Evolution, Development and Environment Toward Adaptation through Phenotypic Plasticity and Exploitation of External Information

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Abstract

Biological organisms have an inherent ability to respond to environmental changes. The response can emerge as organisms that can develop into structural and behavioural different phenotypes. To achieve such properties in an artificial developmental setting external environmental information is included in the gene regulation of the developmental model. This implies interplay between evolution, development and the environment. An experimental approach is taken to investigate this interplay. The test case chosen is evolution of robustness to environmental fluctuations. Development models with and without environmental information included in the gene regulation are compared. Further, the developing organisms of the two models are exposed to environmental fluctuations for a more extensive investigation. The results indicate that including external information in the gene regulation can be favourable and exploitable, particularly for organisms developing in a dynamic environment.

Introduction

A developmental mapping is an example of an indirect mapping. In biological development, an initial unit—a cell, holds the complete building plan (DNA) for an organism. It is important to note that this plan is generative—it describes how to build the system, not what the system will look like. Similarly in a developmental mapping, the artificial organism starts out as a single cell where the genome provides the cell's DNA. The processing of the genome may be based on gene regulation (Lantin and Fracchia, 1995). Each development step, or stage in the mapping, produces a candidate phenotype, i.e. an emerging phenotype. Gene regulation implies that different parts of the genome are expressed in different cells at different times in the emerging phenotype.

An important feature of natural development is that the developing organism develops within an environment. In Tufte and Haddow (2007a) environment was discussed at different levels. Intra-cell environment that the DNA resides in, also referred to as the *cell's metabolism* (Federici, 2004; Gordon and Bentley, 2005). The next level of environment, found in most development models, is the neighbour environment referring to the *inter-cell environment*, enabling communication between neighbouring cells (Bongard and Pfeifer, 2003; Tufte and Haddow, 2003; Miller, 2004; Federici, 2004). Further, the environment may also affect the phenotype emerging from the development process.

Phenotypic plasticity (Larsen, 2004) is a property of organisms which enables adaptation or response to the environment. The adaptation or response is expressed as changes in the phenotypic structure and/or behaviour. It is important to note that this adaptation occurs during the development phase. That is, the genome develops in an environment where the emerging phenotype is influenced by the environment in which it develops. This implies that developing organisms may adapt their structure and/or functionality according to information provided by the external stimulus of the environment — see Tufte and Haddow (2007b).

In an artificial setting, environmental adaptation may be regarded as an emerging tolerance to external fluctuations. In the work of Miller (2003) and Federici and Downing (2006) such robustness appeared to be a shadow effect (Hogeweg, 2000) of evolution and development as it was not specified as a target behaviour or included environmental information in the processes of evolution and development. However, environmental influence may be targeted by evolution to find robust genomes (Tufte and Haddow, 2007a). Additionaly, environmental information can be exploited by development for further adaptation of the emerging organism (Tufte and Haddow, 2007b).

To further investigate the relation between evolution of robustness and possible emergent robustness beyond the scope of the environmental fluctuations induced during evolution, the results of Tufte and Haddow (2007a) are compared to results obtained introducing the possibility of exploiting phenotypic plasticity in the development model. Further, the evolved genomes are exposed to large environmental fluctuations during development to reveal possible emergent robustness to such dynamic environmental fluctuations. As such, the evolved genomes are exposed to different environmental fluctuations during development then what fluctuations the population was exposed to during evolution.

The focus of this paper is to investigate if a developmen-

tal model capable of exploiting environmental information, i.e. phenotypic plasticity, indicates increased tolerance to extended environmental fluctuations compared to a developmental model with no such mechanisms. The possible presence of such extended emergent robustness may indicate exploitation of environmental information in interplay with the development of structure and behaviour. However, the larger goal of the work is toward an understanding of the interplay between evolution, development and environment toward artificial organisms capable of computation. Herein a cellular computational machine Sipper (1997). As such, if the environmental information is treated as data input and output from the functional developing organism a clear separation between the emergent structural organism and the data transformation of the functional parts of the organism may not be feasible or desirable.

