Changing Latent Energy Environments: A Case for the Evolution of Plasticity

Filippo Menczer
Computer Science and Engineering Deptartment
University of California, San Diego
La Jolla, CA 29093-0114
(fil@cs.ucsd.edu)

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1 Introduction

Plasticity can be broadly defined as the capacity for any type of phenotypic change to occur during life. It is often argued that one of the main advantages of plasticity for individuals in evolving populations is adaptation to changing environments (see, e.g., Johnson 1982, Belew 1990). This is independent of other, less direct forms of interaction between evolution and plasticity, such as the Baldwin effect (Baldwin 1896, Waddington 1942, Maynard Smith 1987, Hinton and Nowlan 1987, Belew 1990, Nolfi et al. 1990, Parisi et al. 1992). In this paper the effect of environmental temporal changes on evolution is studied, thus allowing to explore the above hypothesis and quantitatively test it. In particular, this is done by studying the correlation between environmental rate of change and the adaptive advantage of individual plasticity.

2 Model

2.1 LEE

The latent energy environments (LEE) artificial life model lends itself to this type of analysis with relatively little effort. Thus the LEE simulator is used for the experiments described here. For an adequate description of this model and simulator, please see (Menczer and Belew 1993a,b). Instead, the essential features of the model that are relevant to the experiments reported here are briefly described below.

An individual is modeled by a feed-forward neural network that uses information provided by a set of sensors to compute an action executed by a set of motors. Individuals move on a two-dimensional grid and possibly approach atomic elements scattered in the environment. Ambient sensors are used to gather information about atoms within a local range from the individual. The signal mapped by an ambient sensor onto the input of the network is proportional to the quantity of atoms in the range of the sensor, weighed inversely to their distance and independently of their direction. A simple motor allows the individual to perform one of four possible moves: stay still, turn right or left, or move one cell forward.

A population of individuals evolves in time to adapt to their environment. Evolution is modeled by a steady-state genetic algorithm: individuals reproduce asynchronously according to the energy they acquire by approaching elements in the environment. Running out of energy causes death. Reproduction is by cloning with non-lamarckian mutations -- additive uniform deviate on the connection weights of the neural network. Energy is acquired (or lost!) by catalyzing reactions between atoms. Moving also has an energy cost.

2.2 Environment

In the experiments described here there are atoms of two elements (A_1, A_2) uniformly distributed at random in the environment, and the nature of reactions is described in a table with the following form:

	A_1	A_2
A_1	E_{11}	E_{12}
A_2	E_{21}	E_{22}

where a reaction between atoms (i,j) results in energy E_{ij} (i,j=1,2) being acquired by the individual that catalyzes such reaction. Energy can be positive or negative for any reaction, and adaptation consists in evolving a behavior that allows to catalyze exothermic reactions (but not endothermic ones).

Since the description of the environment (or, more precisely, the environmental effect on adaptive behavior) is concisely contained in the reaction table, a very simple way to model a changing environment is by making random changes to the entries of the table, E_{ij}, with the following constraints:

$$\sum_{i,j} E_{ij} = const > 0$$
$$\forall i,j \quad -\alpha < E_{ij} < \alpha$$

where α is the reproduction threshold. These constraints are dictated by the necessity to avoid initial extinction and to normalize the complexity of different environments (Menczer and Belew 1993c). Notice that these changes are easily catastrophic: they amount to completely rewriting the "physics" of the environment, consequently transforming adaptive behaviors into maladaptive ones and vice-versa, with high likelihood.

The possible time scales for these changes are, naturally,

$$\tau_e >> \tau_a$$
$$\tau_e << \tau_a$$

where the time scale of environmental change (e) is compared with that of evolutionary adaptation (a). The first case corresponds to the standard situation in which the environment is effectively fixed with respect to evolution: we can use this situation for "control" experiments. The second case is more interesting for our study of plasticity and evolution in changing environments: adaptation is impossible when the rate of change is too high for the genetic feedback loop to close. This is where we expect plasticity to be advantageous.

