

## Balancing the Costs and Benefits of Learning Ability

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### Abstract

We study the costs and benefits of plasticity by evolving agents in environments with different rates of environmental change. Evolution allows both hard-coded strategies and learned strategies, with learning rates varying throughout life. We observe a range of change rates where the balance of costs and benefits are just right for evolving learning. Inside this range, we see two separate strategies evolve: lifelong plasticity and sensitive periods of plasticity. Sensitive periods of plasticity are found to reduce the learning cost while retaining the benefits of learning. This affects the evolutionary process, by limiting genetic assimilation of learned characteristics, making agents able to remain adaptive after relatively long periods of environmental stability.

### Introduction

Learning has been selected for by the process of natural evolution because it increases the fitness of individuals. This ability has both *advantages* and *costs* associated with it. The costs range from the energetic cost of maintaining a machinery for learning, to the cost having to do some potentially fatal trial and error to enable learning. The result of these costs is that evolution will attempt to minimize the amount of learning and, when possible, replace plasticity with innate strategies. Together, the costs and benefits of learning lead evolution to find a solution that learns just as much as is necessary and at the times in the lives of individuals when learning is most beneficial.

In this paper we study two phenomena related to plasticity regulation, to gain a better understanding of how they affect each other. The first one is the *Baldwin effect*, which describes plasticity regulation across *generations*. The second is *sensitive periods*, which describes plasticity regulation across individual lifetimes. An introduction to these phenomena, and related research on them is given in the next section.

### Background

#### Learning- Costs and Benefits

The benefits of learning are frequently documented in studies of interactions between evolution and learning (see for

instance Floreano and Urzelai (2001), Littman (1995), and Nolfi et al. (1994)). When studying interactions between evolution and learning, it is important to also remember that learning has a *cost*. It is the balance between the cost and benefit of learning that decides the final learning strategies followed by individuals resulting from an evolutionary process. A comprehensive overview of the costs and benefits of learning is outside the scope of this paper. See Mayley (1996a) for a good overview of these factors. An implication of the cost of plasticity, is that plasticity in organisms needs to have *adaptive value*. When possible, natural selection should reduce costs by replacing plastic responses with genetic mechanisms.

Costs and benefits will vary significantly between individuals and even in single individuals in different situations. For instance the benefit of learning will be larger in an infant than an adult who has already learned the most important rules for gathering food and avoiding predators. See Turney (1996) for a comprehensive discussion of the trade-offs between plasticity and stability, and how this changes in different circumstances.

**Modeling the cost of plasticity** Kerr and Feldman (2003) investigated how the reliability of stimuli affects the utility of long-term memory. The authors argued that the key to deciding the evolutionary advantage of learning, is the amount of variability in the environment. They suggested that the relationship between environmental variability and the utility of learning follows “Goldilocks principle”: For learning to be beneficial, environmental variability needs to “just right” – not too high or too low. Based on their results, the authors concluded that under rapidly changing environmental conditions, a short memory span is beneficial, and that a reliable world favors using more memory. Presumably, a completely reliable world would remove the need for memory at all, as responses could be hard-wired, but the authors did not consider multiple generations of individuals, so the possibility of genetically optimized responses was not present.

Dunlap and Stephens (2009) provided the first experimental demonstration, through experiments on populations of *Drosophila melanogaster*, that some types of environ-

mental change favor learning, while others select against it. Through an aversion learning experiment, the authors were able to identify two different types of environmental change that affected the evolved degree of learning in the fruit flies differently. The first type of change, termed *best-action fixity* describes to what degree the best action to take in the environment is always the same. A high value of this parameter indicates that a strategy always performing the same action will be successful. The second type of change, termed *reliability of experience* represents the fixity of the relationship between experience and the best action. This indicates to which degree it is *possible* to do associative aversion learning. The situation that most strongly selects for learning, is the one in which there is a high reliability of experience, and a low best-action fixity. The opposite situation selects for non-learning (fixed) strategies. This theoretical model was confirmed by experiments on a population of *Drosophila* over 30 generations.