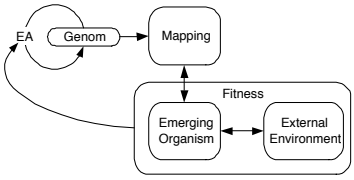
The article is laid out as follows: Section II introduces the roles of environment in artificial development models. The cellular developmental model is presented in Section III. Experimental results are presented in Section IV. Finally, Section V concludes the work.

Environmental Information

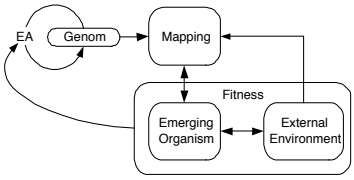
The "environment" of a naturally developing organism usually refers to the external environment affecting the developing organism. In Tufte and Haddow (2007a) this environment was expressed as a combination of both an *initial environment* and an *external environment*. When a cell is grown it is effected by the environment (at that place in the environment) — initial environment. The status of the initial environment thus affects the path of development for any given cell and thus affects the organism as a whole. However, when the organism is developed it has to survive in an environment and thus it is important that the environment beyond the growing organism can affect the developing organism. Such an environment is defined as the external environment. As such, both the growing organism and its "external environment" can be measured during evaluation (Tufte and Haddow, 2007a).

A further implication of emerging organisms is that the phenotype may be evaluated at a given step of development, defined as the finalised phenotype, as in Gordon and Bentley (2005) or at each or any stage during development (Tufte and Haddow, 2003). The latter takes the actual process of developing the emergent structure (Viswanathan and Pollack, 2005) or functionality (Tufte and Haddow, 2003) into the evaluation process i.e. life-time evaluation.

One notable feature of the work presented in Tufte and Haddow (2007a) is that although an external environment is introduced, such an environment only affects the developing phenotype indirectly i.e. through evolution. There is no direct influence on the developing phenotype unlike the initial environment which directly affects the development path of all cells. However, in biology the external environment has a direct affect on the developing phenotype.



(a) Indirect environmental influence through evolution.



(b) Direct environmental influence exploitable by the mapping process.

Figure 1: Evolution of developmental genomes with indirect and direct exploitation of environmental information.

Figure 1(a) illustrates the inclusion of external environment as implemented in Tufte and Haddow (2007a). The organism emerges as a product of the interplay between the genome and the emerging organism. This interplay is represented as the "mapping" box where at any point in time the information about the genome and the organism (at that point in time) are available to the mapping process. Fitness measures the emerging organism together with its environment, as shown, at each stage of the development process. The accumulated fitness, after the mapping process is stopped, is fed back to the evolutionary algorithm (EA). As such, the external environment does not influence the outcome of the development process (mapping) but rather the fitness evaluation thus providing an indirect dependence on the external environmental, i.e. a system with no mutual perturbatory channels (Quick et al., 1999).

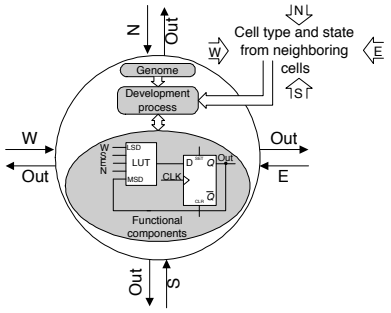
In Figure 1(b) a similar mapping process is described except that the external environment information is available to the development process. As shown, the mapping process can exploit external environment information, in addition to the information coded in the genome and provided by the developing organism. As such, the emerging organism is a product of the interplay between the genome, the organism (at that point in time) and the present environment i.e. mutual perturbatory channels exist. In such systems, a genome can develop into different organisms depending on the environment present, i.e. phenotypic plasticity is achievable (Tufte and Haddow, 2007b).