2.3 Plasticity

While time is one of the independent variables in our experiments, the form of individual change during life is the other. A simple model of plasticity interesting to explore is “developmental noise”, which we can define roughly as a set of stochastic changes to phenotypic traits (connection weights) during the life of an individual. Noise could be viewed as a sort of mutation -- but distributed through time, and *not* inheritable. This "blind" form of plasticity can be quantitatively controlled via both the *amplitude* of noise in the phenotype and its *frequency* (or probability, in the stochastic case).

Developmental noise can assist evolution in changing environments through increased exploration of the adaptive landscape. Support for this view comes from simulations showing that noise helps in the initial phase of evolution (Miglino et al. 1993; see below). Noise is also interesting in the study of development, representing a source of non-invertibility in the mapping from genotype to phenotype (Belew and Parisi 1994).

Another approach to modeling plasticity, not explored in this paper, would be to use prediction learning, as already incorporated into LEE and implemented by back-propagation of error, with the environment acting as a teacher and stimuli sampled from the sensory repertoire of the individual. This sort of "directed" plasticity has been used in many interesting experiments aimed at studying the interactions between learning and evolution (Nolfi et al. 1990, Parisi et al. 1992). The idea behind using prediction learning with changing environments is that the ability to approach atomic elements should be useful independently of the (changing) effects of combining them.

3 Experimental setting

We expect that there is a negative correlation between the time scales of environmental change and plasticity. The higher the rate of change of the environment, the more plastic individuals have to be during their life in order to survive. We explore here the expected orders of magnitude of these time scales, allowing a comparison with the results of the simulations.

Environmental changes considered here are those which span over at least one generations: changes which occur within time periods much shorter than the average duration of a lifetime (l) are not relevant to our analysis of the advantage of plasticity in the *evolutionary* process. This observation, together with the considerations of the previous section, suggests the range for the time scale of changes in the environment in our experiments:

$$\tau_l \leq \tau_e << \tau_a$$

where τ_l and τ_a are measurable in a LEE simulation. The former is estimated by the average age of the population, and the latter is the time required for the population to reach a size reliably and significantly greater than that obtainable with individuals moving at random (in a fixed environment). To relate these measures with plasticity, let us define the rate

$$v_p \equiv \frac{\Pr(noise)}{time \cdot connection}$$

of phenotypic plasticity (developmental noise). Now it is reasonable to assume that when we compare two changing environment, with rates of change

$$\nu_e^1 = \left(\tau_e^1\right)^{-1}, \nu_e^2 = \left(\tau_e^2\right)^{-1},$$

the rates of plasticity in first approximation should be in the ratio:

$$\frac{\nu_p^1}{\nu_p^2} \sim \frac{\tau_e^2}{\tau_e^1},$$

and this gives an idea of the type of functional relationship between environmental change and plasticity, to be explored and validated on the basis of simulation results.

4 Simulation results

A way to study the adaptive advantage of plasticity is by placing it under genetic control and observe the evolutionary conditions under which it is selected for and against. This was done by Miglino et al. (1993) with a "noise gene" (similar to our noise rate) regulating the relative amplitude of noise in each connection of a neural network. A population of such networks evolves to solve an artificial life task -- simpler than the one used here. The results of that paper indicate that, irrespective of initial conditions, the average value of the noise gene in the population initially grows during the adaptive phase in which most change occurs, and then decreases at convergence. It is tempting to draw an analogy between the evolutionary stage at the beginning of the genetic algorithm and those which follow drastic changes in the environment. Consequently, we expect that the amount of phenotypic plasticity to which the population converges should be correlated with the rate of environmental change.

Before testing this hypothesis, we reproduced the experiment of Miglino et al. (1993) with LEE. The environment does not change in this simulation. Developmental noise is defined as follows: at each life cycle of an individual (elaboration of sensory information and production of motor action), the weight w of each connection in its network receives an additive uniform deviate (noise) in the interval

$$\left[-\nu_p|w|, +\nu_p|w|\right],$$

so that relative amplitude and frequency of phenotypic plasticity are collapsed into a unique degree of freedom, i.e., the value of the noise rate parameter. Each individual is initialized with zero noise rate, a condition effectively identical to absence of noise. At reproduction, the noise rate of an offspring is replaced by mutation with a random value in the unit interval, with small probability ($5x10^{-2}$). The result, is qualitatively similar to what was shown by Miglino et al. As illustrated in figure 1, noise does not hinder evolution from the point of view of fitness. To interpret this plot, note that population size is an effective measure of average fitness in LEE: the more fit the behavior of individuals, the more efficiently they can realize latent energy distributed in the environment, the more they can reproduce, resulting in a larger population.