In our experiments, focus will be on regulating best-action fixity – in other words, the action giving the most fitness is subject to change, but the feedback indicating to the agent whether an action was “good” or “bad” is always correct. This ensures that the agent can always learn the best action by association with the feedback signal. We believe Dunlap and Stephens left out part of the truth: as the fixity of best-action decreases sufficiently, learning will be *selected against*. This follows from Kerr and Feldman’s hypothesis that the utility of learning follows “Goldilocks principle”.

### The Baldwin Effect - Regulating Plasticity Across Generations

The Baldwin effect (Baldwin (1896)) is an interesting example of how evolution will regulate plasticity across generations to reduce costs. The effect suggests how learned traits may become encoded into the genome of individuals through an *indirect* mechanism.

The Baldwin effect has two phases. It is initiated by a change to the environment, which forces a population to adapt. In the first phase, learning accelerates the rate of evolution. The reason is that, because learning allows weak individuals to become better, it smooths the fitness landscape, making the “evolutionary search” simpler. This was demonstrated in (Hinton and Nowlan (1987)) for an extreme case where there was only one correct solution, and no fitness gradient to steer the evolution when learning was not present. Adding learning provided a fitness gradient, accelerating evolutionary progress. In this phase, the benefits of plasticity outweigh the costs, leading to an increasingly plastic population.

In the second phase of the Baldwin effect, *genetic assimilation* occurs, meaning that the learned traits gradually become part of an individual’s genotype. This is a result of the cost of plasticity. Mayley (1996b) points out that it is the varying cost/benefit trade-off of plasticity that enforces

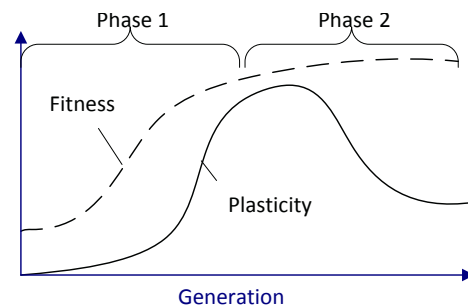


Figure 1: The two phases of the Baldwin effect - First, the benefit of learning leads to an increase in average plasticity. Subsequently, the costs lead plasticity to drop off.

the changes in the levels of learning in an evolving population: Shortly after an environmental change, the benefits of learning are large, and learning is selected for. As the population is full of individuals that can adapt to the environmental change, the cost of learning puts the individuals with innately good strategies at an advantage, and this reduces the overall plasticity in the population. Figure 1 illustrates the Baldwin effect.

**Computational modeling of the Baldwin effect** A few experiments have been done on the Baldwin Effect using simple, evolving individuals. Most of these deal with a *fixed* environment, where an unadapted population is inserted. If the environment is allowed to change during evolution, analyses become more complex. However, as argued by Anderson (1995), it is not sufficient to study the interaction between learning and evolution in fixed environments. Certain interactions between evolution and learning, e.g. the ability of plasticity to act as a “buffer” against changes in the environment, are especially evident in variable environments.

Watson et al. (2002) studied the relationship between the complexity and stability of a learning task and the tendency for genetic assimilation to occur. Genetic assimilation was found to be most complete (eliminating the most learning) when the environment was highly unstable. For more stable environments, the degree of genetic assimilation was lower. These results may seem surprising, but they follow from the relatively short periods of stability the researchers investigated. The most frequent changes were so frequent that evolved responses performed better than learned ones. A slightly more stable environment gave a higher benefit of learning, so the learning rate never reached zero.

Mayley (1996a) studied the effect of two important variables on the amount of learning performed by individuals over many generations of evolution: 1) The cost of learning, and 2) the correlation between genotype and phenotype space. He found that both a *neighborhood correlation* between genotype and phenotype space and an evolutionary *cost of learning* was necessary to observe genetic assimila-

tion.

