under both periodically changing and stochastically changing environments. Second, we extend the model to incorporate random reversible mutations among the three strategies and show that the qualitative results remain similar in the extended model, but that there are also some interesting differences.

## 2. Models and results

### 2.1. The basic model

Assume a population of haploid asexual organisms. A tri-allelic “strategy” locus determines whether an organism is an innate, a social learner, or an individual learner (abbreviated as G, SL and IL, respectively). A social learner copies a random member of the parental generation. Its behavior will be adaptive or maladaptive depending on whether or not the information obtained is appropriate to the current environmental state. An individual learner collects information directly from the environment and its behavior is always adaptive. The behavior of an innate is determined by the allele it carries at the “innate information” locus and is adaptive only if this allele “matches” the present environmental state. The innate information locus is not expressed in individual and social learners. Note that there may be a variety of adaptive behaviors, which by assumption are equally adaptive (i.e. have the same fitness), and similarly for maladaptive behaviors.

We posit a model of mutation and variation at the innate information locus involving two classes of alleles. The “resident” alleles produce behavior that is adaptive in the current environment state, whereas the “mutant” alleles produce maladaptive behavior. Each of the two classes of alleles comprises many selectively neutral variants. A small subset amounting to a fraction  $\rho$  of each class possesses the special property of being adaptive when the environment changes. These variants can be regarded as “preadapted” alleles awaiting environmental change.

Our basic premise with regard to the environment is that when it changes it never reverts to an earlier state

(infinite environmental state model, Feldman et al., 1996). Rogers (1988) assumed that the environment flips back and forth between two states. Comparative analysis of the two environmental state and the infinite environmental state models yielded qualitatively similar results (Feldman et al., 1996). The real world likely comprises a finite but large number of possible states among which transitions can occur. If the environment includes other evolving species, it is a reasonable assumption that the probability of any particular state recurring will be small. The infinite environmental state model is an idealization of this situation, which we introduce for the mathematical simplification it achieves.

In the infinite state model, none of the preexisting behaviors can be adaptive after an environmental change. Innate behavior in our model is the result of an interaction between the allele carried by an organism and the environment. Hence, the behavior of an innate carrying a preadapted allele may differ in the pre- and post-change generations, and consistent with our basic premise, we assume that the behavior in the pre-change generation is maladaptive in the post-change generation. In particular, this implies that a social learner cannot acquire correct behavior by copying an innate with a preadapted allele when the environment changes.

By assumption, individual learners always behave appropriately for the given environmental state, but social learners and innates can get it either right or wrong. Hence, our model distinguishes five phenogenotypes (genotype–phenotype combinations, Feldman and Cavalli-Sforza, 1984), which we abbreviate: GC (genetic correct, i.e., innate with resident allele), GW (genetic wrong, i.e., innate with mutant allele), SLC (social learner correct), SLW (social learner wrong), and IL (individual learner). The five phenogenotypes, their frequencies among reproductive adults, and their fitnesses are summarized in Table 1. The fitnesses are relative viabilities and are assigned to the five phenogenotypes in the following way. There is a baseline fitness of 1 for adaptive behavior, and maladaptive behavior causes the fitness to be reduced by  $s$ . Social learners bear a direct cost of developing and maintaining a nervous system supportive of learning, which is

translated into a fitness loss  $d$ . Individual learners suffer a similar direct cost but in addition they are adversely affected by mistakes made before they mature; the total penalty for them is  $c$ .

In our basic deterministic model, we ignore mutation at the strategy locus and assume that the environment changes with a fixed period  $l$ . The life cycle events are asexual reproduction, learning, and natural selection, in this order. Then, the recursions relating the frequencies of the five phenogenotypes in the offspring generation, indicated by primes, to those in the parental generation can be written as follows.

First, when the environment remains constant between generations the recursions are:

$$\begin{aligned} W_1 u' &= u \\ W_1 v' &= (1 - s)v, \\ W_1 x' &= (1 - d)(x + y)(u + x + z), \\ W_1 y' &= (1 - s - d)(x + y)(v + y), \\ W_1 z' &= (1 - c)z. \end{aligned} \tag{1}$$

Second, when the environment changes between generations they are:

$$\begin{aligned} W_2 u' &= \rho(u + v), \\ W_2 v' &= (1 - s)(1 - \rho)(u + v), \\ W_2 x' &= 0, \\ W_2 y' &= (1 - s - d)(x + y), \\ W_2 z' &= (1 - c)z, \end{aligned} \tag{2}$$

where we used the assumption that the constant fraction  $\rho$  of all alleles at the information locus produces adaptive behavior in the post-change generation. In both recursions,  $W_i$  is a normalization factor for the frequencies. The environment changes every  $l$  generations, so one set of iterations entails  $l - 1$  applications of (1) followed by one application of (2).

