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EVOLUTION OF DEVELOPMENTAL ONTOGENY FOR ROBUSTLY REPRODUCIBLE PHENOTYPES

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Abstract

Development has been used by a number of researchers as an efficient means of nonlinearly decoding genetic information in evolutionary systems. We show that developmental routines which do not utilise cell-cell interactions result in poor performance under noisy conditions. Addition of interactive rules permits self-organisation during development and produces robust mappings from genotype to phenotype even under noisy conditions.

As a case study, we present the evolution of an edge-detecting artificial retina. The model is capable of creating three dimensional, multi-layer neural networks by modelling the development of neuron-to-neuron connectivity. Incorporating interactive overgrowth and pruning is shown to overcome the poor performance of intrinsic-only growth under noisy conditions. Staged evolution (speciation) of these processes is proposed and demonstrated as an effective means of evolving such complex developmental programmes.

1 Developmental Evolution

The use of evolution as a design methodology has been the subject of widespread research for over a quarter of a century [Fogel et al., 1966, Holland, 1975, Rechenberg, 1973], and appears promising for designs involving a large number of discrete parameters. However, such systems often have highly nonlinear parameter dependencies requiring sophisticated gene encoding strategies [Forrest and Mitchell, 1993]. These considerations have led a number of researchers to model development as an efficient nonlinear decoding procedure [Dawkins, 1989, Kodjabachian and Meyer, 1995].

In addition to facilitating nonlinear encoding, development offers memory and computational savings through the use of repeated blocks, hierarchies, and self-organising interactions [Eigen and Winkler-Oswatitsch, 1992, Riedl, 1977]. Given the inexact nature of developmental processes and the need for processes to follow sequentially (ontogeny), developmental decoding of a given genotype could potentially result in different phenotypes in different organisms. Such a scenario would make developmental evolution of large scale and intricate systems difficult since developmental variations would very likely result in poor phenotypes.

We show that self-organising interactions during development can avoid such variability and lead to robustly reproducible phenotypes from a given genotype. Further, we show that mimicking the evolution of increasingly complex species [Dawkins, 1989], it is possible to start with a simple developmental programme, and introduce increasing self-organisation in stages until all robustness criteria are satisfied.

This paper addresses the evolution of artificial neural network (ANN) architectures, a good example of evolving a complex system with sophisticated functionality. The long term aim of our work is to be able to automatically create ANNs of arbitrary complexity, such that they are not limited to stereotyped architectures.

2 Previous Work

We have been implementing a 3D model of neural development, in which neuron-to-neuron connectivity is created through interactive self-organisation [Rust et al., 1997b, Rust et al., 1997a]. Development occurs as a number of overlapping processes including growth governed by intrinsic and interactive factors, as well as growth regulation and pruning based on the effects of spontaneous neural activity [Rust et al., 1997a].

Development occurs in an artificial chemical environment, with an underlying, background chemical gradient which guides initial growth. Developmental processes are defined by a set of interacting rules. These allow neurons in the model to extend axons and dendrites (collectively termed neurites) into the developmental environment. Neurons and their neurites emit chemical gradients, analogous to neurotrophins [Hall, 1992], establishing a complex topographical environment. The tips of growing neurites are modelled as neural growth cones and they navigate under the influence of their localised chemical environment [Purves and Lichtman, 1985]. Interactions between developing neurites result in the formation of neural structures. The model is capable of generating a wide range of neuron morphologies (see Figure 1) and network architectures.

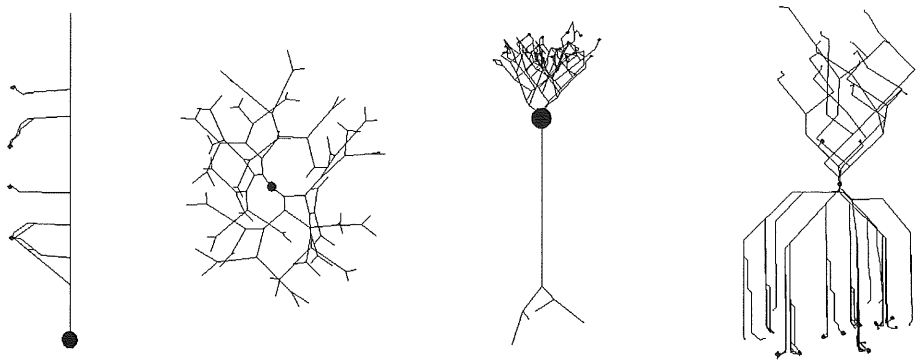


Figure 1: A range of individual neuron morphologies generated by the developmental model. (a) Neuron with an axon which produces side-branches. (b) Stellate cell. (c) Retinal bipolar neuron. (d) Pyramidal cell.

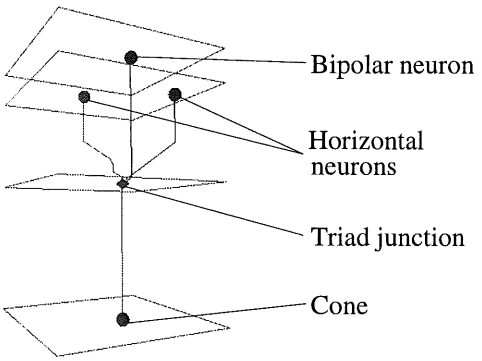


Figure 2: An idealised triad junction.

