# Discontinuity in evolution: how different levels of organization imply pre-adaptation

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## 1. INTRODUCTION

Although sequences of nucleotide bases in DNA and amino acids in proteins appear to mutate at approximately constant rates, evolution seems to have been anything but steady. In fact, most dramatic changes in evolution occurred rather abruptly (Eldredge and Gould; 1972; Gould and Eldredge, 1993).

Gould (1991) claims that in order to explain such radical changes one should abandon the adaptationist or "ultra-Darwinist" paradigm. The idea that all change is gradual and continuous is in fact a consequence of interpreting phenotypic changes as mostly adaptations. Gould (see also Gould and Vrba, 1982) proposed to classify phenotypic traits in three different categories: adaptations (traits that have a well-defined function), preadaptations (traits built for one function and then adapted to another), and exaptations (traits not built as adaptations at all but later adapted for some function) and he claims that the last two categories must greatly exceed adaptations in number and importance.

Of course, no biologist has ever advocated a complete equivalence between retained changes and adaptations. Adaptive changes in some trait may entail correlated but not necessarily functional alterations of other traits (e.g. the human chin appears to be a by-product of functional changes in other parts of the human face during hominization). The architecture of genetic and embryological systems defines channels of possible change. Selection may be required to push an organism down a channel but the channel itself, though not an adaptation, acts as a major determinant of the direction taken by evolution. The real questions then are the relative importance of adaptive versus non-adaptive changes and a better understanding of the mechanisms underlying both types of change.

Using a computational model we will try to show that non-adaptive evolutionary changes may largely outnumber adaptive ones. This fact appears mainly due to the hierarchical organization of the simulated organisms. We will also show how some of these non-adaptive (neutral) changes may subsequently become the basis for further changes which do prove adaptive and therefore how preadaptation phenomena may arise producing sudden evolutionary changes in the behavior of organisms.

## 2. DESCRIBING ORGANISMS AT MULTIPLE LEVELS

It is obvious that biological systems can and should be described at various hierarchical levels. For example, an organism can be described at the genetic level, at the neural level, at the behavioral level, and at the level of fitness. A description of the organism at the genetic level is a description of the genotype of the organism, that is, of the genetic material that the organism has inherited from its parent(s) and that directs the construction of the phenotypic organism. A description at the neural level is a description of the nervous system of the organism, which is just one aspect of the phenotypic organism. A description at the behavioral level is a description of the behavior which is exhibited by the organism, given its nervous system, in a

particular environment. Finally, a description at the level of fitness is a measurement of the fitness obtained by the organism given its behavior in that environment.

A critical role in our understanding of organisms is played by how these different levels interact and how changes at one level are related to changes at other levels. However, a multi-level approach to the study of real organisms is very difficult to realize given the different conceptual and methodological tools traditionally used by genetists, neuroscientists, behavioral scientists, and evolutionary biologists. As a consequence, organisms tend to be studied separately at these different levels and by scientists who belong to different disciplines.

Computational models of evolution (Holland, 1975; Langton, 1992) allow us to analyze the same system, for example a simulated organism, at various levels simultaneously and to investigate how changes at one level are related to changes at other levels. As we will show in the next section one can simulate within the same experiment the genotype, the nervous system, the behavior, and the environment of a particular artificial organism and one can examine what evolutionary changes at one of these different levels accompany changes at other levels.

## 3. THE MODEL

We developed artificial organisms (O) that perform a simple navigation task in a simulated environment (Treves, Miglino, and Parisi, 1992). To each O corresponds a string of genetic material or genotype which specifies a set of developmental instructions. These instructions generate a certain number of neurons and control the growth and branching process of the axons of the neurons (Nolfi and Parisi, 1992). The result of this growing process is a neural network that represents the nervous system of the corresponding O. The inherited architecture and connection weights of such a network determine the way in which O responds to environmental stimuli (the behavior of the network). Such behavior, through interaction with the environment to which O is exposed, determines O's fitness, i.e. O's reproductive chances.