In the work presented the two different principles for exploiting environmental information shown in Figure 1 are

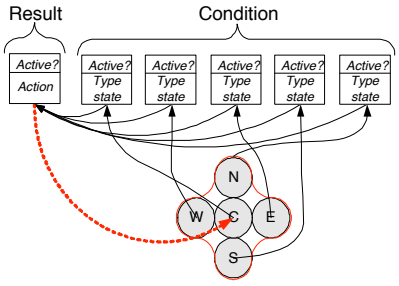
compared to measure the ability to evolve robust phenotypes. The results of the two approaches are taken further by introducing environmental fluctuations during development, i.e. robustness in a dynamic environment.

Development Model

The development model is based on cellular development. This implies that the genome is present and processed autonomously in every cell. In the model, the cell also contains the functional building blocks. For the experiments herein the application sought is that of a digital circuit (phenotype). Figure 2(a) illustrates the developmental system — the cell. The cell is divided into three parts: the genome (the building plan); the development process (mechanisms for cell growth and differentiation) and the functional component of the cell. The information in the functional components represents the type of the cell and the cell's state is described by the outputs of the functional components.



(a) Components of the cell.



(b) Gene regulation shown for a single rule

Figure 2: The basic cell and a rule showing the gene regulation in the cellular development model.

The genome consists of a set of rules. Rules are restricted to expressions consisting of the type and state of the target cell and the types and state of the cells in its von Neumann neighbourhood. There are two types of rules i.e. change and growth rules. Cell growth is a mechanism to expand the organism. A growth rule result provides the direction of growth: grow from north **Gn**; east **Ge**; south **Gs** or west **Gw**. It is important to note that these rules are expressed in terms of where the source of the cell growing into the target cell is. Describing where a cell is growing from enables a fully parallel implementation of the system to be created whilst retaining the possibility that cells in effect may grow in all four directions simultaneously. Growth rules have two restrictions. First, the target cell must be empty – this is to prevent growing over an existing cell and thus specialising the cell with a new cell type. Secondly, the cell to be copied into the target can not be empty.

Differentiation changes a cell's type i.e. its functionality. The result part of a change rule states the type of cell the target is going to be changed into. Cells have the following types: valid cell types, don't care (DC) or empty. However, the empty cell is not a valid target cell type.

Each rule consists of a result and a condition. The conditional part provides information about the cell itself and each of the neighbouring cells. In the development model presented in (Tufte and Haddow, 2005), the type of the cell was applied to describe these cells. However, to introduce external environment, state information is also needed. State information provides a way to include information relating to the functionality of the organism at a given point in time as well as information about the external environment — the empty cells in the environment also have state information. As such, a cell is represented in the condition of a rule by two genes representing its type and its state. However, a target cell is only represented by one gene: it's type for change rules or growth direction for growth rules. The state of cell may be 0, 1 or DC. DC is introduced to provide the possibility to turn on or off this environmental influence. The development model is applied with and without the information from the external environment and functional organism.

Firing of a rule can cause the target cell to change type, die (implemented as a change of type) or cause another cell to grow into it. Figure 2(b) illustrates the process of evaluating a rule. For each cell condition, the cell type and state are compared and if the conditions are true then that part of the rule is active. If all conditions are active then the result will become active and the rule will fire. Activation of the result gene is expressed in the emerging phenotype according to the action specified.

In a development genome multiple rules are present. Multiple rules imply that more than one rule of a given cell may be activated at the same time if their conditions hold. To ensure unambiguous rule firing, rule regulation is part of the development process. If the first rule is activated, the second rule can not be activated. Activation of the second rule prevents activation of the third rule, etc.

The functional components of the cell is an Sblock (Haddow and Tufte, 2000). The content of the look-up table (LUT) defines functionality and is, herein, also used to define the cell type. The LUT is the combinatorial component and the flip-flop is the memory element — capable of storing the cell state. The output value of an Sblock is synchronously updated and sent to all its four

neighbours and as a feedback to itself.

One update of the cell's type under the execution of the development process is termed a development step (DS). A development step is thus a synchronous update of all cells in the cellular array. The update of the cell's functional components i.e. one clock pulse on the flip-flop, is termed a state step (SS). A development step is thus made up of a number of state steps.

