Heterochrony and Adaptation in Developing Neural Networks

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Abstract

This paper discusses the simulation results of a model of biological development for neural networks based on a regulatory genome. The model's results are analyzed using the framework of Heterochrony theory (McKinney and McNamara, 1991). The network development is controlled by genes that produce elements regulating the activation, inhibition, and delay of neurogenetic events. The genome can also regulate the gene expression mechanisms. An ecological task of foraging behavior is used to test the model with an evolving population of artificial organisms. Organisms evolve an optimal foraging behavior and the ability to adapt to changing environments. The adaptive strategy consists in changes of network architecture that are determined by the regulatory rearrangment of neurogenetic events. Results show how heterochronic changes play an adaptive role in the evolution of neural networks.

1 HETEROCHRONY AND DEVELOPMENT IN NEURAL NETWORKS

In living organisms the existence of a variable and plastic ontogenesis is strictly related to the evolution of a regulatory genome, i.e. a genotype whose main role is to control the functioning of simple ontogenetic events. Even though some genes directly codify for structural molecules, most of the genes' product consists of regulatory elements, such as enzymes. These regulatory genes act as ON-OFF switches of the complex chain of biochemical events that constitute the three main phenomena of cellular development: mitoses, cell differentiation, and migration. A regulatory ontogenetic development consists of a variety of interactions between the growing organism and its environment. The interaction acts in, and between, different levels, from the molecular level (genes, proteins, enzymes) to the cellular level (nucleus, cytoplasm), to the inter-cell level (cell assemblies, organs and tissues) and to the organism level (behavior). In such a regulatory development, the timing of the events, i.e. their temporal activation/inhibition, and their rate, i.e. the frequency of occurrence of the phenomena, both have a strong impact. The temporal co-occurrence of two or more events can prove essential for allowing the activation of a biological phenomenon. Even the spatial relation between sub-structures of the developing organism is a key factor. The spatial interaction between cells can induce the phenomena of cell differentiation or cell migration. These classes of interactions, especially the temporal relations occurring during the organism's development, constitute the phenomenon known as heterochronic change. Heterochrony (McKinney and McNamara, 1991) is the study of the effect of changes in timing and rate of the ontogenetic development in an evolutionary context. In particular, heterochonic classifications are based on the comparison of ontogenies that differ for the onset of growth, the offset of growth and the rate of growth of an organ, or a trait or other biological instances. These three kinds of change correspond respectively to the following couples of heterochonic phenomena: Predisplacement and Postdisplacement for an anticipated and postponed growth onset, Hypermorphosis and Progenesis for a late and early offset, and Acceleration and Neoteny for a faster and slower rate of growth (see also Gould, 1977).

Ontogenesis is complex and therefore is hard to be studied only with classical biological sciences. Therefore a complementary modeling method, the synthetic approach of Artificial Life, has been proposed as a possible way for understanding such systems (Langton 1992). Moreover, the advantages of modeling neural and behavioral development through neural networks has been repeatedly stressed (Elman et al., 1996). The modeling of development using neural networks has received a strong impulse in recent years. In the majority of today's development models a single developmental phenomenon is simulated, usually regarding the network connectivity. Some works study the effects of the pruning/adding of connections and units in the neural network (e.g. Ash's 1989 work on node creation for backpropagation networks). In other models the indirect mapping of the network connectivity into a genotype string is studied. For example Kitano (1990) uses rewriting rules to encode the weight connection matrix. Nolfi and Parisi (1995) use a more biologically-based representation of network connectivity. The simulation of the phenomenon of cell division has been studied in different works that use the recursive mapping of Lindenmayer grammars. For example, in Belew (1993) and Gruau (1994) the final topology of the network is determined by the units' duplications which are controlled by the rewriting rules encoded in the genotype.

This kind of models of development has the limit of not dealing with an important aspect of the developing systems, namely the high interaction among the different developmental phenomena. In growing neural systems, the cells interact with each other, so that one cell can induce migration or death in the neighboring cells. Moreover, as we have said, the effect of the regulatory genes in controlling the complex events of cellular development has to be considered.