Each O lives in a simulated environment which is a two-dimensional square divided up into cells (see Figure 1). O has a facing direction and a rudimentary sensory system that allows it to receive as input the angle (relative to where O is currently facing) and the distance of two landmarks situated in the environment. O is also equipped with a simple motor system that provides it with the possibility, at each time step, to move a cell forward, to turn left or right, or to

remain still. O should reach the central area of the world (the food zone) and remain there in order to increase its fitness.
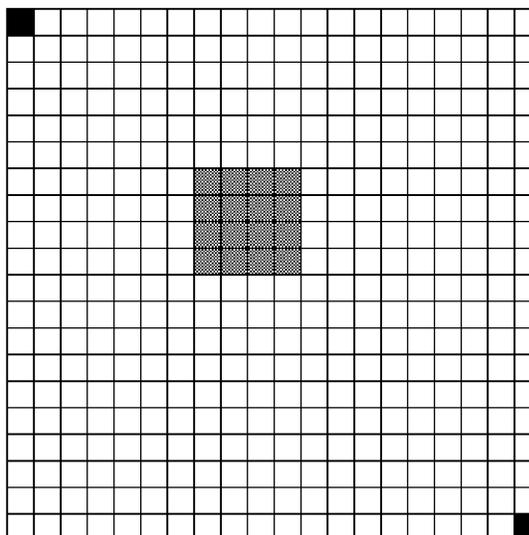


Figure 1: Environment. The two black cells represent the two landmarks and the shaded square in the center of the environment represents the target area that must be reached by Os in order to increase their fitness. The environment is a bidimensional space of infinite size (i.e. Os can go also outside the 20x20 central area displayed in the Figure).



Figure 2: O's genotype.

O's genotype is represented as a string of 0 and 1 (see Figure 2). The string has a fixed length (1600 bits) and is divided up into blocks, each block corresponding to a single neuron that may or may not get expressed during the development process. Each block contains instructions that determine the developmental properties of the corresponding neuron (see Figure 3).

There are three different types of neurons: sensory neurons, internal neurons, and motor neurons. Genotypes are 40 blocks in length; i.e. the nervous system of each O can

include a maximum number of 40 neurons. The first 8 blocks correspond to sensory neurons, the last 5 blocks to motor neurons, and the 27 intermediate blocks to internal neurons.
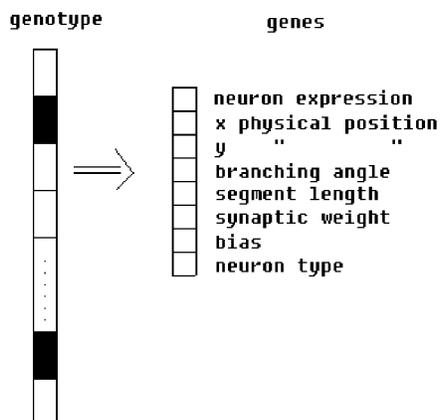


Figure 3: Developmental instructions specified in O's genotype. Inactive blocks which correspond to unexpressed neurons are represented as black cells while active blocks are represented as empty cells.

Each block specifies the following instructions ("genes"):

(a) The "neuron expression gene" determines if the other instructions contained in the block will be executed or not, i.e. if the corresponding neuron will be present or not in O's nervous system.

(b) The two "physical position genes" specify the Cartesian coordinates of the neuron in the bidimensional nervous system of the corresponding O.

(c) The "branching angle gene" and the "segment length gene" determine the angle of branching of the neuron's axon and the length of the branching segments.

(d) The "synaptic weight gene" determines the synaptic weights of all the connections that will be established by the neuron. (All connections departing from the same neuron have the same weight.)

(e) The "bias gene" determines the activation bias of the neuron itself.

(f) The "neuron type gene" determines if a sensory neuron codifies the angle (relative to O's direction) or the distance of one of the two landmarks and if a motor neuron codifies the first or the second motor neuron (i.e. the first or the

second bit of the binary representation of the four possible motor actions that can be performed by O). This implies that each O can have four different types of sensory neurons and two differnt type of motor neurons. More neurons of the same type may be present. When output neurons of the same type are present, the actual motor response is computed by averaging the activation levels of the corresponding neurons.
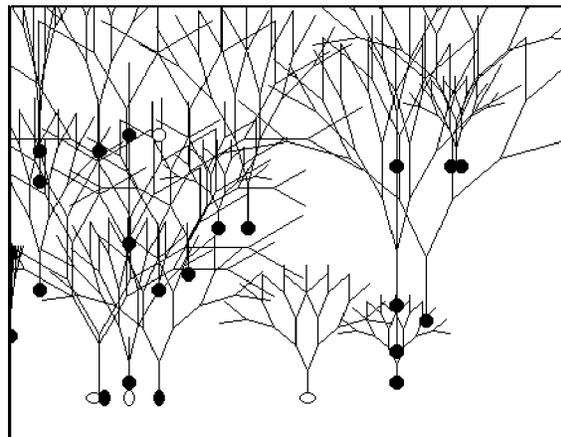


Figure 4: Developmental growth of neurons and neural axons resulting from an evolved genetic string.

