

## The Emergence of Social Learning in a Temporally Changing Environment: A Theoretical Model<sup>1</sup>

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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 in terms of the three distinct ways in which this information can be obtained (Cavalli-Sforza and Feldman 1983*a*, Boyd and Richerson 1985, Laland, Odling-Smee, and Feldman 2000, Henrich and McElreath 2003, Alvard 2003). This trichotomous classification labels behavior as “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 denotes 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). The 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 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. Although social learning is exhibited by a wide variety of animals, there is much debate as to whether any nonhuman species, in particular the chimpanzee, is capable of teaching and imitation (Galef 1992, Tomasello 1994, Boesch 2003). Galef (1992) and Tomasello (1994) argue that teaching and imitation are limited to humans, which is why human culture differs quantitatively and qualitatively from animal “cultures.” Clearly, culture has undergone much elaboration in hominids since their divergence from the chimpanzee lineage and particularly within the past 50,000 years, but it is difficult to identify the cause(s) (Laland, Odling-Smee, and Feldman 2000). We do not seek to contribute to this discussion. Rather, our interest centers on the conditions that might favor the evolution of social learning in its earliest phases.

The utility of social learning (and cultural inheritance) may seem obvious, and the reader may wonder why the question of its origin(s) is raised at all. In fact, although numerous accounts have appeared in the literature, there were few serious attempts to come to grips with the problem quantitatively until the early studies by Cavalli-Sforza and Feldman (1983*a, b*) and Boyd and Richerson (1985) (see also Feldman and Cavalli-Sforza 1976). Even Lumsden and Wilson (1981:330) in their seminal work explain the advent of social learning as “the cosmic good fortune of [hominids’] being in the right place at the right time.”

However, the advantages of social learning are not so clear as to make the question of its origin(s) uninteresting. Two theoretical results obtained by Cavalli-Sforza and Feldman (1983*a, b*) are indicative of the difficulties. First, if both genetic and cultural determination of a selectively favored trait are possible, the former will usually prevail, at least in a constant environment (Cavalli-Sforza and Feldman 1983*a*). Second, when social learning occurs among a small minority of the population, it spreads slowly unless, for example, it occurs between relatives (Cavalli-Sforza and Feldman 1983*b*).

The model of Cavalli-Sforza and Feldman (1983*b*) has been extended by Aoki and Feldman (1987, 1989), Aoki (1990), and Takahasi and Aoki (1995). Cavalli-Sforza and Feldman (1983*b*) define a “communicator” as an organism with the genetically determined ability to acquire and pass on a socially learned adaptive behavior, whereas a “noncommunicator” is unable to do either. Communicators are more likely to spread at the expense of noncommunicators if social learning occurs within families. A “natural” way is for offspring to model their behavior on that of their parent(s), a form of social learning that

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has been called “vertical transmission” (Cavalli-Sforza and Feldman 1981).

Typically in mammals only the mother provides parental care. Modern humans are exceptional in that the father often participates, and a recent analysis of sexual dimorphism in *Australopithecus afarensis* suggests the antiquity of monogamy (Reno et al. 2003). When just one parent is available as a possible model for the offspring, communicators can spread through the population only if the socially transmitted behavior confers at least a twofold advantage on the communicators that acquire it (Aoki and Feldman 1987, 1989). In contrast, with both parents present a small advantage may suffice (Aoki 1990). Hence, it is possible that the human capacity for social learning, with its heavy reliance on vertical transmission (Hewlett and Cavalli-Sforza 1986, Guglielmino et al. 1995), evolved in the context of the monogamous family (Takahasi and Aoki 1995). These results have been obtained assuming environmental constancy.

Boyd and Richerson (1985) explicitly incorporate temporal or spatial variation of the environment. In their model of “guided variation,” organisms use a mixed strategy of social and individual learning. Guided variation entails the initial acquisition by social learning of a behavioral predisposition which is then modified by individual learning before being expressed as mature behavior. The proportions of social and individual learning evolve to an equilibrium at which dependence on social learning will be greater when environmental predictability is higher.

These researchers also ask when it is better to rely on social learning to acquire the initial behavioral predisposition than to inherit it genetically. Given a temporally fluctuating environment that is autocorrelated—autocorrelation being a measure of stability across generations—they find that social learning is favored when this “autocorrelation is high, but not too high. . . . At very high autocorrelations, environments become so slowly changing that genes can track perfectly well, and the advantage of social learning disappears” (Richerson and Boyd 2000:8).