A different modeling approach is the simultaneous simulation of many neurodevelopmental phenomena. One of such models is the work of Dellaert and Beer (1994) on the co-evolution of body and brain in artificial organisms. In their work an organism is developed after many cycles of cell division, differentiation and axonal growth. The design of the developmental events is directly inspired to the biology of development, albeit in a very simplified way. This model shows that the simulation of a complex biologically-inspired development is possible and can be successful. However, the authors point out that adding complexity is more difficult to deal with in this kind of model. In fact, they use hand-written genetic instructions to control the organism's development.

A model of development for neural networks that includes different biological phenomena such as cell duplication and axonal growth have been tested by Cangelosi, Parisi & Nolfi (1994). Here the control of the develoment events is not directly based on biologically-inspired mechanisms, but uses a rewriting rules grammar. Another model of biological development for neural networks had been proposed by Kitano (1995). He tested a new computational model of neurogenesis based on cellular metabolitic processes. The model proved capable of evolving large neural networks and of exhibiting the phenomenon of cell differentiation. Eggenberger (1997) also developed a system for evolving 3D organisms using mechanisms of gene expression. But these two models of organisms' morphology have not been tested with behavior-based neural network simulations.

The model that will be presented here aims at the simultaneous simulation of many biologically-inspired phenomena for the development of neural networks in artificial organisms. The goal is to design a model which permits a high level of interaction between different levels of the developing system, and between the genetically-encoded information and the environment in which the network is growing. For this purpose a regulatory genome is used in which most of the genes produce elements whose role is to control the activation, inhibition, and delay of the developmental events. The phenomena occurring during neural network development (cell duplication, differentiation, migration, axonal growth and synaptogenesis) are directly inspired by their real biological functioning (Purves & Lichtheim, 1985). Due mainly to the present limitations of the simulation techniques, a high level of simplification is used, while retaining the essential features of the biological phenomenon. At present, our goal is not to obtain a completely realistic model of biological development, but to simulate an adaptive behavior model of a developing system which allows a high level of interaction among its substructures, in order to study their role in the evolution of developing neural networks.

2 MODEL DESCRIPTION[1]

The core of this model of biological development for neural networks consists in the encoding of the regulatory genotype, and in the neurogenetic mechanisms that will develop the neural networks using the genetic information.

At the beginning of neural development the organism's neural system consists of a single egg cell with its own genome and a set of 23 elements present in the intercellular environment (see Table 1). Some of these elements act as RECEPTORS for extracellular signaling. Others are STRUCTURAL elements for the activation and execution of developmental events. Others are pure REGULATORY elements for the modulation of gene expression, and do not play any direct role in the development. The structural elements can regulate gene expression, while the receptors cannot.

The physical environment in which the egg cell will grow consists of a 2D grid of 7*20 cells. The grid has a polarized orientation in the y dimension. The upper pole corresponds to the organism's muscle tissue side, and the lower pole to the sensory tissue side. The initial intracellular elements are considered to be inherited from the parent organism. Their distribution, i.e. the initial amount of each element, will function as the zygote's pattern formation mechanism. During development, the amount of these elements, together with the other environmental conditions, will determine the activation, inhibition or delay of the developmental events. Moreover, these elements act also as regulators of gene expression.

2.1 DEVELOPMENTAL EVENTS

Five developmental events occur cyclically during the neural network's growth: Cell duplication, Cell differentiation, Cell migration, Axonal growth, and Synaptogenesis. For example, the cell duplication process

[1] Readers who are interested in this model can download the program that is currently available on the World Wide Web at the URL: http://gracco.irmkant.rm.cnr.it/angelo. In this site it is possible to download the source C files and the compiled program with graphics for XWindows. The data files of some of the simulations described in the paper are also available.

consists in the replacement of the mother cell with two new daughter cells. The physical displacement of the new cells, and their differentiation (i.e. the splitting of the mother cell's elements), is determined by the environment available around the mother cell and by the amount of the two elements responsible for mitosis (see Table 1). The choice of these two elements is inspired by the role played by cyclin and the kinase enzyme, which are known to be the two mayor regulatory proteins for mitosis (Marx, 1989).