The result of the execution of the genotypic instructions of an evolved O is shown in Figure 4. Neurons of different types and in different parts of the O's nervous system are created and connections between neurons are established through the growing process of neurons' axons. (When the growing axonal branch of a particular neuron reaches another neuron a connection between the two neurons is established). The resulting neural network is shown in Figure 5. Figure 6 shows the functional part of the same network, i.e. the same network after isolated (nonfunctional) neurons and groups of interconnected neurons have been removed.
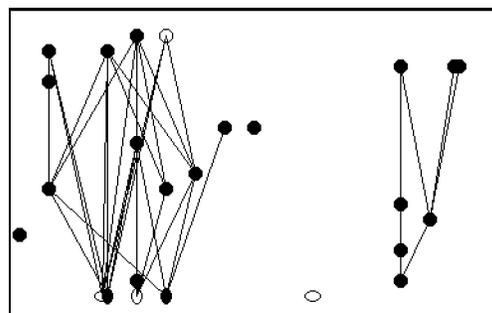


Figure 5: Connections established during the growing process shown in Figure 4. The bottom layer contains

sensory neurons, the upper layer motor neurons, and the remaining layers internal neurons.
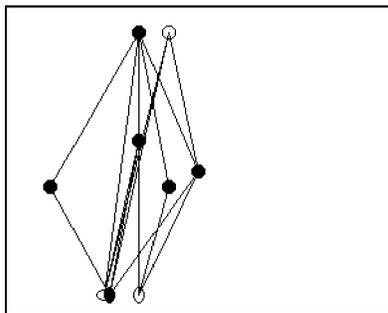


Figure 6: Resulting functional network after elimination of isolated (nonfunctional) neurons and groups of interconnected neurons.

Through interaction with the environment, the functional network determines O's behavior. At each time step, O receives some activation value in the sensory neurons, depending on its position in the environment and its direction. Such an input determines in turn, through a spreading activation process, the activation value of the internal and output neurons. These last neurons determine O's motor reaction to the current input stimulus, i.e. O's behavior. Internal and output neurons have a Heavyside activation function.

It is useful to distinguish between the potential behavior and the actual behavior of an O. The way in which an O reacts to all possible input stimuli is O's potential behavior while the way in which the O reacts to the stimuli it actually experiences during its life is O's actual behavior. In ecological networks (cf. Parisi, Cecconi, and Nolfi, 1990) the stimuli an O experiences during its life are partially determined by O itself through its motor behavior. (Figure 7 shows how a typical O actually visits most of the world's cells in some of the four possible directions only). As a consequence, only the way in which an O reacts to a given (self-selected) subset of all potential input stimuli has a role in determining O's fitness (Nolfi and Parisi, 1993).

While the actual behavior of an O is determined by observing how O spontaneously behaves in its environment, its potential behavior can be determined by testing O in artificial conditions, i.e. by exposing it to all possible stimuli (Figure 8).
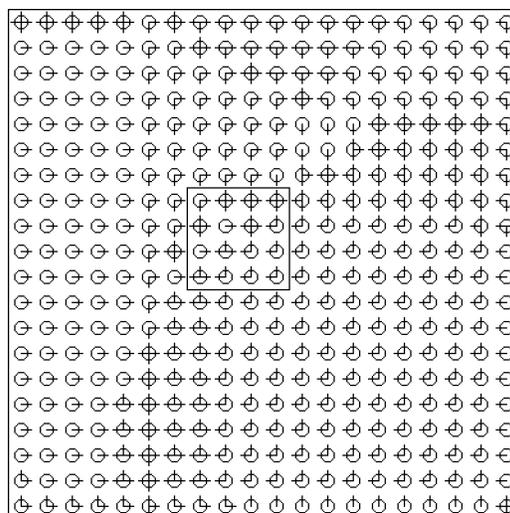