### 2.2. The reduced model and analysis

Aoki et al. (submitted) studied the basic model numerically when  $d < c < s$ . They found that the frequencies of the five phenogenotypes converge to a periodic solution with period  $l$ . Moreover, they showed that the solution as a function of  $l$  shows a sharp transition at a critical value of  $l$ , which we denote  $l^*$ . In other words, the global behavior of the basic model is classified into two modes. When  $l > l^*$ , they found that G dominates; on the other hand when  $l \leq l^*$ , G die out and SL and IL coexist. The transition between the two modes is very sudden and discrete. These results were obtained numerically. In this section we explore the analytic framework and derivation of  $l^*$ .

The social learners are parasitic on the individual learners because only individual learners are able to accurately track the changing environment. Hence, if a

Table 1  
The five phenogenotypes, their fitnesses and frequencies among reproductive adults

| Phenogenotype                | Fitness     | Frequency |
|------------------------------|-------------|-----------|
| GC (genetic correct)         | 1           | $u$       |
| GW (genetic wrong)           | $1 - s$     | $v$       |
| SLC (social learner correct) | $1 - d$     | $x$       |
| SLW (social learner wrong)   | $1 - s - d$ | $y$       |
| IL (individual learner)      | $1 - c$     | $z$       |

population of innates is stable against invasion by individual learners, it should be able to resist invasion by a mixture of individual and social learners. Therefore, consider the competition between innates and individual learners. Let transformation  $\phi$  be

$$\begin{pmatrix} u' \\ v' \\ z' \end{pmatrix} = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1-s & 0 \\ 0 & 0 & 1-c \end{pmatrix} \begin{pmatrix} u \\ v \\ z \end{pmatrix}.$$

As  $u, v$  and  $z$  are frequencies, a normalization operator  $\eta$  follows  $\phi$ . The state after  $t$  generations is therefore given by

$$\begin{pmatrix} u_t \\ v_t \\ z_t \end{pmatrix} = (\eta \cdot \phi)^t \begin{pmatrix} u_0 \\ v_0 \\ z_0 \end{pmatrix}.$$

Environmental changes occur every  $l$  generations. Using the matrix

$$E = \begin{pmatrix} \rho & \rho & 0 \\ 1-\rho & 1-\rho & 0 \\ 0 & 0 & 1 \end{pmatrix},$$

the state after  $nl$  generations becomes

$$\begin{pmatrix} u_{nl} \\ v_{nl} \\ z_{nl} \end{pmatrix} = [(\eta \cdot \phi E)(\eta \cdot \phi)^{l-1}]^n \begin{pmatrix} u_0 \\ v_0 \\ z_0 \end{pmatrix}. \tag{3}$$

In this equation, normalization applies every generation. However, as  $\phi$  is linear, one normalization suffices (see Appendix A). Hence,

$$\begin{pmatrix} u_{nl} \\ v_{nl} \\ z_{nl} \end{pmatrix} = [(\eta\phi E)\eta\phi^{l-1}]^n \begin{pmatrix} u_0 \\ v_0 \\ z_0 \end{pmatrix} = [\eta\phi\eta E\phi^{l-1}]^n \begin{pmatrix} u_0 \\ v_0 \\ z_0 \end{pmatrix},$$

where the latter equality holds since  $E$  and  $\eta$  commute, i.e.  $E\eta = \eta E$ . As  $\phi$  has an inverse matrix and  $\eta\phi\eta = (\eta\phi)^2\phi^{-1} = \eta\phi^2\phi^{-1} = \eta\phi$ , we obtain

$$\begin{pmatrix} u_{nl} \\ v_{nl} \\ z_{nl} \end{pmatrix} = [\eta\phi E\phi^{l-1}]^n \begin{pmatrix} u_0 \\ v_0 \\ z_0 \end{pmatrix} = \eta[\phi E\phi^{l-1}]^n \begin{pmatrix} u_0 \\ v_0 \\ z_0 \end{pmatrix} \tag{4}$$

because  $\phi E\phi^{l-1}$  is linear. Although  $\eta$  is not linear, the global behavior of the system is completely determined by the linear transformation  $E\phi^l$ :

$$\begin{aligned} u' &= \rho(u + (1-s)^l v), \\ v' &= (1-\rho)(u + (1-s)^l v), \\ z' &= (1-c)^l z. \end{aligned}$$

For simpler notation, we define

$$\begin{aligned} A &= (1-s)^l, \\ C &= (1-c)^l. \end{aligned}$$

The transformation  $E\phi^l$  can then be written as

$$\begin{pmatrix} u' \\ v' \\ z' \end{pmatrix} = \begin{pmatrix} \rho & \rho A & 0 \\ 1-\rho & (1-\rho)A & 0 \\ 0 & 0 & C \end{pmatrix} \begin{pmatrix} u \\ v \\ z \end{pmatrix}$$

and the eigenvalues

$$\begin{aligned} \lambda_1 &= \rho + (1-\rho)A, \\ \lambda_2 &= 0, \\ \lambda_3 &= C \end{aligned}$$

are all real and non-negative. The corresponding eigenvectors are

$$\begin{pmatrix} \rho \\ 1-\rho \\ 0 \end{pmatrix}, \begin{pmatrix} A \\ -1 \\ 0 \end{pmatrix}, \begin{pmatrix} 0 \\ 0 \\ 1 \end{pmatrix},$$

respectively.