Figure 1: population dynamics in reproduction of experiment on evolution of noise gene (graphs indicate averages over three simulation runs).

We also reproduced the result that noise is selected for in the initial stage of evolution, and then slowly selected against as the population becomes adapted and stabilizes. Apropos the initial increase in average noise rate, we should point to the role of mutations even in the absence of any selective advantage, since the values are initially set to zero for the whole population. To illustrate this point, a "control rate" gene ν_c is coevolved with the noise gene, undergoing exactly the same mutation dynamics, except that it is never used, making it an adaptively neutral trait. Both ν_c and ν_p are plotted in figure 2.

In agreement with our hypothesis, experiments show that when the environment changes in time, there is selection for a greater amount of plasticity. Figure 3 illustrates this (for three single simulations): as the rate of environmental change increases, the average noise frequency in the population is maintained higher.

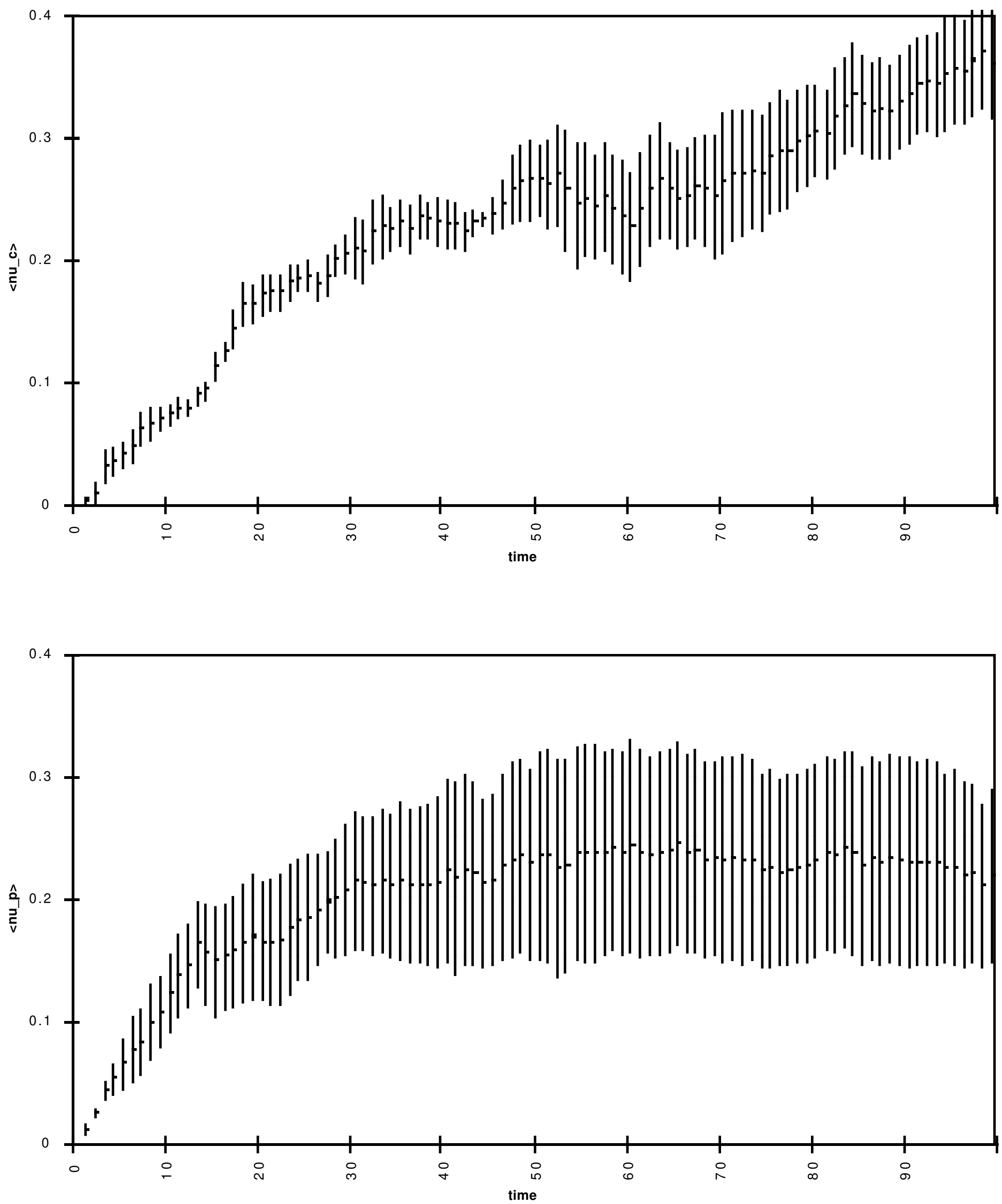

Figure 2: evolution of the noise gene (below) and its control (above). Errors correspond to 1 standard deviation.

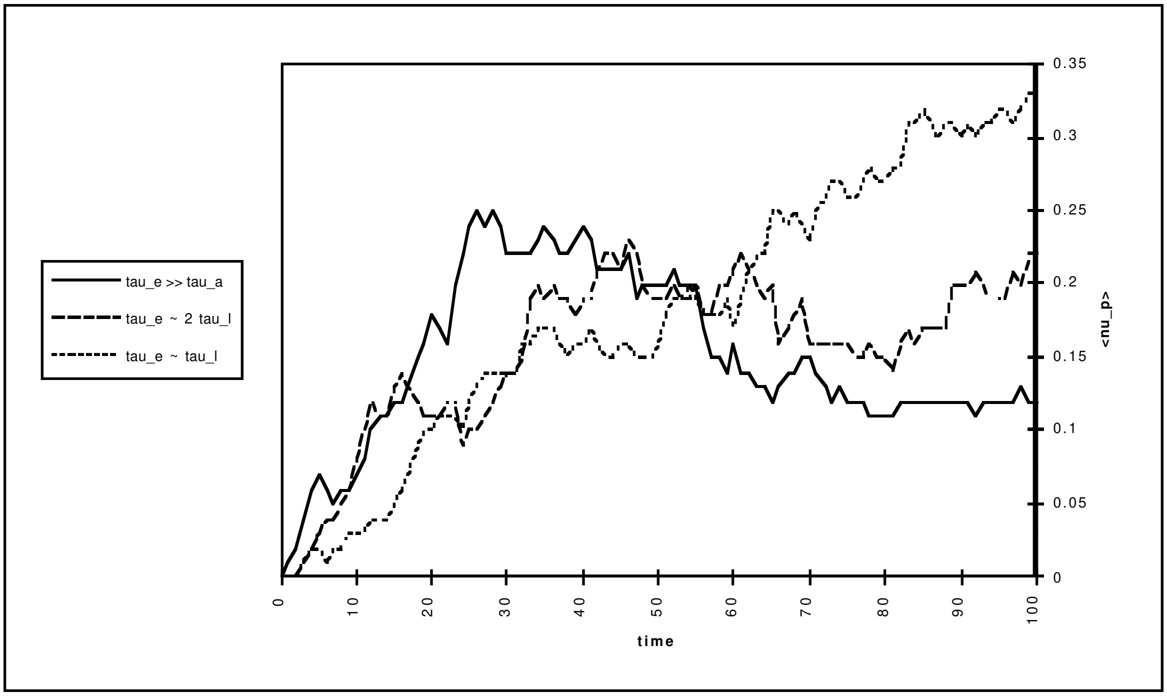

Figure 3: evolution of plasticity in changing environments.