Sasaki and Tokoro (1999) studied how rates of change in an environment affected populations of individuals evolving with different rates of *heritability of acquired characteristics*. The authors saw signs of a Baldwin Effect in the environments with relatively small degrees of dynamic change. For environments with larger degrees of dynamism, however, no genetic assimilation was seen. This indicates that the Baldwin Effect needs a certain *degree of stability* to enter into its second phase. This proposition is supported by findings presented herein.

### Sensitive Periods - Regulating Plasticity Within Individuals

A sensitive period is a period in the life of an individual where environmental stimuli have particular importance in the development of a certain ability (Knudsen (2004)). Hubel and Wiesel's classic paper (Hubel and Wiesel (1970)) illustrates the concept: One eye of a kitten was sutured in various periods throughout life, and it was found that visual deprivation of one eye early in life would make that eye unable to follow the regular path of development. The result would be that the cat was blind on that eye, also when it was opened later in life.

**Computational modeling of sensitive periods** Bullinaria (2003) studied sensitive periods of learning, as part of a simulation of the human oculomotor system. By the use of an evolutionary algorithm, *age-dependent neural plasticity* was generated. The type of age-dependent plasticity arising from these experiments had parallels with biological sensitive periods. For the purposes of our discussion, the most interesting feature of sensitive periods is their ability to reduce the cost of learning, by shrinking the plastic period of individuals. Previous studies on evolution of sensitive periods (Bullinaria (2003), Kirby and Hurford (1997)) have also discussed the cost-reducing role of sensitive periods. In this paper, we want to study this more systematically, by evolving sensitive periods under different balances between the cost and benefit of learning. Also, we want to compare the genetic assimilation happening under sensitive periods with that happening under a constant plasticity, to see if a more focused learning period can in some circumstances reduce the pressure on going through genetic assimilation.

### Hypothesis

The hypothesis of this paper is illustrated in Figure 2, and it proposes a model for how the topics of the Baldwin effect, sensitive periods and the cost/benefit balance of plasticity are connected. The way we regulate the cost/benefit of plasticity is by regulating the *rate of environmental change*. Figure 2 shows how we hypothesize learning strategies are related to the rate of environmental change. In constantly changing environments, learning has no benefits, as there

are no lasting rules to be learned. We hypothesize that the cost of learning would eliminate all plasticity in such a situation. In a fully stable environment, we also hypothesize that learning will be selected against, for obvious reasons.

In between these two extrema, we believe we will find individuals with different degrees of plasticity. Adding some slow changes to the fully stable state will at first be handled by evolution: genetic changes can tackle the environmental fluctuations. But when the environmental change reaches a certain frequency, the limit of genetic assimilation will be reached, and learning will be beneficial, as evolution cannot track the changes by itself. When the changes are relatively slow, we propose that sensitive periods may be enough to handle them, allowing short periods of plasticity in individuals' life, without paying the cost of a lifelong adaptation. Finally, in situations that have a rapid (but not too rapid) rate of environmental change, lifelong re-adaptation will be necessary, and we propose that individuals will evolve to have a high learning rate throughout life, and not just in sensitive periods. In this context, we can view sensitive periods as a *compromise* between the inexpensive but slow adaptation of the genotype and the costly but rapid adaptation allowed by individual learning.

The idea that environmental variability and evolved plasticity are closely connected has been around for a long time (Bradshaw (1965)). However, only a few empirical studies have investigated this connection (see Komers (1997) for a review), and typically only for a couple of levels of environmental variability. A systematic exploration of many scales of environmental change is naturally difficult to implement in a biological experiment. Therefore, this paper attempts to take a middle ground between theoretic approaches and empirical studies, by using evolutionary computation to evolve individuals under a large range of environmental variation.

## Experimental Setup

### The Environment

The setup is a modification of the experiment in (Todd and Miller (1991)), designed for studying the evolution of associative learning. This experiment was concerned with a simple underwater creature that is born into a patch of an environment where it spends its entire life. Substances of two different colors continuously float by, and the only decision the creature needs to make, is whether to eat these substances or not. Substances can be either poisonous or nutritious, and the challenge is for the creature to decide which type of color to consume. The association between color and edibility is a function of the feeding patch the agent was born into, so it is not optimal for all creatures to use the same strategy. The authors studied how evolution and learning together can find good strategies for this associative learning task.