As  $n \rightarrow \infty$ , the system is dominated by the eigenvector associated with the eigenvalue having the largest absolute value. With continuing iteration of  $E\phi^l$  the system asymptotically approaches either

$$k_1 \lambda_1^n \begin{pmatrix} \rho \\ 1-\rho \\ 0 \end{pmatrix} \text{ or } k_2 C^n \begin{pmatrix} 0 \\ 0 \\ 1 \end{pmatrix}$$

where  $k_1$  and  $k_2$  are constants depending on the initial state. It is clear that when we include normalization (i.e., Eq. (4)) the system also approaches either of these two modes. In the first mode ( $\lambda_1 > \lambda_3$ ), the state P1,

$$\begin{pmatrix} u \\ v \\ z \end{pmatrix} = \begin{pmatrix} \rho \\ 1-\rho \\ 0 \end{pmatrix}$$

is the unique globally stable equilibrium. Convergence to P1 means that innates outcompete individual learners. The frequency of GC is small ( $\rho$ ) at P1 because P1 is the state just after the environment changes. In the second mode ( $\lambda_1 < \lambda_3$ ), the state P2,

$$\begin{pmatrix} u \\ v \\ z \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 1 \end{pmatrix}$$

is the unique globally stable equilibrium. Convergence to P2 means that individual learners outcompete innates.

The transition between the two modes occurs at  $l = l^*$ , which is determined by  $\lambda_1 = \lambda_3$  or

$$\rho + (1-\rho)A = C. \tag{5}$$

Solving (5) for  $l$  gives the analytic expression of  $l^*$ . As  $l \rightarrow \infty, A \rightarrow 0$  and  $C \rightarrow 0$ . Thus, for sufficiently large  $l, \lambda_1 > \lambda_3$  and P1 is globally stable. Assume  $s > c \gg \rho$ , then  $\lambda_1 < \lambda_3$  when  $l = 1$ . Both eigenvalues are monotonically decreasing functions of  $l$ , and  $\lambda_1$  converges to  $\rho$  faster

than  $\lambda_3$  converges to zero. This means that there exists a unique solution of (5) in an interval  $[1, \infty)$  (Fig. 1). In other words, there exists a unique integer  $l^*$  such that P1 is always approached when  $l > l^*$  and that P2 is always approached when  $l \leq l^*$ .

Convergence to P1 or P2 in the reduced model implies convergence to the periodic solution with period  $l$  in the full model (Eqs. (1)–(2)). Here we discuss whether the differences between the reduced and full models are negligible or not. With regard to the first mode, stability of P1 (fixation of G) in the reduced model shows that IL cannot invade by itself in the full model. Intuitively, we expect that presence of SL at a low frequency should not facilitate invasion by IL, since SL are parasitic on IL, but we cannot rule out this possibility. On the other hand, it can be rigorously shown that SL cannot invade the population of G in the full model, whether or not IL are also present (see Appendix B).

For the second mode, stability of P2 (fixation of IL) does not necessarily entail that IL will be fixed, as SL may coexist with IL in the full model. Nevertheless, the important point is that G cannot invade. In fact, the fitness of IL is always  $1 - c$  regardless of the frequencies of the other phenotypes, and at the equilibrium periodic solution the geometric mean fitness of SL should equal  $1 - c$ . (This condition determines the equilibrium ratio of SLC to SLW.) Hence, it will be equally difficult for G to invade a polymorphism of IL and SL as for it to invade a monomorphism of IL. When P2 is stable, the geometric mean fitness of G is less than  $1 - c$ , whence G cannot invade.