The approach taken by Boyd and Richerson (1985, 1988) is realistic in recognizing the *facultative* nature of individual and social learning—most organisms capable of learning use both strategies—but the price of this realism is lack of amenability to detailed mathematical treatment (but see Feldman, Aoki, and Kumm 1996). Rogers (1988) proposes a much simpler model of competition between *obligate* individual and social learners in a temporally variable environment. His assumptions, similar in spirit to those made by Boyd and Richerson (1985), are as follows: 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. (The term

“copy” is used broadly to include all means by which an accurate transfer of information may occur.)

Since only the individual learners can 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, Aoki, and Kumm (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.

Recent reviews of the factors contributing to the emergence of social learning emphasize the role played by a changing environment (Laland, Odling-Smee, and Feldman 2000, Richerson and Boyd 2000, Alvard 2003, Henrich and McElreath 2003). A consensus has been reached among these writers on the “strategy” appropriate to any given degree of environmental stability: individual learning, social learning (from the parental generation), and innate determination of behavior are favored by natural selection when environmental changes occur at short, intermediate, and long generation intervals, respectively. This proposal is quite reasonable in view of the results described above (Boyd and Richerson 1985, 1988; Rogers 1988; Feldman, Aoki, and Kumm 1996). However, the obvious study has not yet been done of simultaneously comparing individual learners, social learners, and organisms behaving innately when they are in direct competition with each other.

The purpose of this paper is to fill this theoretical lacuna. After extending the model of Feldman, Aoki, and Kumm (1996) to include innate behavior, we show by way of numerical examples that this consensus view is basically true for both periodically and randomly changing environments, provided that certain conditions are met. However, we also find significant differences between the predictions of the periodic-environmental-change model and the random-environmental-change model. In addition, our numerical work suggests that social learners may lack the opportunity to copy a genetically inherited behavior and therefore such a behavior is not likely to become part of a species’s cultural repertoire unless “reinvented” by individual learners.

#### ENVIRONMENTAL CHANGES AND PHENOGENOTYPES

Feldman, Aoki, and Kumm (1996) assume a population of haploid asexual organisms with two genetically determined strategies, social and individual learning. We extend their model to include innate behavior. Thus, in our model a tri-allelic “strategy” locus determines whether an organism is an “innate,” a social learner, or

an individual learner. Social learners acquire their behavior—or, rather, the information required to express the behavior—from an organism of the parental generation. Their behavior will be adaptive or maladaptive depending on whether the information obtained is appropriate to their current environmental state. Individual learners collect information directly from the environment and always achieve the adaptive behavior on their own. The information needed for innate behavior must be stored genetically. Accordingly, we posit an “innate information” locus with two classes of alleles, the “resident” alleles producing behavior that is adapted to the current environmental state and the “mutant” alleles producing maladaptive behavior. When an innate carries a resident allele at the innate information locus, its behavior is adaptive. Carrying a mutant allele results in maladaptive behavior. Each of the two classes of alleles comprises many selectively neutral variants. Hence, there may be a variety of adaptive behaviors, which by assumption are equally adaptive (i.e., have the same fitness), and similarly a variety of maladaptive behaviors. 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. The innate information locus is not expressed in individual and social learners.

By assumption, individual learners always behave appropriately for the given environmental state, but social learners and innates can get it either right or wrong. Therefore our model distinguishes five phenogenotypes (genotype-phenotype combinations [Feldman and Cavalli-Sforza 1984]): 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. 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—though not necessarily equivalent—direct cost and are also adversely affected by mistakes made before the mature behavior is realized; the total penalty is  $c$ .

In the periodic-environmental-change model, the environment changes every generations. In other words, one (postchange) generation experiences a different environmental state from the previous generation, and  $l-1$  subsequent generations experience the same state as the previous generation. Larger values of  $l$  imply more environmental stability. Rogers (1988) posits two states between which the environment alternates. However, the number of possible environmental states is likely to be large. As an idealization this number is assumed to be infinite, so that when the environment changes it never reverts to an earlier state (Feldman, Aoki, and Kumm

TABLE 1  
*The Five Phenogenotypes and 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)	$1-c$	$z$

1996). None of the preexisting behaviors can be adaptive after an environmental change. The infinite-state model may be a realistic representation of long-term environmental change, particularly if the environment is assumed to include other evolving species.