Figure 7. Actual behavior of an evolved O. The picture shows all the directions with which an evolved O happens to step on each world cell. The trace is the result of O's natural movements after being placed in all the peripheral cells of the world. As can be seen, very few cells are visited in all the four possible directions.
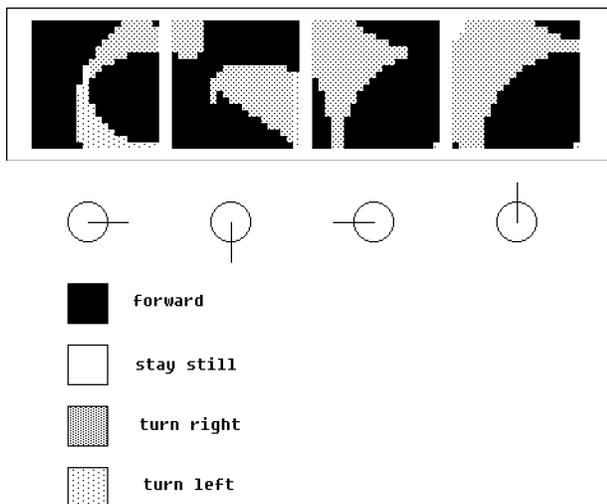


Figure 8. Potential behavior of an evolved O. Each picture shows the reactions of this O in all the world cells for each of the four possible directions.

It is important to notice that at each level (genotype, nervous system, behavior) a functional component can be distinguished from a nonfunctional component. At the genetic level, only the blocks that are actually expressed (i.e. that have their expression gene set to 1) are functional in determining the nervous system (see Figure 3). Similarly, at the nervous system level, only the neurons that are

interconnected and contribute to determining the motor responses to environmental stimuli are functional in determining O's behavior (see Figure 5 and 6). And finally, only the motor responses that an O produces to stimuli it actually experiences during its lifetime are functional in determining O's fitness (see Figure 7 and 8).

The overall picture (see Figure 9) is a system organized in four hierarchical levels (genotype, nervous system, behavior, and fitness) in which the functional component of each level determines both the functional and the nonfunctional component of the next higher level. The genotype determines the nervous system that in turn determines the behavior that in turn determines the fitness. This implies that individuals that have the same fitness can differ at some level of their organization for two reasons; (a) they can have two different structures in the functional component at one level that result in the same structure at the next higher level, or (b) they can have different structures in the nonfunctional part of one level because, by definition, these differences do not affect the higher levels.
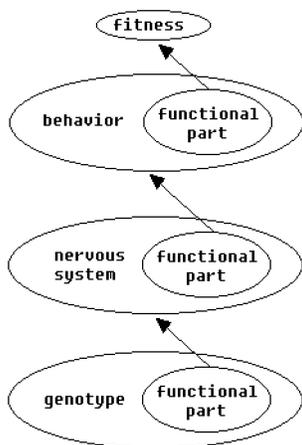


Figure 9. Hierarchical organization of an O. The functional component of the genotype is the subpart of the genotype that is expressed and that determines the nervous system. The functional component of the nervous system is the subpart of the developed neural structure that contributes to determining O's motor reactions. The functional component of the behavior represents the motor responses to the stimuli that O actually experiences during its lifetime.

## 4. RESULTS OF SIMULATIONS

We have run a set of simulations using the model described above. Each simulation begins with 100 randomly generated different genotypes resulting in 100 Os with different architectural and behavioral characteristics. This is generation 0 (G0). G0 networks are allowed to "live" for a total of 2400 actions divided into 80 epochs. Each epoch consists of 30 actions starting from a randomly chosen cell located at the periphery of the environment. (Os are free to move out of the 20x20 environment even if they can increase their fitness only by remaining in the environment). Os are placed in individual copies in the environment (i.e. they live in isolation) and they do not change during the course of their life. In other words, the development of the nervous system is supposed to be instantaneous. (For a different approach see Nolfi and Parisi, 1992). Fitness is calculated by counting +10 points for each cycle spent in the target area, +1 point for each movement forward, and -1 point for each cycle spent outside the 20x20 cell area.