In conclusion, in the full model we expect the innates to dominate in the first mode ( $l > l^*$ ) and to go extinct in the second mode ( $l \leq l^*$ ). With Aoki et al.'s parameters ( $s = 0.1$ ,  $c = 0.02$  and  $\rho = 10^{-6}$ ), (5) gives  $l^* = 683$ , which is exactly the same as in the numerical result (Fig. 2). A comparison between the numerical results of

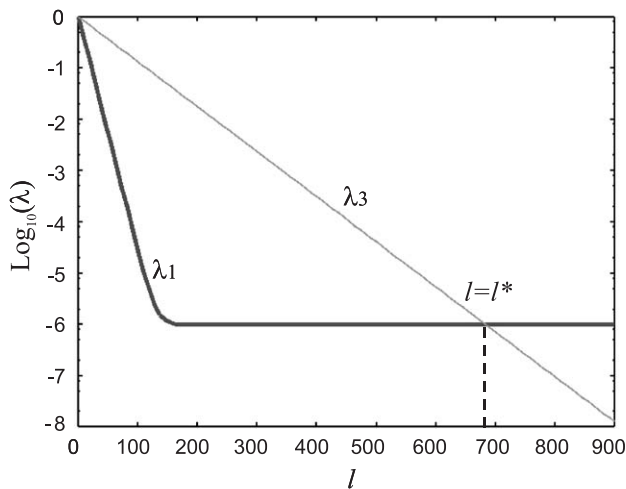


Fig. 1. Eigenvalues as a function of period. Parameters are  $s = 0.1$ ,  $c = 0.02$  and  $\rho = 10^{-6}$ .

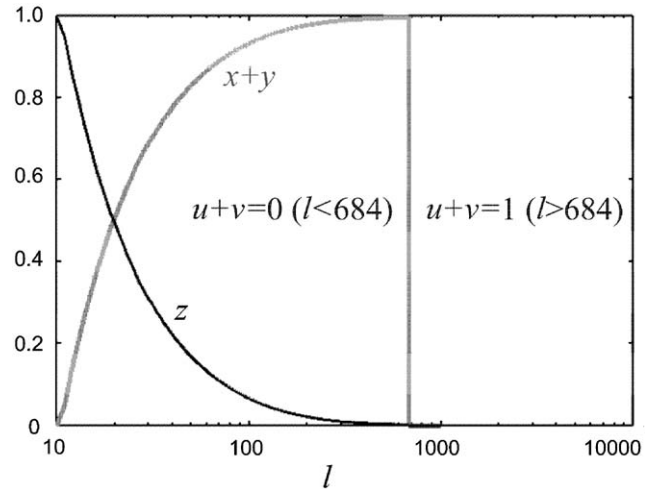


Fig. 2. Frequencies of individual learning, social learning, and innate behavior, averaged over one period at equilibrium, are plotted against the period length ( $l$ ) on a log scale for the periodic environmental change model. The curves are labeled by the frequencies:  $z$  for individual learners,  $x + y$  for social learners, and  $u + v$  for the innates. Parameters are  $s = 0.1$ ,  $c = 0.02$  and  $\rho = 10^{-6}$ .

Table 2  
Comparison of numerical and analytical results

| Parameters |      |      |           | Results |                |
|------------|------|------|-----------|---------|----------------|
| $s$        | $c$  | $d$  | $\rho$    | $l^*$   | $l^*$ analytic |
| 0.1        | 0.02 | 0.01 | $10^{-6}$ | 683     | 683            |
|            |      | 0.1  |           | 683     | 683            |
|            | 0.05 | 269  | 269       |         |                |
| 0.2        | 0.08 |      | $10^{-6}$ | 165     | 165            |
|            |      |      |           | 683     | 683            |
|            |      |      | $10^{-7}$ | 797     | 797            |

$l^*$  and  $l^*$  analytic are derived by the numerical iteration of (1)–(2) and from (5), respectively. Parameters are  $s = 0.1$ ,  $c = 0.02$ ,  $d = 0.01$ ,  $\rho = 10^{-6}$  unless otherwise specified.  $l^*$  analytic is monotone decreasing in the parameters  $\rho$  and  $c$ , monotone increasing in the parameter  $s$  (proofs not shown), and independent of the parameter  $d$ . Rows 1 and 5 of the table predict the same apparent value of  $l^*$  analytic although  $s$  has been varied, because  $(1 - s)^{l^*} \ll (1 - c)^{l^*}$  holds for the given parameters.

the full model and the analytical results of the reduced model is summarized in Table 2. Our analysis gives the exact  $l^*$  value in all cases tested.

### 2.3. A stochastic model and analysis

Aoki et al. (submitted) also dealt with the case where environments change with probability  $p$  at each generation. In this case also, they observed two modes, although the transition was continuous. Here we try to clarify whether a threshold  $p^*$  exists and to derive it analytically.



We study the reduced stochastic model in which the transformation with stasis is  $\eta\phi$  while the transformation with change is  $\eta E\phi$ . Let us consider the asymptotic behavior of the ratio of the frequency of individual learners relative to the frequency of innates, i.e.  $z/(u+v)$ . In the deterministic model, if the environment does not change for  $l-1$  generations and then changes ( $l$  generations in total), this ratio changes by the factor of

$$g(l) = \frac{C}{\rho + (1-\rho)A}.$$

This is because the component in the second eigenvector corresponding to the eigenvalue  $\lambda_2 (= 0)$  disappears. Fortunately, the first and third eigenvectors do not depend on the period, and the IL/G ratio is also multiplied by  $g(l)$  in the stochastic model.