The initial condition is applied before development starts. This means that all empty cells are set or reset depending on the given initial condition. To avoid empty cells updating their output values from their von Neumann neighbourhood, all cells of type Empty are set to update their outputs based on only their own output value at the previous clock pulse. A empty cell will retain its initial state — environmental information, until the emerging organism grows into it.

Experiments

The experiments are separated into three different experiments. In the two first experiments each genome was exposed to a set of ten different randomly generated environments. As such, the development of a given genome is repeated ten times, one for each environment. The fitness score was calculated as the mean fitness of the genome in the ten different environments. A genome is thus explicitly being evaluated and, therefore, evolved to tolerate different environments. Ten runs were conducted resulting in a collection of the ten best developmental genomes and their respective developed organisms. The use of environmental information in the development model for the two experiments is illustrated in Figure 1(a) and 1(b).

Extending the developmental model to include environmental information in the gene regulation has several implications. The environmental information requires an extension of the information processing in the gene regulation. As such, the genomes for experiment one and two may not be directly comparable. The larger genome required to include environmental information changes the search space. The genome with no environmental regulation may be defined with parts, e.g. genes, set to don't care to maintain an even genome size, i.e. a redundant representation. Another possibility is to remove the genetic parts that are included in the environmental regulation. In the work of Shipman et al. (2000) and Rothlauf and Goldberg (2003) such redundant representation was shown to be non-favourable or to decrease the performance of the EA. As such, the later solution was chosen.

Further, the resulting genomes from the two experiments were re-developed and re-evaluated in ten other randomly generated environments. Each genome's performance on each of the ten new environments was then compared to the fitness value obtained from the base experiments.

In the third experiment genomes of the two first experiments were re-developed and re-evaluated in an environment were changes was introduced during the life time of the organism. The change in external information was inserted at three fixed steps during development of the organism.

Experimental Setup

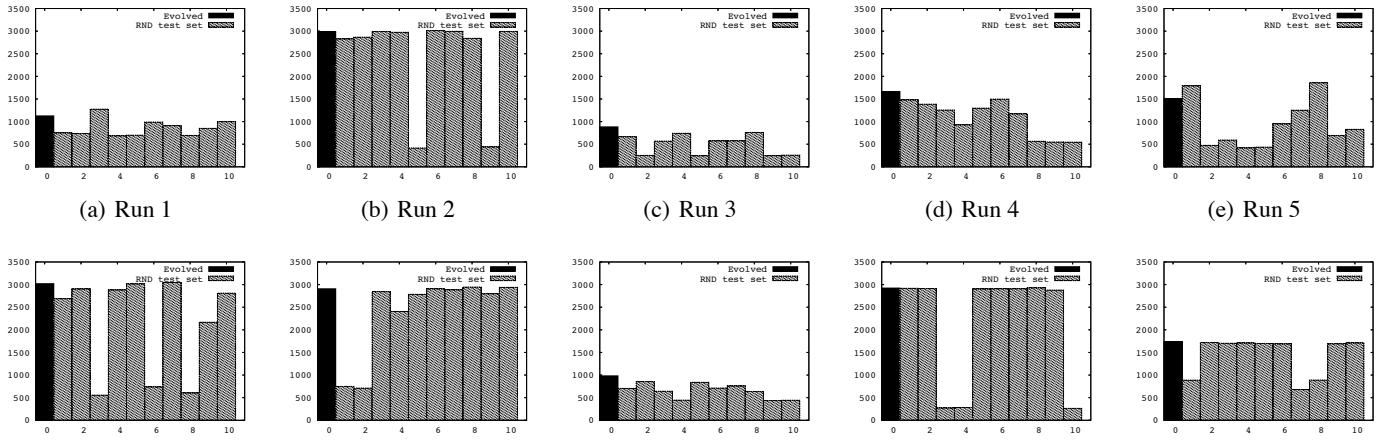
The number of available cell types was set to thirteen including the empty cell type. Available cell types was based on Sippers universal non-uniform CA (Sipper, 1997) and threshold elements (Beiu et al., 2003). Table 1 provides the set of available cell types, together with their functional LUT definition and graphical symbol. For signal directions and LUT addresses refer to Figure 2. The first single cell which the multicellular organism develops from was defined to be of type 5 (NAND).