In this paper, the same setup is used to study the relationship between plasticity and degree of environmental change.

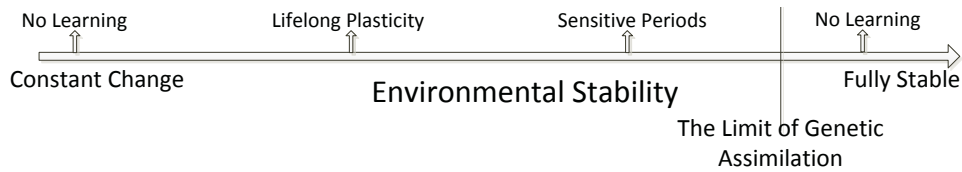


Figure 2: A hypothesized spectrum mapping the level of environmental stability to learning strategies in individuals.

Two important extensions to the experiment have been performed: 1) Learning is associated with a *cost*, simulating the biological costs of learning, and 2) The environment changes at regular intervals. The second extension means that instead of varying across *feeding patches*, associations vary across *time*. The environmental change is the same: a reversal of the color/edibility association. We regulate the change rate of the environment using a single variable, the *stability period* of the environment. This variable decides the number of generations between changes. Setting this below one means we have several changes per generation. For instance a stability period of 0.1 entails 10 changes per generation.

The timing of changes within a generation is randomly chosen. However, in *which generations* the change occurs is fully controlled by the given stability period. We do not add randomness to which generations see environmental changes, because we want the generational interval between changes to be fixed, in order to study genetic assimilation systematically.

**The Agents**

As pointed out by Mayley (1996b), two conditions are necessary in any experiment on genetic assimilation:

1. The plasticity of agents needs to be under genetic control.
2. The characteristics expressed by plasticity must also be possible to express genetically.

In this experiment, these conditions were met by an artificial neural network (ANN) capable of both employing *hard-coded rules* and *neuromodulated learning* when deciding which substances to eat and which to avoid. An evolutionary algorithm decides the initial *connection weights* and the *learning rates* along the same connections in the network, meaning it can evolve both hard-coded and plastic individuals.

The neural network is shown in Figure 3. The dotted connections are plastic links, which have evolvable initial weights and learning rates. The other connections are hard-wired in the experiment. The connections attaching to other connections are *neuromodulators*. That means that they modify the learning rates in the links they affect. This way, reinforcement learning driven by the perception of rewards and punishments is achieved. When the associations in the

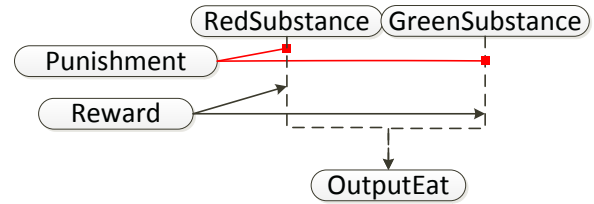


Figure 3: The neural network performing the substance association task. Rounded rectangles represent neurons. Arrows represent connections.

environment change, the agent will notice that actions lead to different reinforcing feedback than before, and alter its preferences based on the neuromodulated plasticity.

Arcs in the network are updated by the following learning rule:

$$\Delta w_{ij} = \eta * mod * |x_i x_j| \tag{1}$$

where  $\eta$  is the evolved learning rate, *mod* is the strength of incoming neuromodulation and  $x_i x_j$  is the product of pre-synaptic and post-synaptic activity, in other words a regular Hebbian update term.

As the equation shows, it is the *absolute value* of the hebbian update that is used in the calculation of the new weight value, since we want the *modulatory signal* to decide the direction of the weight change: negative modulation means whatever action was taken was a bad idea, so the weight of the link causing the action should be decreased. Positive modulation should have the opposite effect. In the absence of modulation (in other words, if  $mod = 0$ ), weights are not updated.