The probability that the interval between an environmental change and the next one is  $l$  is

$$P(l) = (1-p)^{l-1}p.$$

After sufficiently many generations, we expect that the initial IL/G ratio is multiplied by

$$\prod_{l=1}^{\infty} g(l)^{P(l)}.$$

Therefore, if

$$\sum_{l=1}^{\infty} P(l) \ln g(l) < 0 \tag{6}$$

then the population of innates is stable against invasion by individual learners (and most likely social learners). By this analysis, we expect that there exists a threshold  $p^*$  and the system essentially has two modes. The inequality gives an analytic estimate of  $p^*$ . With Aoki et al.'s parameters ( $s = 0.1$ ,  $c = 0.02$ ,  $d = 0.01$  and  $\rho = 10^{-6}$ ), (6) gives  $p^* = 0.0016$  while the transition occurs around  $p = 0.0015$  in our numerical calculation of the full stochastic model (Fig. 3).

*2.4. Reversible mutations at the strategy locus*

Given that innate behavior was the primordial state, neither individual nor social learning could have arisen without mutation. Hence, introducing reversible mutation among the three strategies enhances the realism of our model. When an individual learner (IL) or a social learner (SLC or SLW) mutates to an innate (G), the allele it carries at the innate information locus will be expressed. Hence, it is necessary to keep track of the class of allele, resident or mutant, occurring at the innate information locus in individual and social learners as well as in the innates. We do this by distinguishing the frequencies of non-innate organisms with resident and mutant alleles by subscripts  $r$  and  $m$ , respectively. Thus, for example, the frequency

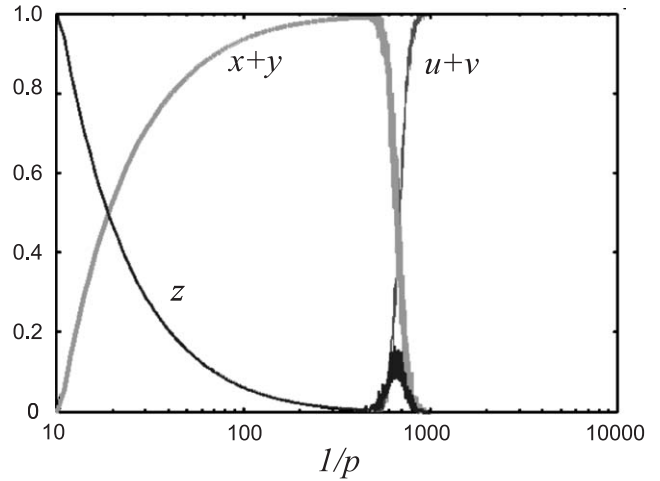


Fig. 3. Average frequencies of individual learning, social learning, and innate behavior in the stochastic environmental change model. The values at the initial 50,000 generations are discarded to eliminate the effect of the initial values and the average of the subsequent 50,000 generations are used. This process is repeated for 100 different random number seeds and the average result is plotted. The horizontal axis,  $1/p$ , is a mean interval of environmental changes. The curves are labeled by the frequencies:  $z$  for individual learners,  $x+y$  for social learners, and  $u+v$  for the innates. Parameters are  $s = 0.1$ ,  $c = 0.02$  and  $\rho = 10^{-6}$ .

of a SLC with a resident allele is denoted by  $x_r$ . There are a total of eight variables, seven of which are independent.

Recall that resident alleles produce adaptive behavior whereas mutant alleles produce maladaptive behavior in the current environmental state. The class, resident or mutant, is defined relative to the environmental state. When the environment changes, each organism inherits the parental allele but the class of the allele changes. We assume that a small fraction ( $\rho$ ) of all alleles at the innate information locus becomes resident alleles in the post-change generation, regardless of the status in the pre-change generation. In other words, the class of an allele at the innate information locus is reset when the environment changes: it becomes a resident allele with probability  $\rho$  and a mutant allele with probability  $1-\rho$ .

Let the mutation rate at the strategy locus be  $\mu$ . We assume reversible unbiased mutation among the three strategies, G, SL and IL, which occurs before asexual reproduction. The frequencies of genotypes after mutation are denoted by

$$\begin{aligned} u^* &= u(1-\mu) + (x_r + y_r)\mu/2 + z_r\mu/2, \\ v^* &= v(1-\mu) + (x_m + y_m)\mu/2 + z_m\mu/2, \\ x_r^* + y_r^* &= u\mu/2 + (x_r + y_r)(1-\mu) + z_r\mu/2, \\ x_m^* + y_m^* &= v\mu/2 + (x_m + y_m)(1-\mu) + z_m\mu/2, \\ z_r^* &= u\mu/2 + (x_r + y_r)\mu/2 + z_r(1-\mu), \\ z_m^* &= v\mu/2 + (x_m + y_m)\mu/2 + z_m(1-\mu). \end{aligned} \tag{7}$$