Table 1: Definition of cell types and their functionality

Cell type	LUT hex	Function name	Graphical representation
0	$0xFFFF0000$	$no\ change\ Emty$	
1	$0x66666666$	$XOR_d\ W \oplus S$	
2	$0x3D3D3D3D$	$XOR_c\ E \oplus S$	
3	$0x0FF00FF0$	$XOR_b\ N \oplus E$	
4	$0x55AA55AA$	$XOR_a\ W \oplus N$	
5	$0x55FF55FF$	$NAND\ \overline{W \bullet N}$	
6	$0xFF00FF00$	$\downarrow SouthPropagation$	
7	$0xCCCCCCCC$	$\uparrow NorthPropagation$	
8	$0xF0F0F0F0$	$\leftarrow EastPropagation$	
9	$0xAAAAAAAA$	$\rightarrow WestPropagation$	
10	$0xE8808000$	$T \geq 4$	
11	$0xFEE8E880$	$T \geq 3$	
12	$0xFFFEFEE8$	$T \geq 2$	

The evolutionary algorithm chosen was a Genetic Algorithm (GA), a modified version of a GA found in Spears (1991). The GA's crossover operator was modified such that a gene was undisturbed and a variable number of crossover points was implemented. The genome size was set to consist of 32 rules and the population size was set to 16. The initial population consisted of random generated valid rules. However, invalid rules may arise through the application of genetic operators. Crossover rate was set to 0.5 and the mutation rate for each gene was set to 0.0017. The GA was set to terminate after 100 000 generations.

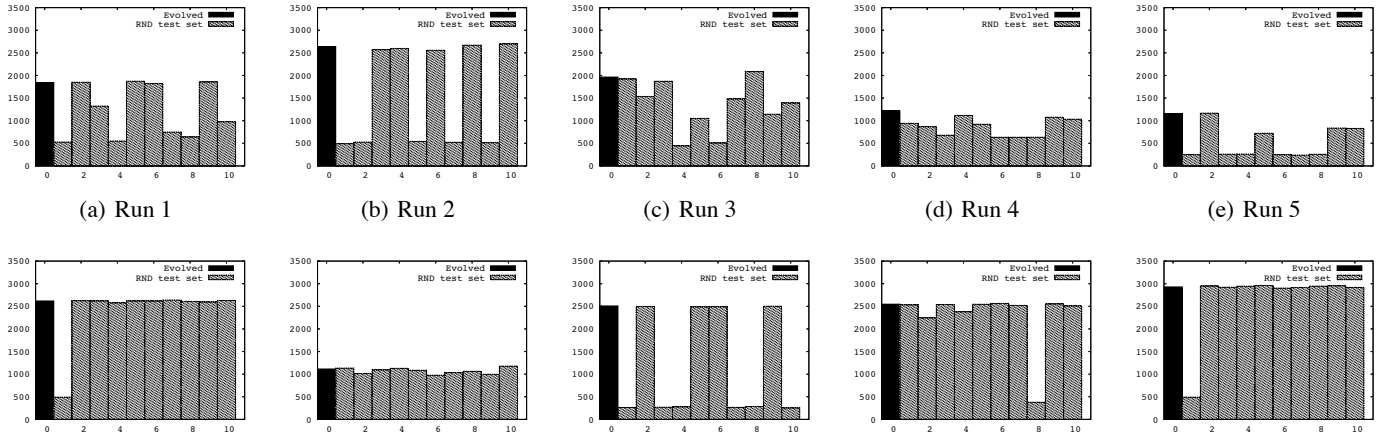
The fitness considers how well an organism function in a set of environments. The application is a sequential counter where counting is based on the state information of the entire cellular space and the sequential operation of the functional components of the cells. The application thus places a requirement on the tuning of the development genome (by evolution) and the emerging phenotype (by development) for such sequential digital circuit behaviour. A counting sequence is defined in the cellular array as the number of logical "1"s in the cellular array increasing by one for each state step. The goal being to achieve counting behaviour in all environments applied, i.e. the same functionality. In this case, a life-time fitness evaluation was used. This is similar to those performed in Tufte and Haddow (2007a) where