**Plasticity**

An important question in these experiments is how the ability to employ age-dependent plasticity, potentially forming sensitive periods, affects the balance between genetic and neural adaptation. We ran the experiments with two different types of plasticity. In the first type (“static” plasticity), plasticity was constant throughout the lifetime of an individual, and regulated by a single evolved learning rate. In the second type (“dynamic” plasticity), a function was evolved, which controlled the plasticity level throughout agents’ lives with a 2 timestep interval - meaning plasticity levels could

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Parameter	Value
Generations	200
Adults	15
Children	25
Crossover probability	0
Mutation probability	0.01
Genes per individual	3 (static) or 60 (dynamic)
Bits per gene	8
Elite fraction	0.1
Culling fraction	0.1

Table 1: Parameters of the Evolutionary Algorithm

change at most 50 times in the agents’ 100-step lifetimes. To produce a somewhat smooth age-plasticity mapping, the evolved function was smoothed with a window size of 8 around the current timestep. For each timestep, a value between  $-2$  and  $2$  was evolved, and this was averaged with the 7 following values to produce the plasticity value for that timestep.

### Evolutionary Algorithm

The system SEVANN was used for evolving learning rates in these experiments. SEVANN is a flexible system for designing experiments allowing evolution of neural network parameters and topologies. For details, see Downing (2010). The parameters of the evolutionary algorithm are given in Table 1.

Results were found to be most stable and evolvable when crossover was turned off. However, for adding realism to the model, investigating further how crossover affects these results is interesting for future studies. Evolved individuals employed either static or dynamic plasticity regulation, and this required a different number of evolved genes. In both cases, two of the genes coded for the innate strategy of individuals. The remaining encoded the plasticity for the rest of individuals’ lives.

## Results

### Change Rates and Learning Effort

To investigate the hypothesis illustrated in Figure 2, we evolved the learning efforts and innate weights of individuals under many different rates of environmental change. We did this both for learning rates allowed to vary throughout the lifetimes of individuals and for learning rates that remained constant throughout life.

Figure 4 shows the resulting evolved learning effort. The measured learning effort is proportional to the sum of learning efforts made in each timestep for an individual. When the learning effort is “dynamic” (in other words, allowed to vary with the age of an individual), we can identify four main learning strategies, corresponding to the four strategies we hypothesized in Figure 2. For changes occurring too

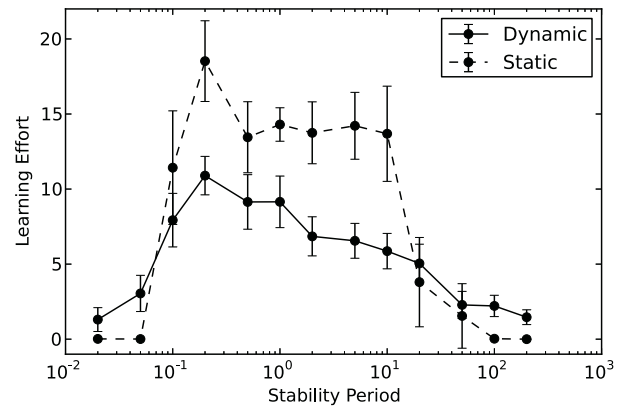


Figure 4: The learning effort made by individuals evolved under different rates of environmental change. Dots are measured values, the lines interpolate between measurements. “Dynamic” indicates a learning effort allowed to vary throughout the lifetime of individuals, while “Static” indicates a constant learning effort throughout life. Change rates are given as number of generations between each change. – Averages over 20 runs. Error bars show a 95% confidence interval of the means.

slowly or too rapidly, there is no benefit to learning. These observations are in line with the suggestion (Kerr and Feldman (2003)) that the utility of learning in a varying environment follows “Goldilocks principle”: Change rates need to be *just right* for learning to evolve.