At the end of their lives (2400 actions) Os are allowed to reproduce. However, only the 20 individuals which have accumulated the most fitness are allowed to reproduce by generating 5 copies of their genotype. These 20x5=100 new Os constitute the next generation (G1). 20 random mutations are introduced in the copying process (crossover is not applied). For each mutation a random bit of the genetic string is chosen and a new value, randomly generated, is substituted for the original value. Because there is a 50% of possibility of extracting the same value of the original bit the actual number of changes in the genotype is a number stochastically distributed around 10.

After the Os of G1 are created they are allowed to live for 2400 cycles. The behavior of these Os will differ slightly from that of the preceding generation (G0) as a result of two factors. First, the 100 individuals of G1 are the offspring of a subset of the individuals of G0. Secondly, the offspring themselves differ slightly from their parents because of the mutations. These differences lead to small differences in the mean fitness of G1 with respect to that of G0. At the end of their lives the 20 best individuals of G1 are allowed to reproduce to form G2. This process continues for 1400 generations.

The evolved Os are able to reach the target area efficiently. The individual O represented in Figures 5, 6, 7, and 8 is one of the best of the last generation of Simulation 1. It succeeds in reaching the target area starting from almost any peripheral cell.

If we take the best individual of the last generation we can reconstruct the entire lineage of the individual until the single originator of the lineage in the first generation is reached. We will call this lineage the successful lineage. If we look at how fitness changes in the successful lineage across generations (see Figure 10) and we test all the

individuals of the lineage in the same environmental conditions (i.e. if we place all the individuals in all the peripheral cells of the environment once) we obtain an interesting pattern: periods of stasis, which can last hundreds of generations, are followed by rapid increases in fitness.
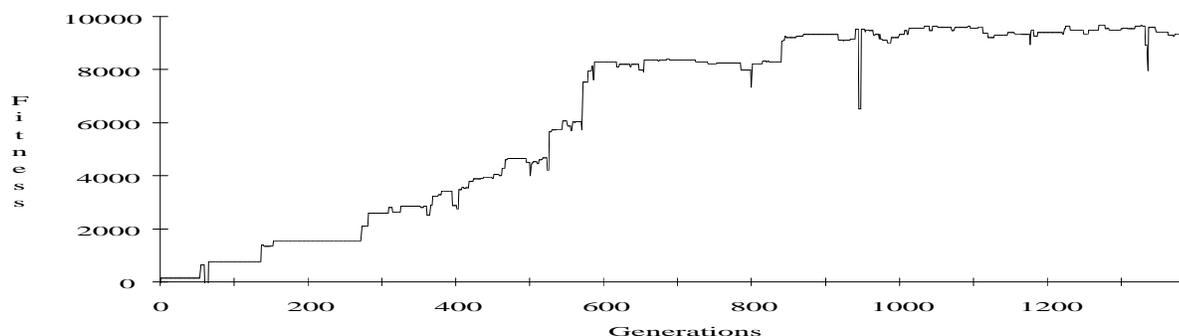


Figure 10. Fitness of the successful lineage of Simulation 1 tested in the same environmental conditions. Os are placed once in each of the 76 peripheral cells of the 20x20 central area of the environment facing the target area. The total number of startings was 80 because Os were placed in each corner cells with two different orientations.

We then compared the two members of each parent/offspring pair of the successful lineage at the different levels of organization of these organisms. What we found is that the number of changes that are retained by Os of successive generations decreases significantly when one goes up from lower to higher levels of organization. Figure 11 shows the proportion of cases in which an offspring differs from its parents because mutations have changed (1) its genotype, (2) its functional genotype, (3) its overall neural network, (4) its functional neural network, (5) its potential behavior (i.e. way of responding to all possible environmental stimuli), (6) its actual behavior, (7) its fitness. Only less than 1% of successful Os were not affected by mutations in the functional part of the genotype. On the other hand, almost 50% of the same Os did not differ at the functional nervous system level; 80% did not differ at the potential behavior level, and almost 90% did not differ at the fitness level with respect to their parents. This implies that most of the retained mutations do not affect the fitness level and, as a consequence, are not adaptive.