The recursions for environmental stasis are

$$\begin{aligned}
 W_1 u' &= u^*, \\
 W_1 v' &= (1 - s)v^*, \\
 W_1 x'_r &= (1 - d)(x_r^* + y_r^*)(u + x_r + x_m + z_r + z_m), \\
 W_1 x'_m &= (1 - d)(x_m^* + y_m^*)(u + x_r + x_m + z_r + z_m), \\
 W_1 y'_r &= (1 - s - d)(x_r^* + y_r^*)(v + y_r + y_m), \\
 W_1 y'_m &= (1 - s - d)(x_m^* + y_m^*)(v + y_r + y_m), \\
 W_1 z'_r &= (1 - c)z_r^*, \\
 W_1 z'_m &= (1 - c)z_m^*.
 \end{aligned} \tag{8}$$

The recursions for environmental change are

$$\begin{aligned}
 W_2 u' &= \rho(u^* + v^*), \\
 W_2 v' &= (1 - s)(1 - \rho)(u^* + v^*), \\
 W_2 x'_r &= 0, \\
 W_2 x'_m &= 0, \\
 W_2 y'_r &= (1 - s - d)(x_r^* + y_r^* + x_m^* + y_m^*)\rho, \\
 W_2 y'_m &= (1 - s - d)(x_r^* + y_r^* + x_m^* + y_m^*)(1 - \rho), \\
 W_2 z'_r &= (1 - c)(z_r^* + z_m^*)\rho, \\
 W_2 z'_m &= (1 - c)(z_r^* + z_m^*)(1 - \rho).
 \end{aligned} \tag{9}$$

The model is rather complicated, but the recursions for mutation and the recursions for innates and individual learners are still linear. Therefore, we can perform an analysis similar to the previous one. First, we consider periodically changing environments. Consider the reduced dynamical system in  $(u, v, z_r, z_m)^T$ . Using matrices

$$M = \begin{pmatrix} 1 - \mu & 0 & \mu & 0 \\ 0 & 1 - \mu & 0 & \mu \\ \mu & 0 & 1 - \mu & 0 \\ 0 & \mu & 0 & 1 - \mu \end{pmatrix},$$

$$\xi = \begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & 1 - s & 0 & 0 \\ 0 & 0 & 1 - c & 0 \\ 0 & 0 & 0 & 1 - c \end{pmatrix},$$

and

$$F = \begin{pmatrix} \rho & \rho & 0 & 0 \\ 1 - \rho & 1 - \rho & 0 & 0 \\ 0 & 0 & \rho & \rho \\ 0 & 0 & 1 - \rho & 1 - \rho \end{pmatrix},$$

the state after  $nl$  generations is given by the following transformation:

$$\begin{aligned}
 [(\eta \xi FM)(\eta \xi M)^{l-1}]^n &= [(\eta \xi FM)\eta(\xi M)^{l-1}]^n \\
 &= [\eta \xi FM(\xi M)^{l-1}]^n = \eta[\xi FM(\xi M)^{l-1}]^n,
 \end{aligned}$$

where we used  $M\eta = \eta M$ ,  $F\eta = \eta F$  and  $\eta \xi \eta = \eta \xi$ . Thus,  $\xi FM(\xi M)^{l-1}$  determines the behavior of the system. The

transformation is linear, but it is too complicated to deal with analytically. We numerically examined the largest eigenvalue and the corresponding eigenvector of  $\xi FM(\xi M)^{l-1}$  by the power method (assuming parameter values  $s = 0.1$ ,  $c = 0.02$ ,  $\rho = 10^{-6}$  and  $\mu = 10^{-6}$ ). For most  $l$  values, the dominant eigenvector changes gradually as  $l$  is varied. However, it changes very sharply from  $(10^{-9}, 0.003, 10^{-6}, 0.996)$  to  $(10^{-6}, 0.979, 10^{-8}, 0.02)$  as  $l$  changes from 683 to 684. Such a transition occurs only once and we estimate  $l^* = 683$ . Associated with this transition, the average frequencies of innates and individual learners over  $l$  generations, derived from

$$\frac{1}{l} \sum_{i=0}^{l-1} (\xi M)^i \mathbf{h},$$

where  $\mathbf{h}$  is a dominant eigenvector, change from  $(10^{-4}, 0.999)$  to  $(0.354, 0.645)$ . These results mean that the overall behavior remains similar when we introduce reversible mutations at the strategy locus. On the other hand, a major difference predicted by the reduced model is that individual learners will coexist with innates at significant frequency ( $\gg \mu$ ) when  $l > l^*$ . A possible reason for this polymorphism of individual learners and innates is that the rate of increase (or multiplication factor) of the individual learners is no longer a constant (i.e.,  $1 - c$ ) divided by the mean fitness, but depends on the frequencies of the other phenogenotypes (Eq. (7)). This frequency dependence, although weak, may maintain the individual learners in a polymorphic state even when  $l > l^*$ , particularly in the neighborhood of the critical period  $l^*$  where selection favoring the innates is also weak.