NAME	EFFECTS
DUP_time	Cell duplication timing
DUP_posi	New cell position
MIG_pote	Migration movement
MIG_pole_R	Sensitivity to migration signal
MIG_subA	Migration signal of type A
MIG_subB	Migration signal of type B
MIG_subA_R	Sensitivity to migration signal A
MIG_subB_R	Sensitivity to migration signal B
DIF_sens_R	Sensitivity to input tissue
DIF_moto_R	Sensitivity to output tissue
AXO_adhA	Adhesion molecule of type B
AXO_adhB	Adhesion molecule of type B
AXO_adhA_R	Sensitivity to adhesion molecules A
AXO_adhB_R	Sensitivity to adhesion molecules B
SYN_trop	Synaptogenesis and weight value
SYN_ach	Excitatory synapses and weight
SYN_gaba	Inhibitory synapses and weight
SYN_ach_R	Receptor for excitatory synapses
SYN_gaba_R	Receptor for inhibitory synapses
REG_A	Gene regulation function
REG_B	Gene regulation function
REG_C	Gene regulation function
REG_D	Gene regulation function

Table 1 - List of cellular elements. For each element is reported its typology and function. The name indicates the developmental events the element takes part in (first three capital letters) and its specific role (the other four letters). Elements with a final R are receptors.

2.2 GENE REGULATION

An additional and basic developmental event is the gene expression mechanism. The genotype structure consists of a binary string which can be divided into 23 segments, or genes. Each gene has an operon structure, that is a regulatory region, and an expression region. The regulatory region is used during gene expression. The element is also constituted by a binary string. The element is structured in a regulatory region and a structural region. The element's regulatory region will match the genes' regulatory string segment. The element whose regulatory region matches completely the binary sequence of the inductor region will be the inductor. The element matching the inhibitory region will be the inhibitor. Depending on the presence of one or both regulatory elements, the gene will be expressed or inhibited. As a result if its expression, some complementary copies of the structural region of the gene will be released into the intracellular environment. The number of copies is proportional to the amount of the inductor element.

2.3 NEUROGENESIS

Given this element and genotype structure, and having defined the way the five developmental events function, the process of the neural network growth can be described as follows. An external clock signals the 10 discrete time steps. During each time step the five developmental events and the gene expression process are executed in sequence. Gene expression is the first mechanism to be executed. It will determine the new distribution of elements in the intracellular and extracellular environment. This change constitutes the major cell differentiation process. All following events will be a function of this differential distribution of elements. Cell division follows the genotype expression, and then cell migration happens. The axonal growth and synaptogenesis are executed in parallel. They start at time step 10.

Each developmental process implies a drop (cost) in the amount of elements involved. A distinction must be made concerning the metabolitic cost of the process. For example, cell division, being a more global mechanism for the cell, has a higher cost, i.e. it causes a larger decrease in the element's amount. Other processes, such as the elongation of single axonal segments, have a lower cost. The criterion for defining the process costs cannot be completely biologically plausible. The parameters have been chosen in such a way to equilibrate the different processes and to facilitate the development of feedforward neural networks.

3 SIMULATION

A genetic algorithm (Holland, 1975; Goldberg, 1989) is used for evolving populations of artificial organisms. An ecological neural network (Econet) framework is implemented (Parisi, Cecconi & Nolfi, 1990). Organisms live in a simple 2D environment. A neural network controls organism's behavior. The genotype of the initial population is randomly initialized, and the initial distribution of elements in the egg cell is assigned at random. The 100 organisms of the population are developed and tested individually in each generation.

After the fitness test, organisms are ordered on the basis of their fitness value. The 20 individuals with the highest fitness are selected and reproduce 5 offspring each. The genetic operator is applied to the new 100 (20*5) organisms and then the cycle of development-evaluation-selection and reproduction is repeated.

In the simulation reported here, the reproduction is agamic and the genetic operator is the single bit mutation. An average rate of mutation of 0.4 % is used (range between 0 and 0.8%). The reason for this low mutation rate is the high sensitivity of a regulatory genome to mutations. In fact the effect of single mutations in a model with a complex and indirect genotype-phenotype has been shown to be a critical factor for the evolution of organisms with an optimal behavioral performance (Cangelosi, Parisi & Nolfi, 1994). In other simulations, the crossover was also used.