Mutations that do not affect the fitness level do not have any role from the perspective of the individual's reproductive chances. However, these mutations produce a great number of changes at the lower levels and this can have long term consequences for the evolutionary process. In order to understand the role of mutations that do not affect the fitness level one can examine the changes which occur in Os at different levels of their organization during an evolutionary period in which the fitness level is stable. If fitness does not increase generation after generation, no adaptive mutations arise and therefore changes in Os' organization reflect only the effect of mutations that are not adaptive.
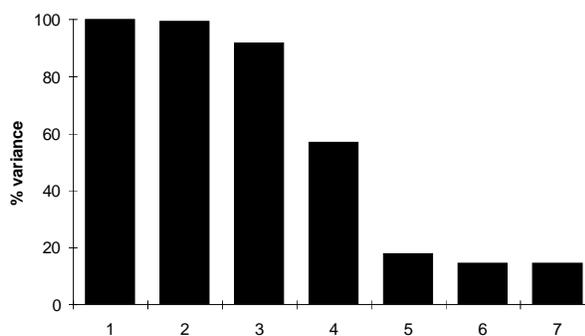


Figure 11. Percentage of variance in parent/offspring pairs at different levels of organization; (1) genotype, (2) functional genotype, (3) overall nervous system, (4) functional nervous system, (5) potential behavior, (6) actual behavior, (7) fitness. Each black bar represents the average result of 10 different simulations.

In Simulation 1 we have a quite long stretch of evolutionary of time (from generation 154 to generation 272) in which the fitness level of the successful lineage does not change at all (cf. Figure 10). During this phase of 118 generations which is stable from the point of view of
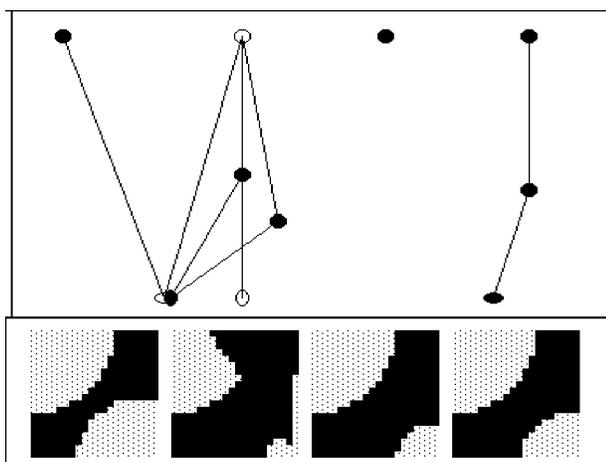
fitness, 54 of the 118 Os differ at the functional neural level and 17 Os differ at the level of their potential behavior (as measured in artificial conditions; cf. above) with respect to their parents. Figure 12 shows the functional neural network and the potential behavior of eight of these Os that most significantly differ from their parents. (These Os represent Generations 154, 168, 188, 190, 225, 234, 246, and 257, respectively.) The first O (representing Generation 273) in which an adaptive mutation occurred and that, as a consequence, obtained a higher fitness value than its 118 predecessors, is also shown.

If we examine the behavior of these eight Os (leaving aside the O of Generation 273) we observe some changes in how they respond to the input in some areas of the environment (more precisely, in the NW area) but these changes in behavior do not lead to any change in fitness. These Os oscillate between two alternative solutions (e.g. the behavior of the O representing Generation 154 is different from the behavior of the O representing Generation 168 but it is almost identical to the behavior of the O representing Generation 257) but these solutions are equivalent from the point of fitness.
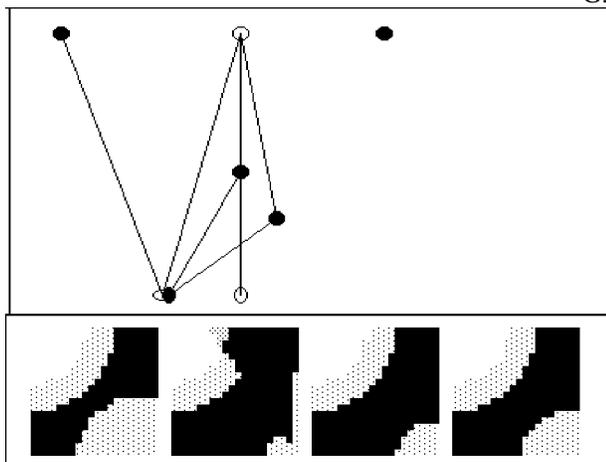
On the contrary, at the level of the functional nervous system we see an interesting process going on. If we look at the neural architectures of the two Os representing Generation 154 and 257, respectively, we see that these architectures are very different despite the fact that they generate the same behavior. However, if we look at the architecture of the O of generation 273, i.e. the first O that received an adaptive mutation, we observe that its architecture is almost identical (except for a single connection) to an architecture already present in the population since Generation 246. This means that the architecture of the O of generation 273, that is, of the first O which was able to produce a more adapted behavior after 118 generations, was pre-selected or pre-adapted at least 27 generations before.