The results of the numerical iterations of the full model (Eqs. (7)–(9)) are shown in Fig. 4. The threshold occurs at  $l = 684$ , which is in good agreement with the predicted value of  $l^* = 683$ . Individual learners and innates dominate when  $l > 684$  (the first mode), while individual and social learners dominate when  $l \leq 684$  (the second mode). The frequency of individual learners in the first mode is non-negligibly large as is predicted by the reduced model. Due to the mutations at the strategy locus, social learners also exist in the first mode but their frequency is of the order of mutation rate,  $\mu$ , and similarly for the frequency of innates in the second mode. Thus, at the evolutionary equilibrium, interactions between social learners and innates are rare.

Lastly, we study the model including both stochastically changing environments and mutations at the strategy locus. The numerical analysis shows that the overall tendency is similar to the previous models (Fig. 5). The only difference is that the overlapping region is larger.

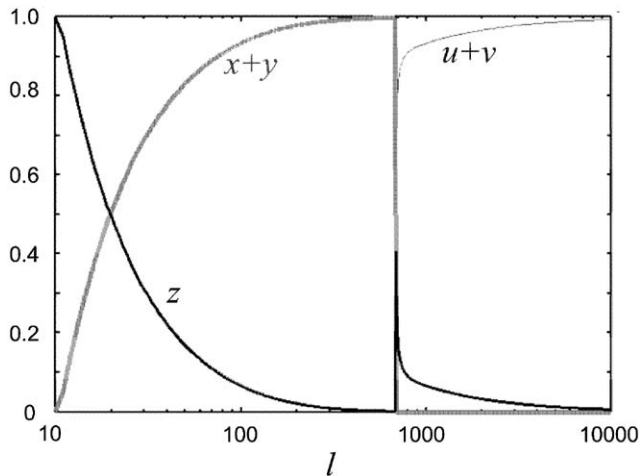


Fig. 4. The result of the model with mutations at the strategy locus and periodic environmental changes. The graph is drawn in the same way as Fig. 2. Parameters are  $s = 0.1$ ,  $c = 0.02$ ,  $\rho = 10^{-6}$  and  $\mu = 10^{-6}$ .

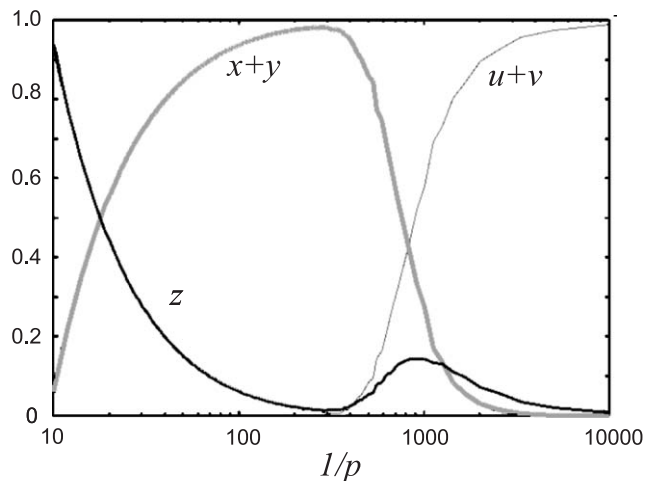


Fig. 5. The result of the model with mutations at the strategy locus and stochastic environmental changes. The graph is drawn in the same way as Fig. 3. Parameters are  $s = 0.1$ ,  $c = 0.02$ ,  $\rho = 10^{-6}$  and  $\mu = 10^{-6}$ .

### 3. Discussion

Building on the work of Boyd and Richerson (1985, 1988), Rogers (1988), and Feldman et al. (1996), Aoki et al. (submitted) showed that individual learning, social learning, and innate determination of behavior are favored by natural selection when environmental changes occur at short, intermediate, and long intervals, respectively. In this paper, we analyzed and extended Aoki et al.'s models in order to give more strong evidences supporting the hypothesis. First, we carried out a mathematical analysis of the model. Analyzing the reduced linear dynamics, the evolution of learning ability is described in terms of the eigenvalue problem.

The analysis not only supports the hypothesis but also explains the sharp transition of two modes and gives an analytic expression for the critical frequency of environmental change. Second, we introduced more biologically realistic assumptions including reversible mutation at the strategy locus, which was ignored in the basic model. The general model also supports the hypothesis.