#### EVOLUTIONARY DYNAMICS WITH PERIODIC ENVIRONMENTAL CHANGES

Given that the state of the environment after a change is unprecedented, the innates will be rapidly eliminated from the population unless variant alleles segregate at the innate information locus that “anticipate” the environmental change. As described above, we assume that a small fraction,  $\rho$ , of all alleles at the innate information locus have the serendipitous property of being “preadapted.” They become resident alleles when the environment changes regardless of their status before the change. The remaining fraction,  $1-\rho$ , of all alleles then become mutants.

The behavior of an innate in our model is the result of an interaction between the allele it carries and the environment it experiences. In particular, an innate carrying a preadapted allele behaves differently in the pre- and postchange generations. Consistent with our basic premise—that none of the preexisting behaviors can be adaptive after an environmental change—we assume that its behavior in the prechange generation is maladaptive in the postchange generation. This implies that a social learner cannot acquire correct behavior by copying an innate with a preadapted allele when the environment changes.

The life-cycle events are mutation, asexual reproduction, learning, and natural selection, in that order. 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 changes between generations they are

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

TABLE 2  
An Example of a Periodic Solution

Number of Generations after Environmental Change	<i>u</i>	<i>v</i>	<i>x</i>	<i>y</i>	<i>z</i>
1	0.0000	0.0000	0.0000	0.5063	0.4937
2	0.0000	0.0000	0.2579	0.2378	0.5043
3	0.0000	0.0000	0.3844	0.1078	0.5078
4	0.0000	0.0000	0.4438	0.0482	0.5080
5	0.0000	0.0000	0.4718	0.0215	0.5067
6	0.0000	0.0000	0.4857	0.0096	0.5047
7	0.0000	0.0000	0.4933	0.0043	0.5024
8	0.0000	0.0000	0.4981	0.0019	0.5000
9	0.0000	0.0000	0.5016	0.0009	0.4975
10	0.0000	0.0000	0.5046	0.0004	0.4950
11	0.0000	0.0000	0.5074	0.0002	0.4925
12	0.0000	0.0000	0.5100	0.0001	0.4899
13	0.0000	0.0000	0.5126	0.0000	0.4874
14	0.0000	0.0000	0.5151	0.0000	0.4849
15	0.0000	0.0000	0.5177	0.0000	0.4823
16	0.0000	0.0000	0.5202	0.0000	0.4798
17	0.0000	0.0000	0.5227	0.0000	0.4773
18	0.0000	0.0000	0.5253	0.0000	0.4747
19	0.0000	0.0000	0.5278	0.0000	0.4722
20	0.0000	0.0000	0.5303	0.0000	0.4697

NOTE: Parameter values are  $s = 0.1$ ,  $c = 0.02$ ,  $d = 0.01$ ,  $l = 20$ ,  $\rho = 0.000001$ . Innate behavior is absent at this equilibrium ( $u = v = 0$ ). The frequency of SLC ( $x$ ) increases monotonically after the environmental change. This pattern repeats itself, and in the twenty-first generation the frequency of SLC, for example, returns to 0.0000.

where  $V = [\rho + (1-s)(1-\rho)(u + v) + (1-s-D)(x + y) + (1-c)z]$ . Second, when the environment remains constant between generations they are

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

where  $W = u + (1-s)v + (1-d)(x+y)(u+x+z) + (1-s-d)(x+y)(v+y) + (1-c)z$ . Note that  $u + v + x + y + z = 1$  and each  $V$  and  $W$  normalizes the corresponding recursions so that  $u' + v' + x' + y' + z' = 1$ .

We now explain the derivation of these recursions; the recursions with environmental stasis (2) are easier to explain, so we will deal with them first. Since reproduction is asexual, each offspring is genetically identical to its parent. Hence the frequencies of GC, GW, social learners, and IL among newborns are  $u, v, x + y$ , and  $z$ , respectively. (SLC and SLW cannot be distinguished genetically.) The naïve social learners acquire their behavior by copying a random member of the parental generation. Since GC, SLC, and IL of the parental generation are behaving adaptively, the fraction  $u + x + z$  of the naïve social learners becomes SLC, and the remainder,  $v + y$ , become SLW. The multiplicative factors  $1, 1-s, 1-d, 1-s-d$ , and  $1-c$

are the fitnesses of GC, GW, SLC, SLW, and IL, respectively; they define the surviving fractions of each phenotype after viability selection. Finally, normalizing by  $W$  gives the frequencies among reproductive adults of the offspring generation.