This pre-adapted architecture was not obtained in any purposeful way. It was not selected against other architectures because it did allow some further advantage in adaptive terms. It was selected by chance and then it was retained because it was able to generate a more fit O through a single or a few mutations. Furthermore, it should be noted that it might have been impossible to generate more fit Os given the structure of the preceding Os. The fact that more fit Os did not arise for a long period of more than 100 generations implies that adaptive mutations in these Os were very improbable. Therefore, the nonadaptive mutations that affected the nervous system level were crucial in determining the successive adaptive ones.
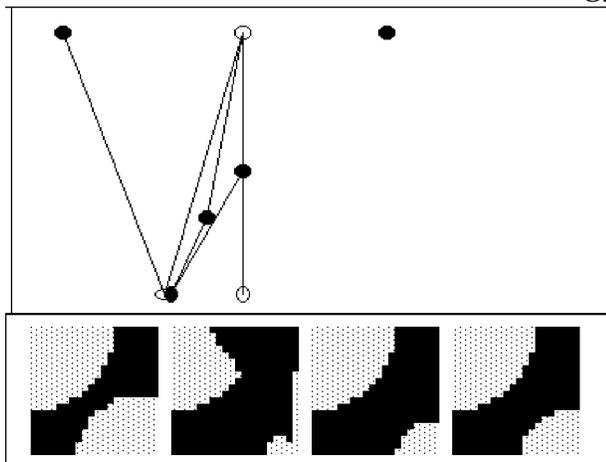
Without such nonadaptive (neutral) changes it might have been impossible for the evolutionary process to generate more adaptive Os.