(a) Run 1 (b) Run 2 (c) Run 3 (d) Run 4 (e) Run 5

(f) Run 6 (g) Run 7 (h) Run 8 (i) Run 9 (j) Run 10

Figure 3: Evolved in a set of initial random environment. Exposed to random environments. No phenotypic plasticity



(a) Run 1 (b) Run 2 (c) Run 3 (d) Run 4 (e) Run 5

(f) Run 6 (g) Run 7 (h) Run 8 (i) Run 9 (j) Run 10

Figure 4: Evolved in a set of initial random environment. Exposed to random environments. Phenotypic plasticity introduced

different environments were used but here environment may also affects the developing phenotype directly.

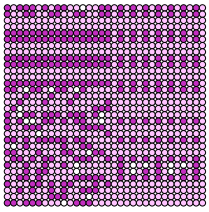
In all experiments the final fitness score was based on the organisms counting behaviour throughout its life time. The development process was apportioned 100 development steps. Each development step was set to include 100 state steps. The maximum size of the organism was set to 1024 cells in an array of 32 by 32 cells.

The experiments were executed on a cPCI machine including a PC running the GA. The development process and functional behaviour of the cellular array was executed on an FPGA (Tufte and Haddow, 2005).

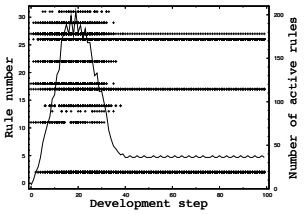
Experiment one: no Phenotypic Plasticity

The first experimental results are taken from Tufte and Haddow (2007a). In this work no environmental information was included in the gene regulation. The work compared the robustness of evolved organisms developed in environments with different degree of environmental fluctuations. The span of environments ranged from a single environment for all organisms to set of environments as used herein. The goal of the experiment was to evolve genomes that could develop into organisms that survived in different environments. This was archived by exposing the evolving organisms to different environments. The presented results are for comparison with results obtained by a development model that can include environmental information in the gene regulation.

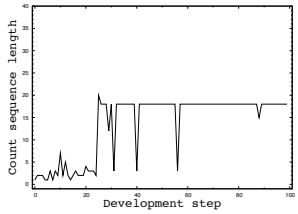
In Figure 3 the results of the experiment in Tufte and Haddow (2007a) are shown. The plots show the results for each of the ten runs. The fitness score of the respective evolved genome is plotted in black in



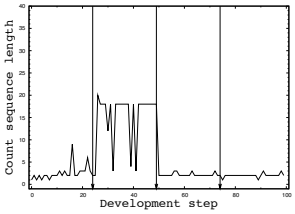
(a) Phenotype at DS 100.



(b) Gene activity.



(c) Behaviour with no environmental fluctuations.



(d) Behaviour with environmental fluctuations.

Figure 5: Comparing behaviour of a developing organism with and with out applying environmental changes. No environmental information in the gene regulation.

each run plot. The grey bars show the performance of the genome if re-developed in ten new randomly generated environments.

These genomes have not specialized to a given environment and their behaviour are quite similar for most of the environments the genomes was re-developed in. Some runs, i.e. *run1* and *run8*, show a short counting sequence. However, the deviations from the evolved results are low.

Experiment two: Including Phenotypic Plasticity

In this experiment environmental information was included in the gene regulation. The extension to include environmental information may be illustrated by changing the information available for the development process from the set-up in Figure 1(a) to 1(b).