The recursions with environmental change (1) can be obtained by modifying the above argument. Among newborns the frequencies of GC and GW are  $\rho(u + v)$  and  $(1-\rho)(u + v)$ , respectively (lines 1 and 2). No members of the parental generation are behaving adaptively as viewed by members of the offspring generation, and therefore the fractions of naïve social learners that become SLC and SLW are 0 and 1, respectively (lines 3 and 4). IL are unaffected by environmental change and line 5 remains the same.

The evolutionary dynamics of the five phenotypes were investigated numerically. Corresponding to the environmental periodicity  $l$ , one set of iterations entails one application of 1 followed by  $l-1$  applications of 2. This procedure was repeated until the five variables,  $u, v, x, y$ , and  $z$ , converged to a solution of period  $l$ . Such a periodic solution is an equilibrium of the set of iterations in the sense that the pattern, once established, is repeated indefinitely. An example of a solution with period 20 is shown in table 2. Although it is conceivable that the equilibrium reached depends on the initial values assigned to the variables, in the cases tested the same equilibrium was reached regardless of the initial conditions.

Figure 1 illustrates the dependence on period length,  $l$ . On the horizontal axis,  $l$  is given on a log scale. On the vertical axis are plotted the frequencies, averaged over one period at equilibrium, of innates (GC and GW

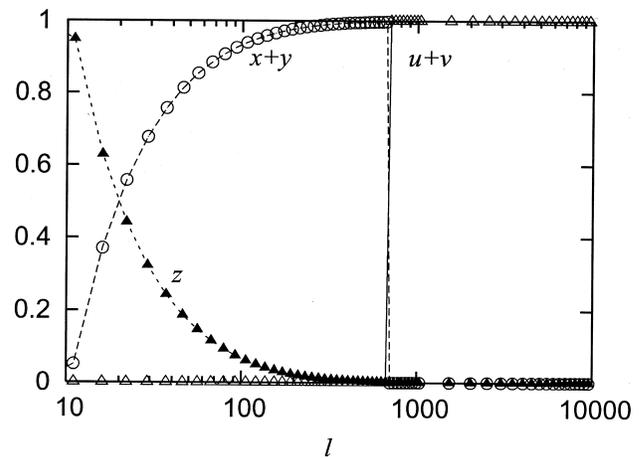


FIG. 1. Frequencies of individual learning, social learning, and innate behavior, averaged over one period at equilibrium, plotted against the period length ( $l$ ) on a log scale for the periodic-environmental-change model. Closed triangles and  $z$ , individual learners; open circles and  $x + y$ , social learners; open triangles and  $u + v$ , innates.

combined, frequency  $u + v$ ), social learners (SLC and SLW combined, frequency  $x + y$ ), and individual learners (IL, frequency  $z$ ). The values of the other parameters are  $s = 0.1$ ,  $c = 0.02$ ,  $d = 0.01$ , and  $\rho = 0.000001$ . Three properties of the plots are worth noting. First, individual learners, social learners, and innates dominate (i.e., reach high frequencies) at short, intermediate, and long periodicities, respectively. This result clearly supports the consensus view (Laland, Odling-Smee, and Feldman 2000, Richerson and Boyd 2000, Alvard 2003, Henrich and McElreath (2003) Second, a critical period length,  $l^*$ , exists such that innates are absent when  $l \leq l^*$  and individual and social learners are both absent when  $l > l^*$ . In this particular example we find that  $l^* = 683$  generations. Third, social learners always coexist with individual learners, on whom they are parasitic, and their frequency increases continuously as period length increases up to the threshold  $l^*$ . Together the second and third properties imply that at equilibrium social learners do not acquire their behavior by copying the innates. Caution is required in generalizing from the results of numerical work, but the features noted above apparently hold whenever  $d < c < s$ , as in this example. This ordering entails that the direct cost of social learning is small compared to the total cost incurred by the individual learners and both are smaller than the fitness loss due to maladaptive behavior.