The feasibility of regulatory development for adaptation to environmental changes is the hypothesis we want to test. For this reason a two-stage, two-task simulation setting is used. In the first evolutionary stage, the organisms are selected according to their performance in a foraging task (Food Task). The fitness formula corresponds to the number of foods collected. In the second evolutionary stage the behavioral task is complicated by changes in the environment. Dangers are introduced, together with food (Food&Danger Task). This task requires that organisms adapt their food approaching strategy to a new behavioral pattern for approaching only foods and avoiding dangers (fitness = number of collected food minus number of touched dangers). To do this, organisms need to restructure their neural network, for example by adding or readapting some sensory and hidden neurons to the new processing needs. The way to re-adapt the neural network is by modifying its architecture.

The first stage takes 250 generations to evolve organisms for the foraging task. After the last generation, the best 33 organisms are selected and reproduce 3 offspring each. The new population lives in the new environment for another 250 generations in order to evolve a proper behavioral strategy for the second task. In each generation, the organisms are tested for 5 epochs, that is they live in five environments with different distributions of food, or food and danger elements. Once an element is reached, it disappears and the fitness of the organism is updated. The organism is allowed to make 150 moves per epoch.

The sensory information for the input layer of the neural network is the Euclidean distance and the angle of orientation of the closest food. The angle of orientation is the absolute angle with respect to the face of the organism. In the second task, another bit of information is available to signal the "quality" (food=0, danger=1) of the perceived element. In order to input the distance, orientation, and quality of food, the neural network must develop the specialized type of sensory unit. The type of input unit is decided during the functional differentiation that occurs once the cells reach the lower pole of the developing grid. A similar functional differentiation is used for the output units, where two types of motoneurons can develop. The binary pattern of activity of the two types of motor units will determine one of the four possible moves: go one cell forward (activations: 1 1), turn 90 degrees right (0 1) or left (1 0), or do nothing (0 0).

4 RESULTS

To test the robustness of the model a large amount of data were collected. The experimental plan included the two-stage two-task simulations plus other tests with different parameters (e.g., continuous axon growth compared to discrete growth). In this paper we will concentrate on the comparison of the two-stage results.

Within the 250 generations of the first evolutionary stage the probability of evolving successful populations of good foragers is quite high (p=0.87, 13 out of 15 replications). By way of example, the left side of the chart on figure 1 (from generation 1 to 250) shows the fitness curves of 3 successful populations. The data refer to the average performance of the best 20 individuals in each run. The number of generations necessary to reach an optimal fitness level is variable, with an average of 128 generations, and a range from 25 to 230. Indeed, in one simulation the organisms evolved an optimal behavior after only 25 generations, maintaining this good performance until the 250th generation.

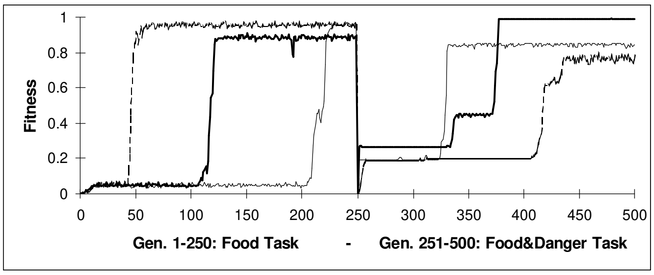

Figure 1: Fitness curves of 3 sample populations in the two-stage two-task simulations. The curves refer to the average fitness of the best 20 organisms in each population.

The fitness curve is characterized by sudden increases followed by stable periods. Each fitness jump takes only one or very few generations. This sudden increase corresponds to a functional change in the organism's behavior and in its neural network. This is a clear case of punctuated equilibrium (Gould, 1977). The evolutionary process does not follow a continuous increase in the level of adaptation to the environment, but it is characterized by a prolonged period of stable fitness, followed by a sudden increase in the fitness value. In the genetic algorithms and neural network literature, this nonlinear, punctuated trend is known to be associated with models using an indirect genotype-phenotype mapping (cfr. Miglino, Nolfi & Parisi, 1996). The regulatory genome for a biological development used here is an advanced form of this class of complex genotype-phenotype mapping.