When the change rate is within the range needed to evolve learning capacity (here, that range is from about 0.1 to 50 lifetimes between each change), we can identify two main strategies for the dynamic learners. The first main strategy is to stay plastic throughout life. This strategy is adapted for environments where change rates are so high that a sensitive period of learning would not allow an individual to keep track of environmental changes. We see this strategy evolve when there are from 1 to 10 changes per generation. Figure 5 shows the learning strategies of evolved individuals. The situation for a stability period of 1 represents a turning point, where individuals go from being plastic their whole life to having a sensitive period of learning early in life. For changes occurring less frequently than once per generation, individuals adopt the strategy of having a short period of plasticity early in life and staying non-plastic otherwise. This gives the benefit of being able to adjust to the current environment, while not incurring the cost of lifelong plasticity.

The results discussed so far are presented in a more compact form in Figure 6. This figure shows how the evolved learning efforts through life vary with the rate of environmental change. The same results were seen in Figure 4, but then without the “age”-dimension. Seeing how learn-

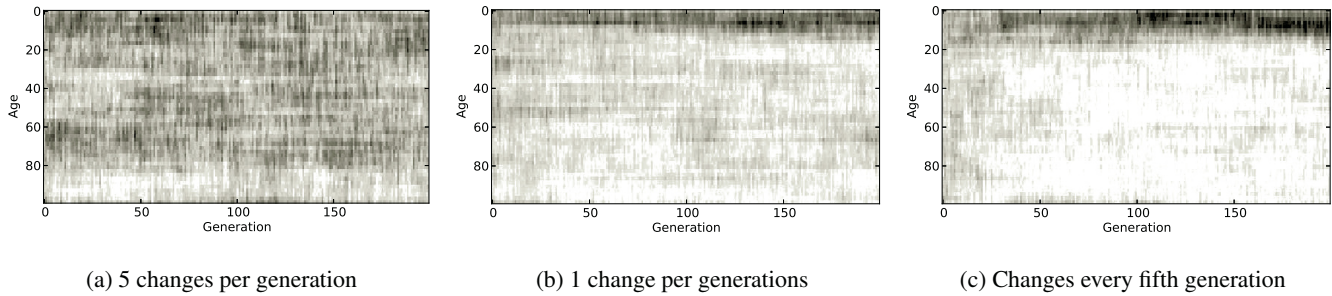


Figure 5: Average learning rate (brightness - darker means higher learning rate) through their 100-timestep lifetimes (y-axis) for the winner individuals of each generation of evolution (x-axis). – Averages over 20 runs.

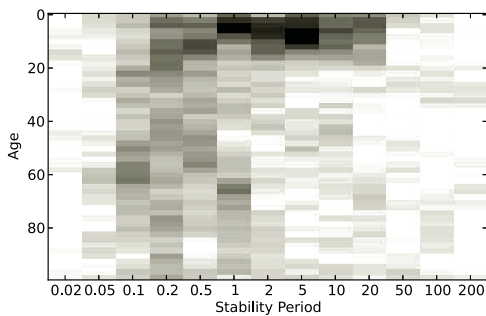


Figure 6: The learning effort made by individuals evolved under different rates of environmental change. Dark rectangles indicate a high learning rate - so a column with a few dark and many bright rectangles indicates that this individual has evolved a sensitive period of learning. Change rates are given as number of generations between each change. – Averages over 20 runs.

ing efforts vary with age and change rates, confirms the four strategies we identified earlier. For too low and too high change rates, little effort is made to learn, as seen by the bright values at the left and right edge of the plot. The relatively uniform gray columns (stability periods from 0.1 to 0.5) indicates individuals learning throughout life. Finally, the columns with stability period from 1 to 20 shows individuals with evolved sensitive periods.

**Static or Dynamic Plasticity**

Comparing “dynamic” (plasticity varying throughout life) and “static” (fixed plasticity throughout life) individuals helps clarify the role of sensitive periods in plasticity when balancing the costs and benefits of learning. It reveals some of the aspects we miss by making the simplifying assumption of a lifelong, constant learning rate, as has been common in studies of the evolutionary regulation of learning efforts.