#### CONSTRAINTS ON THE FITNESSES

As we have seen, the fitnesses of SLC, GW, and IL are  $1-d$ ,  $1-s$ , and  $1-c$ , respectively. If  $d < c < s$ , SLC has a higher fitness than either GW or IL. Hence, provided that most social learners are SLC rather than SLW and most innates are GW rather than GC, the social learners will on average “do better” than either the innates or the individual learners. Such a situation obtains at intermediate environmental periodicities—when the period is long enough for most social learners to acquire the adaptive behavior but too short for most innates to be carrying the resident allele at the innate information locus.

There are six ways in which the three quantities,  $s$ ,  $d$ , and  $c$ , can be ordered, including the case  $d < c < s$  already considered. Let us briefly indicate why social learning cannot evolve in the five remaining cases. If  $s < d$ , the fitness of a social learner can never exceed the fitness of an innate. Similarly, if  $c < d$ , the fitness of a social learner is always less than the fitness of an individual learner. Hence, if either inequality holds (i.e., if  $s < d < c$ ,  $s < c < d$ ,  $c < s < d$ , or  $c < d < s$ ), the social learners will be eliminated. This leaves the case  $d < s < c$ , but then the individual learners lose in competition to the innates and as a result the social learners, parasitic on the individual learners, will also disappear. Thus, the only condition that permits the evolution of social learning is

$$d < c < s. \quad (3)$$

Clearly, the statement that individual learners, social

learners, and innates dominate at short, intermediate, and long periodicities, respectively, must be qualified.

#### EVOLUTIONARY DYNAMICS WITH RANDOM ENVIRONMENTAL CHANGES

We have been assuming environmental changes at regular intervals of  $l$  generations. Real environments, however, do not change according to a fixed schedule even when there is an underlying periodicity; for example, this is true of the onset of the four seasons. An extreme alternative to the periodic-environmental-change model is the random-environmental-change model, which assumes that in any generation the environment changes with probability  $p$ . To facilitate comparison between the two models, we set  $p = 1/l$ . Then *on average* the environment will change every  $l = 1/p$  generations. As before, recursions of the first kind apply when the environment changes and recursions (2) apply when the environment is constant. However, the iterations do not follow a fixed order, since the timing of environmental changes is random.

The model of random environmental changes was simulated numerically by generating one uniform random number,  $R$ , between 0 and 1 per generation. If  $R < p$  (i.e., with probability  $p$ ) recursions (1) were applied. If  $R > p$  (i.e., with probability nonnegligible frequencies even at intermediate average period lengths.

We repeated the numerical work with other parameter sets satisfying inequality 3. The differences noted above between the periodic and the random model appear to hold in general.

#### CONCLUDING REMARKS

Building on the work of Boyd and Richerson (1985, 1988), Rogers (1988), and Feldman, Aoki, and Kumm (1996), we have shown 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. This prediction is qualitatively true whether the timing of the changes is deterministic or random but is subject to the constraint that the selection coefficients  $s$ ,  $c$ , and  $d$  must satisfy  $d < c < s$  (inequality 3). Our approach differs from previous studies in that it simultaneously compares the three strategies in direct competition with each other.

The conditions favoring the evolution of social learning in its earliest phases are not excessively stringent, and therefore the wide phylogenetic distribution of primitive social learning is not a mystery (Laland and Hoppitt 2003). However, we emphasize in this regard that only the behaviors that can be “invented” by individual learning processes can be socially transmitted; social learners cannot “plagiarize” innate behavior. This is because at equilibrium social learners coexist with the individual learners but not the innates, except possibly when the environment changes randomly and the average period lies in the narrow boundary layer. Hence, the “content

of culture" is limited by the capacity for individual learning as much as by the capacity for social learning.

There remains the task of testing the predictions against data on the phylogenetic distribution of social learning. Clearly, this would be a formidable undertaking. First, the relevant environmental factors would have to be identified. What exactly is changing that might make it profitable to employ a social learning strategy? Second, the timescale of these environmental changes relative to the generation length of each species would have to be determined, and we need to know whether these changes occur regularly or at random. Third, we would require estimates of the strength of natural selection acting on the three strategies. Quantitative predictions on the period length that might favor social ( $1-p$ ) recursions (2) were applied. This was continued for 100,000 generations. The first 50,000 generations were discarded to allow for the possibility that "equilibrium" had not been reached, and the phenogentype frequencies were evaluated over the remaining 50,000 generations. Since our interest is in the average tendencies rather than the results unique to each realization of the stochastic process, we ran 100 such simulations.