The results of experiment two are shown in Figure 4. The plots for each run are obtained and presented in the same way as for the previous experiment.

The fluctuation in performance for some runs, e.g. *run5* and *run8*, is product of evolved dependency on specific environmental data. Such dependency can cause poor performing phenotype structures or competing counters cancelling out each other.

In Figure 7 the best evolved genomes, i.e. longest counter performance, of the two experiments are compared to the mean performance of the same genome developed in ten random environments. In addition the mean performance for all experiments developing in a random environment is shown. Comparison of the results for phenotypic plasticity vs. no plasticity shows an improvement for the best genomes including environmental information in the gene regulation when re-developed in a set of new environments. However, the mean of all runs shows an almost identical performance.

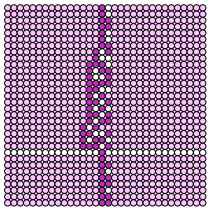
Experiment three: Exposure to Environmental Fluctuations during Development

The third experiments may be an extreme case for environmental fluctuations. The genomes evolved in experiment one and two are re-developed in an environment where fluctuations are enforced during development. External information is applied as an enforced random state to $1/4$ of the cells (empty or within the organism) available. The external changes in cell state are applied at an early stage of development (DS 25), in the middle of the organisms life time (DS 50) and at a late stage of development (DS 75). The cells influenced are defined as an array of 16 x 16 cells in the centre of the cellular array.

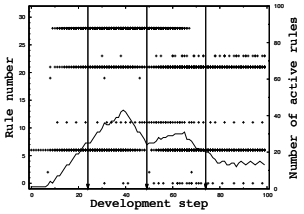
In nature most organisms of a given species develops in a rather uniform environment. The species has evolved within an environment where the species is a result of evolution and possible environmental changes over time. As such, large unpredicted fluctuations on the single individual level is not the main concern. However, if artificial cellular organism for computation are considered with the external information used as data. The external information enforced into the system is on the individual level, i.e. an organism as a computational machine.

Figure 5 presents the result of introducing changes enforced externally to a genome from experiment one (no phenotypic plasticity). The resulting phenotype is shown in Figure 5(a). Since the development model used in this experiment does not take the environmental information into the gene regulation the phenotype structure is equal for all environments. Figure 5(b) illustrates the gene activation for the presented phenotype. The plot presents the gene activation pattern during development together with the number of active rules at each development step. Rule numbers from 0 to 31 are placed on the left Y-axis. The mark (+) in the plot indicates that the rule was activated at the given development step. The right Y-axis shows the number of cells in the organism with an active rule on a given development step. The number of active rule cells is illustrated by the plotted line. The gene activity is constant for all environments.

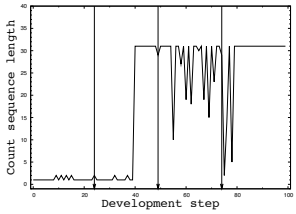
The plot in Figure 5(c) show the counting sequence length achieved at each development step with no enforced environmental changes. As shown the organism develops a fluctuation counting between DS 26 and 58 there after the counting sequence is stabile throughout the life time of the organism. If the genome develops in a changing environment the result is quit different as illustrated in Figure 5(d). The environmental changes are enhanced by the arrow lines. In



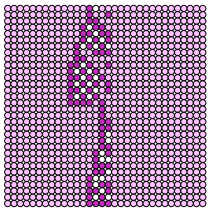
(a) Phenotype at DS 100 with environmental fluctuations.



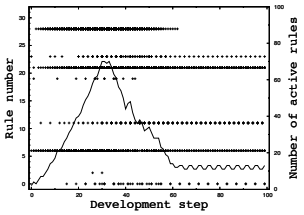
(b) Gene activity with environmental fluctuations.



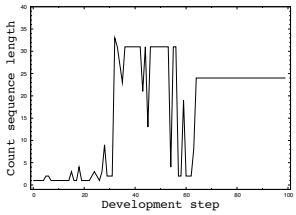
(c) Behaviour with environmental fluctuations.