As seen in Figure 4, the most striking difference between the two types of individuals is that dynamic learners can adjust their learning rate much more smoothly to the different rates of environmental change. Static learners, on the other hand, operate in an “on/off” mode. Too rapid or too slow changes lead to individuals evolved to avoid learning. Intermediate rates of change lead to individuals that invest very much in learning. The inability of static learners to tune their learning efforts through life also means that they will have to shut off their learning ability earlier as learning becomes less beneficial. Dynamic learners, on the other hand, will retain some learning ability also under conditions that are relatively poorly suited for learning. This can be seen at the extreme ends of the spectrum of change rates, where the learning efforts of dynamic learners fall quite slowly towards zero.

Another interesting way to compare static and dynamic individuals is to look at their respective *fitness values* before and after environmental changes. This comparison indicates how well individuals balance their learning efforts to reap the benefits but avoid the costs as much as possible. Figure 7a shows fitness values for the best individuals in the *generation before* environmental change. For instance, for individuals evolved with a stability period of 50, this means the last 49 generations of their evolution happened under stable environmental conditions. We see that dynamic plasticity regulation gives a significant fitness increase when change rates are in the region from every second to every tenth generation. This is also the region where sensitive periods are most important. For higher change rates, a lifelong plasticity is most beneficial, as we saw in Figure 5. For lower change rates, no learning is most beneficial, because individuals will have *genetically assimilated* their learned traits in this generation immediately before the next change, allowing them to reduce their cost of learning.

In the generation *after* environmental change, the situation is different, as seen in Figure 7b. Individuals with a dynamically regulated learning rate now have a benefit over

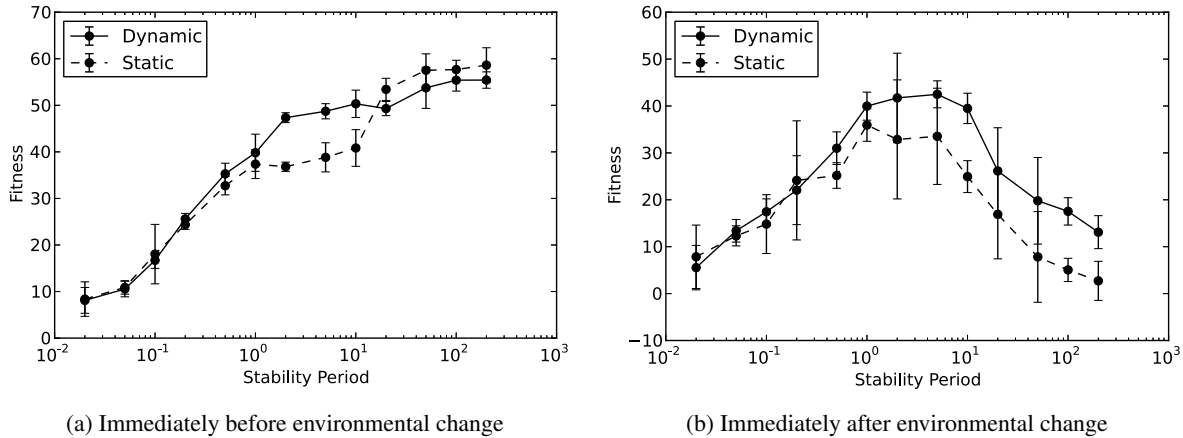


Figure 7: Graphs showing the difference in fitness values between the best evolved individuals with dynamically and statically regulated plasticities throughout life. Shown immediately before and after an environmental change. – Averages over 20 runs. Error bars show a 95% confidence interval of the means.

the static ones also when the environment has been stable for a long time. The reason is that static individuals rely more and more on genetic assimilation the longer the period of stability – meaning they are unable to respond well to the environmental change. Also notice the increase in variability between the plots, as seen in the error bars. This is a natural consequence of the environmental change: the best individual before the change will have converged to the same behavior in most runs – but their behavior in the new environment may not be the same.