G.154



G.168

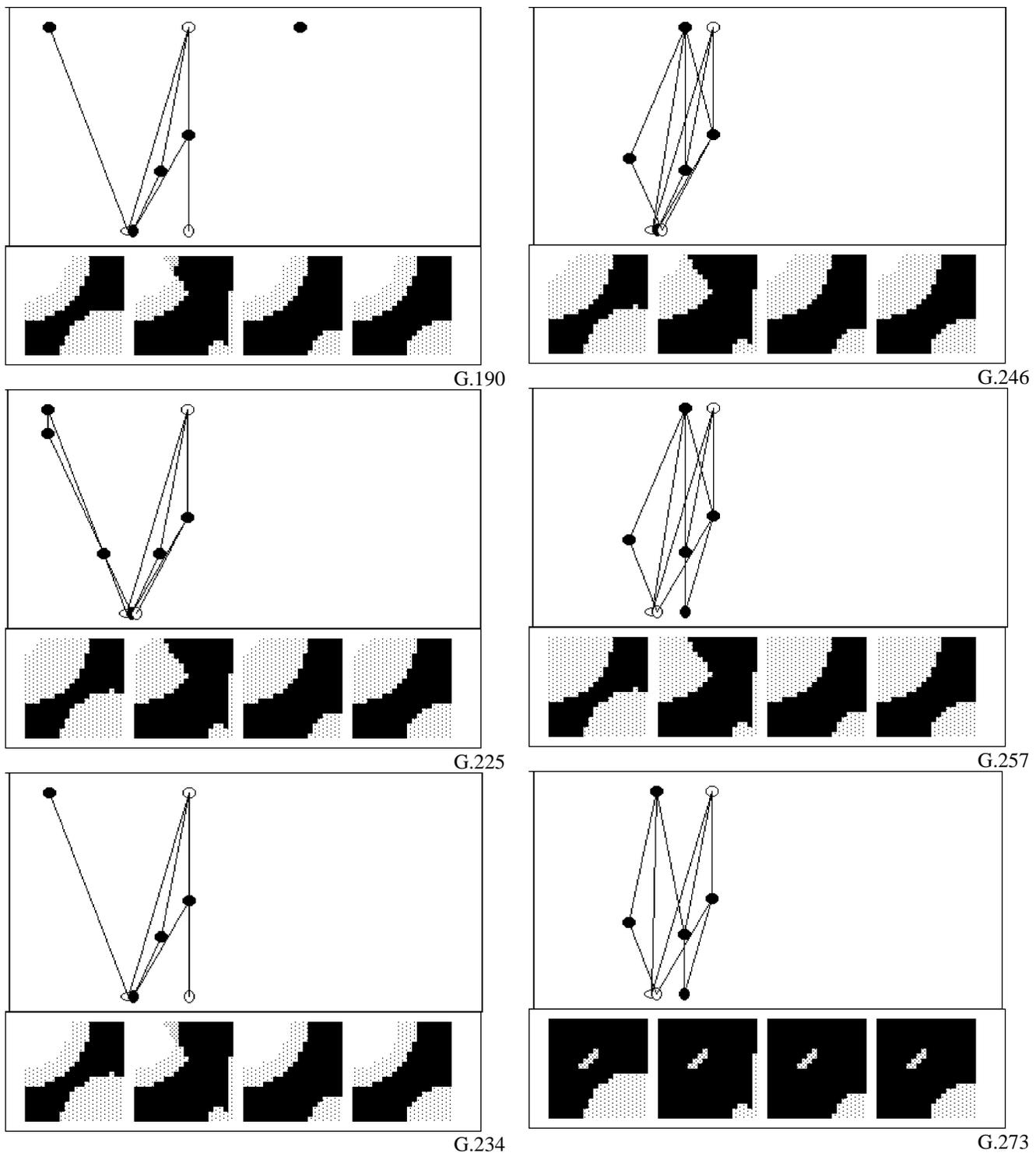

G.188

G.190

G.246

G.225

G.257

G.234

G.273

Figure 12. Functional neural architecture and potential behavior (see Figure 7) of 8 Os of the successful lineage in a phase of the evolutionary process in which fitness is stable. The ninth O is the first O in which an adaptive mutation that causes a sudden increase in fitness occurs after such a stable period. The number at the bottom of each picture represents the generation of the corresponding O.

## DISCUSSION

Biological systems can be described at various hierarchical levels. For example, an organism can be described at the genetic level, at the neural level, at the behavioral level, and at the fitness level. Each level determines the structure of the organism at the successive level but not all changes that occur at a certain level cause corresponding changes at higher levels. Since only part of the structure at each level (the functional part) is responsible for determining the structure at successive levels, only changes that affect these functional parts can cause changes at successive levels.

If we examine the lineage of the best individual of the last generation in an evolutionary simulation with growing neural networks and we compare the two Os in each parent/offspring pair we see that different levels change at different rate. While at the genetic level almost all offspring differ from their parents, the probability that the two members of a pair differ at higher levels gradually decreases as one ascends levels. This implies that most of the mutations do not affect the fitness level and as a consequence should be considered nonadaptive or neutral. However, these mutations may produce changes at other levels and this can have long term consequences for the evolutionary process.

Since most mutations do not affect fitness and, this notwithstanding, may be maintained in the population, this implies that evolution is to a significant extent neutral. In other words, changes occur in the population and are retained in successive generations which are not adaptive in the sense that they do not increase fitness. Insofar as these changes determine the future course of evolution, these changes are selectively neutral.

Some neutral changes, as we have shown in our simulations, may subsequently become the basis for further changes which do prove adaptive. Hence, preadaptation phenomena may arise. The population may turn out to be pre-adapted to these further adaptive changes. These preadaptation phenomena may explain the discontinuous and abrupt changes observed in our simulations. Neutral mutations can accumulate in the nonfunctional components of a particular level without affecting in any way the next higher level. However, due to some new mutation a portion of the changed nonfunctional component of the lower level can become suddenly functional and, as a consequence, visible at the next higher level.

We have shown that higher levels of organization have a high degree of stability because they are mostly immune to genetic mutations. This fact can result in a drawback in rapidly changing environments. Phenotypic plasticity having the chance to directly affect higher levels of organization (for example the nervous system through learning) can be seen as a way to overcome this problem. In order to obtain phenotypic plasticity we plan to modify the model described in this paper allowing the genotype to determine the development of the nervous system during all individual lifetime and making the developmental process sensitive to the external environment. We believe that this is a very promising direction that simulative models should pursue. A direction that for example may shed some light on fundamental questions like: how and in which conditions phenotypic plasticity has evolved?

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