For the populations subjected to the second stage of evolution (Food&Danger Task), the probability of evolving an optimal behavior within the 250 generations is 0.83 (N=12). Even in this case, we observe sudden jumps of fitness in the range of one or a few generations (figure 1, generations 251-500). The average evolutionary time needed to achieve a significant fitness increase is 90 generations.

The behavior of the evolved organism is optimal in both evolutionary stages. The Food Task is accomplished very well, since the good forager organisms are able to reach all the perceived food elements. In the discriminative Food&Danger Task of the second stage, the behavioral performance is also quite optimal. In the 10 simulations, during the organism's lifetime an average of only 2 danger elements are touched, versus the collection of an average of 20 food elements.

5 DISCUSSION

There is a large number of variables that can be monitored during the gene regulation process and the network neurogenesis. Moreover, the model is quite complex, and it implies the co-occurrence and interaction of different factors (genetic, cellular and environmental). To make the presentation of the development data and their discussion and interpretation more effective, we will focus on the developmental events which occurred during the process of adaptation between the tasks of the two evolutionary stages. The organism's neural networks are evolved, in the first stage, according to their performance in the foraging behavior. That is, during evolution a developmental pattern is selected that is able to produce a functional network. This network should develop at least two sensory units that can detect the position (angle and distance) of the food, some motor units for approaching it, and a pattern of connection including or not a hidden units pathway. Because of the environmental change during the second stage, i.e. the introduction of dangers, some modifications in the neural developmental process will be necessary. A dramatic solution could be the total substitution of the already evolved neurogenetic process with a completely new ontogenesis. But the evolutionary cost of this operation is too high, since the second task is related to the foraging behavior. In fact at least some of the neural structures are still necessary for controlling the approaching behavior towards the foods. A completely new development would require rebuilding even this functional structure. Instead, a more economic solution is to readapt the already evolved functional development to the new behavioral demands of the changed environment. The evolutionary algorithm can be useful to try to evolve some changes in the development process that will cause the re-adaptation of the organism's neural network.

We analyzed the distribution of neurogenetic changes that allowed organisms to successfully restructure and readapt their neural networks for the new Food&Danger task . Frequency data in the 10 populations suggest that all developmental events, except the migration, were involved to readapt the ontogenesis for coping with new behavioral requests. The events related to axon growth and synaptogenesis were the one most frequently used. In fact even small adjustments of the connectivity pattern can prove very functional for the evolution of good networks.

Now we will use a theoretical schema to analyze these data. In the initial section we have introduced the Heterochrony theory as a framework for the comparison of different ontogenies. This framework uses the evolutionary changes in the ontogenetic development as a meaningful criterion for classifying the role of the developmental changes and for analyzing the flux of interactions regulating ontogenesis. The heterochonic changes are the changes in the rate, onset, and offset of growth of single traits. Our model includes a basic property of the biological system, that is a development at the cellular level based on a regulatory genome. Therefore we can use this framework to account for the functional role of the developmental changes in the neural network's adaptation to environmental changes. For example, the distinction between global and local heterochronies can be used here. It is useful to distinguish the role of the developmental changes according to the way they affect the ontogenesis. The global heterochronies include those changes that affect the very early stages of development, and whose consequences are significant in all organisms. For example, a change in the first stage of cell duplication can have effects on more than one trait or organ. The local heterochronic changes, instead, act later and affect only a limited part of the developing system. Global heterochronic changes were normally non functional because they resulted in a non-fully connected neural network. The functional heterochronies that we observed in the simulation were mainly local, since they affected only substructures of the neural networks, such as the input units level, the axon growth process in few units, late cell divisions, etc... This can be explained by the fact that the second behavioral task is closely related to the first, and so the developmental changes that are necessary for adaptation must be small, i.e. local. In the case in which environmental changes required the development of completely new, unrelated neural structures, we would expect more global phenomena, such as a large addition of new cells to build different processing pathways.