Figure 2 illustrates the dependence on the probability of environmental change,  $p$ . On the horizontal axis the reciprocal of this probability,  $l = 1/p$ , is given on a log scale, facilitating comparison with figure 1. On the vertical axis are plotted the frequencies of innates (GC and GW combined), social learners (SLC and SLW combined), and individual learners (IL). Each point represents an average over 100 runs for generations 50,001 through 100,000. The other parameters are as before:  $s = 0.1$ ,  $c = 0.02$ ,  $d = 0.01$ , and  $\rho = 0.00001$ . The overall picture is remarkably similar to figure 1. Thus, *on average*, we see that individual learners, social learners, and innates dominate when the value of  $l$  is small, medium, and large, respectively.

However, we note several differences. First, there is a "boundary layer" of finite width between the regions where social learners and innates are on average dominant. The average frequencies of social learners and innates change continuously in the boundary layer, whereas in the periodic-environmental-change model a sharp transition was observed at the threshold,  $l^*$ . This result is attributable to the considerable variance among the 100 runs in the frequencies of social learners and innates for any value of  $p$  in the boundary layer.

Second, the boundary layer is centered to the left of  $l^*$ , although the deviation is small. In fact, the intersection of the curves labeled  $x + y$  and  $u + v$  occurs at  $p = 0.00148$  corresponding to  $l = 676$ , whereas  $l^* = 683$ . However, since the boundary layer is finite in width, the upper bound on the average period for which social learning dominates is significantly smaller when the environment changes randomly (the frequency of social learners approaches 1 when  $l = 465$  [fig. 2]). Since real environments do not change at regular intervals, predictions derived from deterministic models that make this assumption may be qualitatively but not quantitatively applicable.

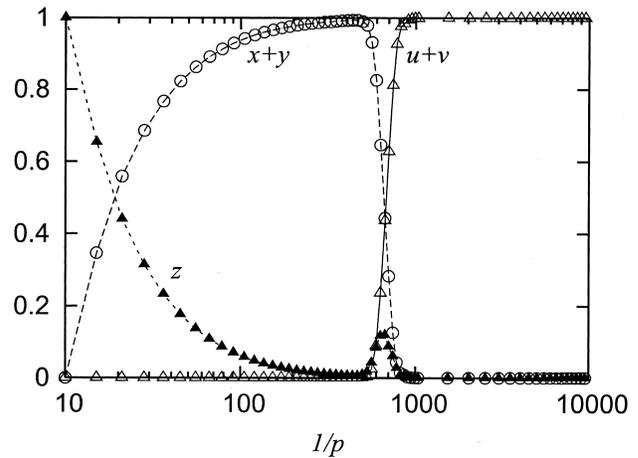


FIG. 2. Average frequencies of individual learning, social learning, and innate behavior plotted against the average period length ( $1/p$ ) on a log scale for the random-environmental-change model. Closed triangles and  $z$ , individual learners; open circles and  $x + y$ , social learners; open triangles and  $u + v$ , innates.

Third, the average frequency of individual learners shows a secondary peak in the boundary layer. The maximum, 0.162, occurs at  $p = 0.00149$  corresponding to  $l = 670$ . Once again there is considerable variance among the 100 runs in the frequency of individual learners for any value of  $p$  in the boundary layer. In fact, individual learners temporarily dominate in some realizations of the stochastic process. Hence, in a randomly changing environment, individual learners may sometimes reach learning cannot be made without information on the selection coefficients.

Finally, we mention one complication that cannot be ignored. Given that innate behavior was the primordial state, neither individual nor social learning could have arisen without mutation. Hence, introducing mutation among the three strategies enhances the realism of our model. When recursions 1 and 2 are appropriately modified to incorporate this assumption and then iterated with periodic environmental changes, we find that individual learners coexist with the innates when  $l > l^*$ . When the modified recursions are iterated with random environmental changes, we observe a significantly wider boundary layer than for the case of no mutation at the strategy locus (Wakano, Aoki, and Feldman 2004).<sup>2</sup>

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