In the basic model, we have shown that only innates dominate and both social and individual learners go to extinction when the period of environmental change is long ( $l > l^*$ ). The introduction of reversible mutations results in the coexistence of strategies. The frequency of each strategy is maintained above a certain level supported by the continuous flow of mutations. As the mutation rate is low, we would not expect mutation to have a major effect on these frequencies. However, our analysis shows that the equilibrium frequency of individual learners is significantly larger than that expected by the mutation rate alone. This is not only mathematically interesting but also reminds us that simplifications (such as neglecting rare mutations) do not always produce the expected outcome. In conclusion, when we assume a low mutation rate at the strategy locus, innates and individual learners coexist when the period of environmental change is long.

When the environment changes periodically, social learners and innates do not coexist at significant frequencies. Therefore, only those behaviors that can be “invented” by the individual learning process can be socially transmitted. The “content of culture” is limited by the capacity for individual learning as much as by the capacity for social learning. This argument was originally made by Aoki et al. (submitted), and the present study shows that it is valid even when we introduce mutations at the strategy locus. On the other hand, when the environment changes stochastically, the transition of two modes is more gradual. Moreover, the overlapping region is larger when we introduce mutations among the strategies. These results suggest that the content of culture basically comes from what individual learners invented, but it may also come from innate behaviors when the environment changes randomly.

There remains the task of testing the predictions against data on the phylogenetic distribution of social learning. This would be a formidable undertaking, and we do not attempt it here. One problem lies with our modeling approach, where we have followed Rogers (1988) in assuming that behavior is obligate. Any real behavior cannot easily be classified as innate, socially learned, or individually learned, and many behaviors will actually involve all three processes. Hence, the predictions of our models serve a heuristic purpose but cannot readily be applied to data. Boyd and Richerson (1985, 1988) have introduced more realistic models that recognize the facultative nature of behavior. Unfortun-



nately, the price of this realism has been lack of amenability to detailed mathematical treatment (but see Feldman et al., 1996).

**Acknowledgments**

We thank the anonymous referees for helpful comments. Research supported in part by NIH Grant GM28016.

**Appendix A**

A normalization operator is defined as

$$\eta : \mathbf{x} \mapsto \frac{\mathbf{x}}{\|\mathbf{x}\|},$$

where  $\mathbf{x} = (x_1, x_2, \dots, x_N)$  is an arbitrary vector and

$$\|\mathbf{x}\| \equiv \sum_{i=1}^N x_i$$

is a scalar. Here we prove

$$(\eta\zeta)^n \cdot \mathbf{x} = \eta\zeta^n \cdot \mathbf{x} \tag{A.1}$$

for any positive integer  $n$  and any linear transformation  $\zeta$ . Note that

$$\eta \cdot (c\mathbf{x}) = \frac{c\mathbf{x}}{\|c\mathbf{x}\|} = \eta \cdot \mathbf{x}$$

and

$$\zeta \cdot (c\mathbf{x}) = c\zeta \cdot \mathbf{x}$$

for any non-zero scalar  $c$ . The proof uses the principle of mathematical induction. When  $n = 1$ , Eq. (A.1) is true by definition. If it is true when  $n = m$ , then it is also true when  $n = m + 1$  because

$$(\eta\zeta)^{m+1} \cdot \mathbf{x} = \eta\zeta \cdot \frac{\zeta^m \mathbf{x}}{\|\zeta^m \mathbf{x}\|} = \eta \cdot \left( \frac{1}{\|\zeta^m \mathbf{x}\|} \zeta^{m+1} \cdot \mathbf{x} \right) = \eta\zeta^{m+1} \cdot \mathbf{x}$$

This completes the proof, of Eq. (A.1).

**Appendix B**

Here, we prove that social learners cannot invade a population consisting mostly of innates but in which individual learners may also be present at a low frequency. Recursions (1) can be rewritten as

$$\begin{aligned} W_1 u' &= u, \\ W_1 v' &= (1 - s)v, \\ W_1 x' &= (1 - d)(x + y)u, \\ W_1 y' &= (1 - s - d)(x + y)v, \\ W_1 z' &= (1 - c)z, \end{aligned}$$

when  $x, y, z \ll 1$ . Substituting the explicit expression for  $W_1$ , we obtain

$$x' + y' \approx \frac{(1 - d)u + (1 - s - d)v}{u + (1 - s)v} (x + y) \approx \frac{1 - d - sv}{1 - sv} (x + y),$$

where we neglected the higher-order terms of  $x, y$  and  $z$ . This equation means  $x + y$  decreases while the environment remains constant. When the environment changes,

$$\begin{aligned} W_2(u' + v') &= (1 - s + s\rho)(u + v) \\ W_2(x' + y') &= (1 - s - d)(x + y) \end{aligned}$$

and thus  $x + y$  decreases. This completes the proof. Notice that the result is independent of parameter values.

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