In the 10 successful two-stage, two-task populations, different examples of local heterochronic changes were found. To explain how these heterochronies work, and to show their adaptive value, we will use few examples. In the first case (population 6, generation 326 and following) we have a case of adaptive local Progenesis and contemporaneous cell-cell induction effect due to spatial interaction. At generation 326, all the individuals of the population maintain the strategy of reaching every element they see, even if the danger elements cause a fitness decrease. This is because there is no input unit for the detection of the information of food "quality" (danger/food). All the cells that reach the lower sensory row differentiate into detectors of the food's orientation angle. A few mutations in the descendant of the best organism were enough to cause significant changes in development. In the ancestor, the two sensory cells for the input of orientation originate from a common founder cell. In the descendant, this founder cell stops duplicating at time step 6, leaving two free spots in the sensory area of the developing grid. This is a case of local Progenesis, because the offset of the mitotic sequence is anticipated. At the same time, there is a change in the cell displacement of other cell duplication branches. In the upper side of the developmental grid, two new cells, coming from a different mitosis branch, occupy the space left free in the sensory area. What happens in the descendant is that at time step 7 a newly formed cell will change position moving to the lower row. This new displacement will induce a dividing cell to place one of its daughters in the lower input area. Because of these spatial interactions, the progeny of this cell ends up in the two spots left free by the Progenesis. These ontogenetic phenomena are shown more clearly in the morphogenetic tree in figure 2. The morphogenetic tree is a graphic representation of a cell duplication tree using the two dimensions of time and space. It facilitates the understanding of the developmental events, and their temporal and spatial interactions (see Arthur, 1984).

Another example of local heterochronic changes is the rearrangement of the connectivity pattern in a different population. A prolongation (Hypermorphosis) of one or more axon trees causes the addition of new connections, or the linking between distant cells. Instead, an early offset of the axonal growth (Progenesis), localized in only few cells, can function as a mechanism of connection pruning. At generations 309 and 310 of the population 2, we observed the simultaneous phenomena of local Hypermorphosis and Progenesis of the axon growth. The axon starting from two hidden units and one input unit is longer in the descendant and determines the adding of new functional connections that were not present in the ancestor's neural network. At the same time some connections are pruned in other hidden units. All these changes are the results of the same few changes in the regulatory genome.

In later generations of the same population another interesting example or heterochrony for temporal interaction during development was found. A change in the temporal order of the synaptogenesis event caused the adjustment of some functional connection weights. This derived by a case of local Predisplacement between the ancestor's and descendant's neural developments. During neurogenesis many events happen simultaneously, such us the axon growth in different neurons. In our model, because implementation does not allow parallel execution of events, it is necessary to find a serial solution. When developmental events occur in parallel, the units are ordered according to the amount of the elements involved in the event regulation. This order is used for the sequential execution of the events. For example, the axonal growth at the last time step should be executed in parallel for each neuron. Therefore the system orders the cells according to the amount of the axon potentiality element. The growth of the first axonal segment starts from the cell with the highest element amount to that with the lowest level. Then the second axonal segment is grown using the same order, and so on. The weight of a connection is a function of the distribution of many intracellular elements, such as the trophic element in the cell receiving the synapses (see Table 1). The order in which an axon reaches the target cell's body is relevant to the strength of the connection. Earlier connections will have higher weight values because of the greater availability of elements in the two connecting cells. If an axon reaches a cell after some delay, it has less chance of establishing a strong connection.