(d) Phenotype at DS 100 no environmental fluctuations.



(e) Gene activity no environmental fluctuations.



(f) Behaviour no environmental fluctuations.

Figure 6: Comparing gene regulation and behaviour of a developing organism with and with out applying environmental changes. Environmental information included in the gene regulation.

the example the organism tolerate the first shift in the environmental information. However at DS 50 when the second change is enforced the organism's functionality is hardly present as the counting sequence drops. The last environmental change at DS 75 does not cause any major change in behaviour.

The result of applying external information during development for the development model capable of phenotypic plasticity is shown in Figure 6. In contrast to the results presented for no phenotypic plasticity the environment influence on gene regulation results in a possibility for environmental influence on the cellular composition of the phenotype. As such, the resulting phenotype depends on the environment present. Figure 6(a) show the phenotype developed in an environment with fluctuations. In Figure 6(b) the gene activation plot for the phenotype is presented. The enforced environmental fluctuations are illustrated by the arrow lines. The emergent counter sequence is presented in Figure 6(c).

To highlight the presence of environmental information in the gene regulation a candidate phenotype for the same genome developed in an initial random environment, i.e. developed with no enforced fluctuation, are shown in Figure 6(d). The corresponding gene activation plot for the shown phenotype is given in Figure 6(e). Figure 6(f) show the emergence of counting behaviour for the presented phenotype developed in the given random environment.

In contrast to the results presented for the development model with no environmental influence phenotypic plasticity can here be observed by the two different phenotypes arisen from the same genome. The source for the variation in phenotypic structure is the difference in gene activation caused by the extra environmental information. If the gene activity in Figure 6(b) and 6(e) are compared the affect of the fluctuations during development alter the timing of activation of different rules and the number of cells with active rules at different stages of the development of the organism.

The functionality of the organism given in Figure 6(c) and 6(f) show that the counting sequences are not identical but here the fluctuations introduced are not causing permanent damage to the functionality. The enforced changes may cause fluctuations in the counting sequence length but the developing organism achieves a stable behaviour.

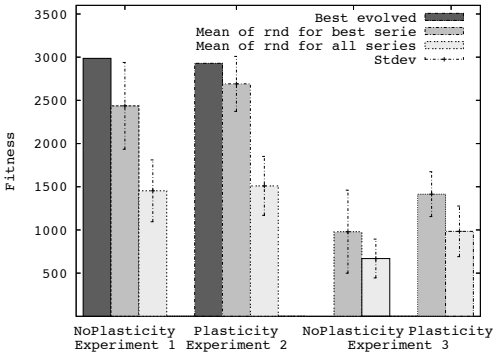


Figure 7: Experiments with possible phenotypic plasticity compared with the development model with no such feature.

In Figure 7 the result of introducing enforced environmen-

tal changes to the sets of best genomes are shown. In experiment three there are no evolved best result. As such, the mean of the best series and the mean of all runs with and without the possibility to exploit phenotypic plasticity are presented.

Conclusion

Including environmental information into the gene regulation mechanisms itself may be a way to achieve organisms that can respond to environmental changes during development. Organisms that can dynamically tune the cellular structure by development in an interplay with the environment. The environmental information is not only influencing the phenotypic structure but also included in the making of the behaviour, i.e. computation, of the artificial organism.

The results show a successful integration of evolution, development and environment toward adaptive organisms. Further, the introduction of additional external environmental information, during development, shows how a developmental system can dynamically respond and adapt. This adaptation is a result of the possibility to create dynamic phenotypes. Such phenotypes change their phenotypic structure as a response to external stimulus, here robust computational behaviour.

In experiment one and two the expansion of the development model to include environmental information found individual genomes that have an increased performance. However the general result of all runs in the experiments are almost identical. As stated, comparing these two results are difficult due to the change in search space and the extended regulation caused by the environmental information. As such, the fact that the inclusion of environmental information results in better individual solutions and that the EA was capable of keeping up the performance with the increased genome size indicate that the environmental information is exploitable.

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