The same effect can be seen by studying the fitness curves of individuals. In this case, we look at their fitness values *without* an imposed cost of plasticity. The fitness values we study here are proportional to the amount of foods the agent eats subtracted by the amount of poisons it eats – an indication of exactly how well it performs the association task. Figure 8 shows fitness values plotted over 200 generations of evolution. The sudden drops in fitness value are due to environmental changes, and the following climbs show re-adaptation of the individuals. Static individuals show much larger drops in fitness values as the environment changes, indicating that they have relied heavily on genetic assimilation of learned traits and eliminated much of their learning capacity. This is seen also in dynamic individuals, but to a much smaller degree - they are able to retain their learning ability for more generations, because it is not as costly.

For changes with a frequency above once per generation, the same pattern does not emerge. With such a high frequency of change, keeping a lifelong plasticity is beneficial, and static individuals often end up with a higher fitness as such a strategy is easier to evolve for them than for dynamic ones.

### Conclusion

By studying the evolution of learning strategies across a wide range of environmental change rates, we have observed four main strategies: For both too frequent and too infrequent changes, no learning evolves, as the cost of learning outweighs its benefits. For environmental change rates in the range suited for the evolution of learning, the two main strategies are 1) Lifelong plasticity, which is preferred when change rates are high, and 2) Sensitive periods of plasticity, which is preferred for relatively low change rates.

We have also seen that the ability to regulate plasticity through the lifetime of individuals has two important features that separate these individuals from those with a static learning rate: 1) Dynamic individuals show a less complete genetic assimilation when environmental changes are infrequent and 2) Dynamic individuals can gain the same benefit from learning while paying a lower cost when environmental changes have an intermediate frequency, by employing sensitive periods of learning.

These results illustrate that genetic assimilation and sensitive periods in learning have similar roles: reducing the cost of plasticity, while retaining its benefits. Because of their similar roles, they affect each other – for instance, sensitive periods reduce the need for genetic assimilation. Therefore, studying them together in the same model, is necessary to get a full understanding of the roles of these two phenomena.

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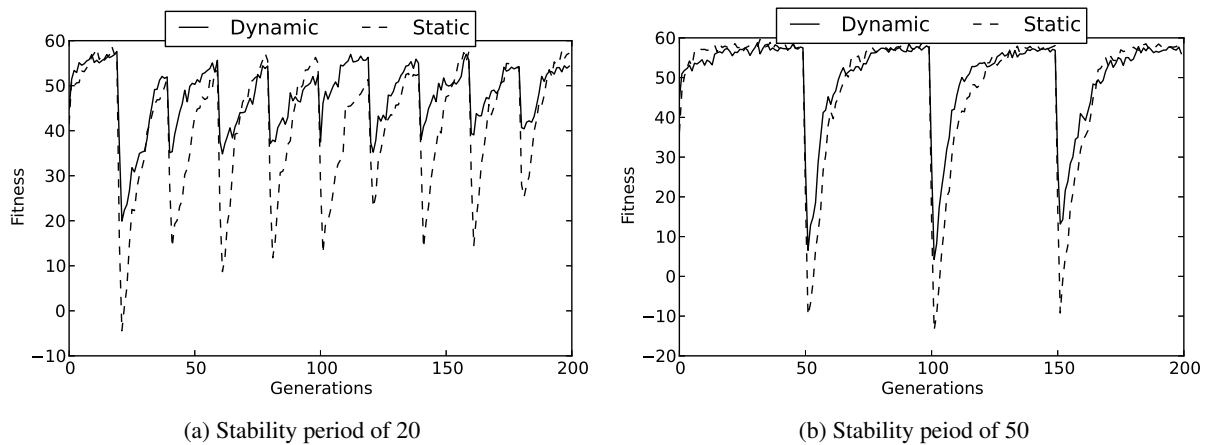


Figure 8: Fitness values plotted against generations of evolution for static and dynamic individuals. The shown fitness values are without an explicit cost to plasticity - meaning it indicates the actual performance of individuals on the association learning task. The difference between static and dynamic individuals we observe here was similar for all stability periods associated with the evolution of sensitive periods. – Averages over 20 runs.

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