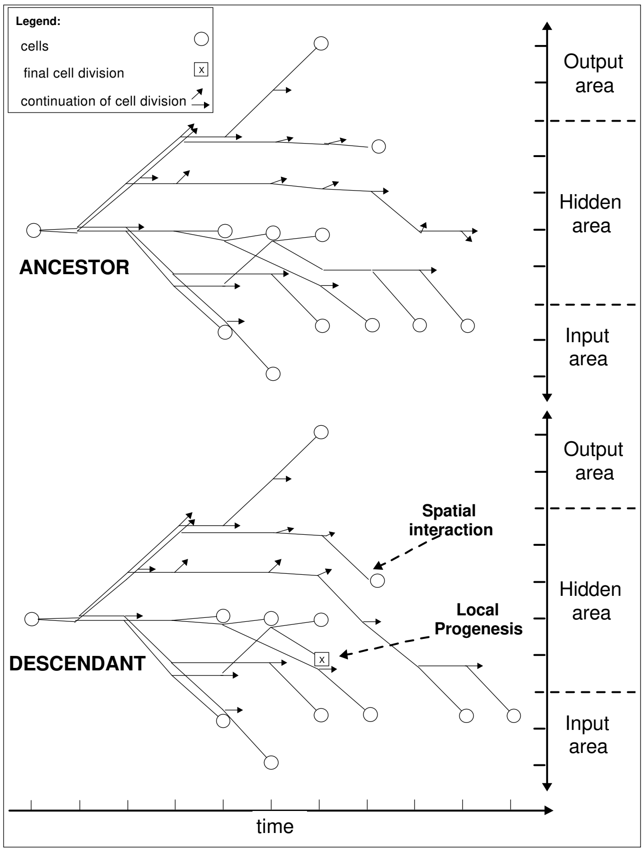

Figure 2: Morphogenetic trees for the neural network development of the best organism in population 6 (ancestor in generation 326 and descendant in generation 327). See text for explanation.

This is the phenomenon that occurs during generations 326 and 327 of the population 2. In fact, two cells that connect to the same target neuron switch the order in which their axon reaches the target unit. The cell that connected early in the ancestor's neural network, in the descendants' network will connect later, and therefore its connection strength is lowered (from -1.47 to -1.43). At the same time, the cell that in the ancestor's network connected later, now anticipates the synapse causing a weight increase (from -1.50 to -1.54). This phenomenon, the only relevant change occurred in the development of the two organisms, determines a significant improvement in the Food&Danger behavior. Because of these weight changes, the descendant organism is better adapted to the environment. In fact its fitness increases significantly because the organism stops before it approaches the danger elements. In the ancestor it was not able to avoid reaching the danger. The changes in the temporal order of the axon growth (Predisplacement of axons) is the mechanism that explains this significant adaptive change, and as we explained, it depends on the intracellular amount of structural elements acting as axon potential.

Among the observed adaptive ontogenetic changes, the phenomena of the single or multiple connection weight adjustment, depending on changes in the development course, are found frequently in the simulations. Another common developmental change is the differentiation of some sensory cells from detectors of the element position, to detectors of the food/danger quality. This is because in the behavioral task it is essential to evolve and use this information on the perceived element in order to choose between the approaching and avoiding strategy.

6 CONCLUSIONS

The simulation results suggest that the model is robust enough, at least for the class of problems required by the simulated behavioral tasks. Through genetic algorithm it is possible to evolve populations of organisms with optimal task performance. In similar models with complex genotype-phenotype mapping (e.g. Cangelosi et al, 1994) the probability of evolving optimal behavior was much lower. In the present work, even though the model is based on a regulatory genotype for the control of complex biological development, functional neural networks are easily selected and evolved.

Another important conclusion suggested from the analysis of heterochronic changes, is that the introduction of a model of biological development based on a regulatory genome is a good resource for adaptation. Data analyses showed the adaptive role of mechanisms of neural plasticity in response to the behavioral requests of a changing environment. With a classical neural network training algorithm, such as a back-propagation method, or even a genetic training method for fixed architectures, the re-training of a neural network to accomplish new behavioral requests would require almost a complete re-initialization of the learning process. The introduction of development, instead, provides a different approach by allowing the adaptive mechanisms of ontogenesis to evolve new functional structures. The introduction of a flexible model of development could prove useful in overcoming some of the limitations of current connectionist models, such as the scaling problem. Here the quantitative advantage for a developmental-based model is not immediate or obvious for small-scale problems, such as the foraging tasks. However is our feeling is that there could be benefits in larger scale problems. The resources of developmental mechanisms could help overcoming some of the limitations of current neural network models.

Further testing and enhancements of this model could take different directions. A first approach could be trying out its suitability for problems of greater complexity. It would require the use of some analytical method to assess and quantify the objective advantages of utilizing a developmental-based model versus fixed-architecture models. A second direction could regard the simulation of evolutionary theories and phenomena. The data reported show the possibility of studying some interesting heterochrony phenomena. Therefore, the simulation of a specific and well known example of Heterochrony could promote a fuller understanding of the evolutionary mechanisms of natural selection. Moreover, a final direction could use this simulation method to study biological development and the mechanisms of gene regulation.

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