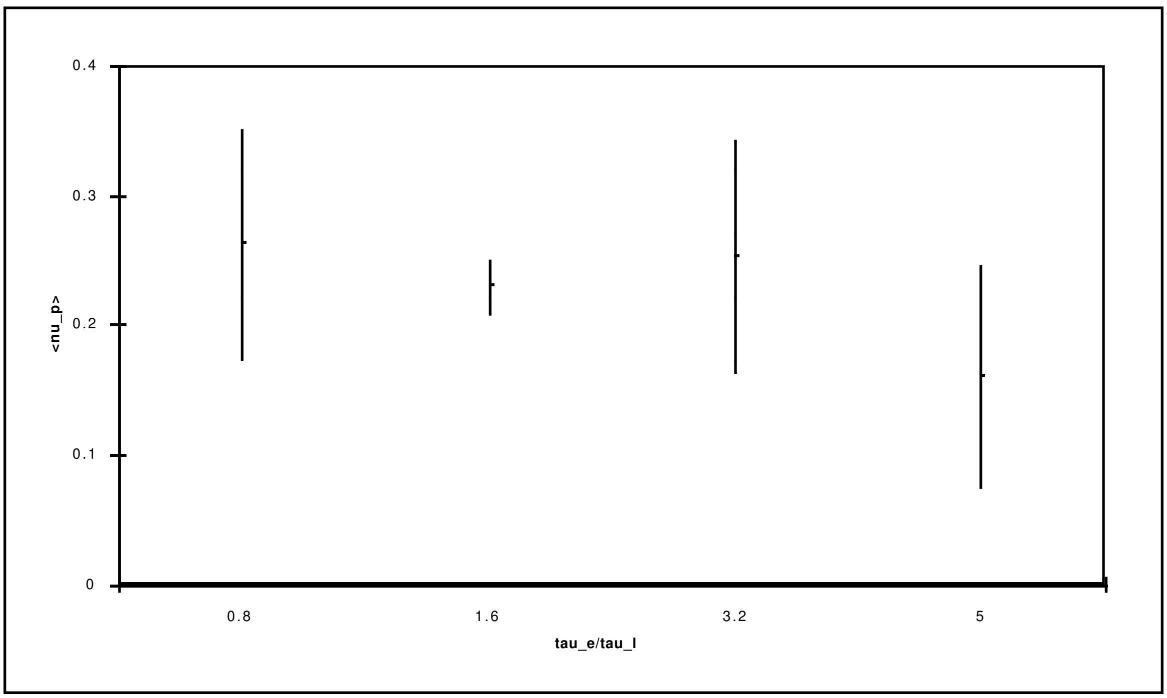

Figure 4: correlation between τ_e and ν_p (errors correspond to 1 standard deviation).

To analyze how the adaptive amount of developmental noise varies with the rate of change of the environment, we have plotted in figure 4 the evolved noise rate (averaged over the population) as a function of τ_e , after a fixed evolutionary time (~$10\tau_l$). The negative mean slope is in agreement with the expected decreasing behavior predicted in section 3, although the very large errors make this preliminary result somewhat inconclusive.

5 Conclusion

The simulations illustrated in this paper illustrate the effects of developmental noise, a "poor man's" version of plasticity, in adaptive evolution. While its presence does not hinder evolution in fixed environments, it appears to favor adaptation to changing environments. An alternative interpretation of the effect of plasticity is that it makes the adaptive landscape appear smoother to the evolutionary process. Thus a transformation of such landscape, caused by a change in the environment, may have less catastrophic consequences.

The ways in which phenotypic plasticity and changing environments have been modeled in this paper are quite crude. One direction for further work is to try other, more plausible forms of environmental change and phenotypic plasticity. It would also be critical to reach a higher degree of confidence in the simulation results, which remain quite "noisy" as presented here. Another direction would be to capture a more precise measure of how much selective advantage can be provided by plasticity in changing environments: such data could be obtained by direct comparison between the performance of simulations with and without plasticity, in the presence of environmental change.

Even with the limited and preliminary results presented here, however, the use of artificial life techniques has allowed us to obtain at least partial quantitative evidence in support of an important hypothesis: that plasticity is helpful for populations of evolving individuals in the course of their adaptation in changing environments. This idea, while largely agreed upon among theoretical biologists, has remained without experimental support for a long time.

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