The developmental rules are controlled by parameters, much in the same way as genes can be thought of as parameters for biological development [Goodwin, 1994]. Evolution then becomes the identification of optimal sets of the developmental parameters. We have previously carried out some preliminary investigations on evolving the growth parameters using a genetic algorithm [Rust et al., 1997b]. The remainder of the paper addresses evolving the developmental processes in stages.

3 The Retina Model

The modelling of the mammalian retina has been chosen as the testbed application. The retina was chosen as it has been extensively studied and does not require learning through synapse modification, which simplifies initial modelling. The aim has been to model the on-centre/off-surround response in the retina in order to perform edge detection [Dowling, 1987].

We are specifically modelling the formation of triad junctions, which are thought to be responsible for the edge detection response. In the current implementation triad junctions are formed using two phases of outgrowth. Initially a layer of cones and a layer of bipolar cells grow together. The junctions formed by this outgrowth phase become the targets for horizontal cell outgrowth. A valid triad junction is one innervated by two different horizontal cells. A single triad is shown in Figure 2. Invalid triad junctions are automatically pruned.

Implicit in our modelling procedure is that the required functionality of the retina is determined by its underlying structure. Cones transmit input signals to their triad junctions. Horizontal cells average the signal value they receive through their connections to the triad junctions. The response of bipolar cells is determined by the input signal levels from the cones (centre) and horizontal cells (surround),

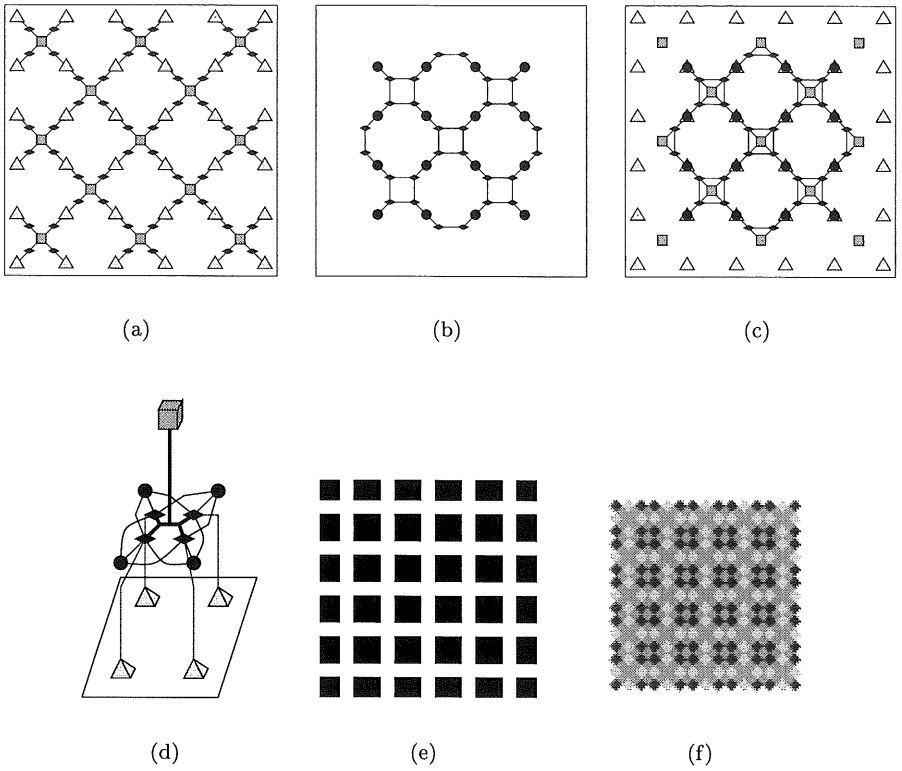


Figure 3: Architecture and functionality of the target retina. (a) to (d) are structural diagrams for the evolved 6x6 retina. (e) and (f) are functional examples for a 32x32 retina. (Cones are shown as triangles, bipolar neurons as squares, triads junctions as diamonds and horizontal neurons as spheres.) (a) Cone-to-bipolar connections. (b) Triad junctions formed by horizontal neurons with the synapses in (a). (c) Complete retina combining (a) and (b). (d) A 3D sketch of the central bipolar neuron and associated connections. (e) Test input image. (f) Target output image for 16x16 array of bipolar neurons. Outer bipolar neurons have a 'white' response due to edge effects.

namely:

$$bipolar\ output = \sum c_{i\pm1,j\pm1} - k \sum h_{i\pm1,j\pm1} \quad (1)$$

where c is the response of a cone, h the averaged response of a horizontal neuron, k is a constant of proportionality, and i and j are vertical and lateral indexes respectively, relative to the position of the bipolar neuron. The desired functionality is illustrated in Figures 3 (e) and (f).

3.1 Fitness Function Design

In this implementation, a retina's functionality is directly related to its geometry. Hence, we are investigating whether evolution can be driven by a fitness function derived entirely from a target retinal geometry. We therefore use fitness functions based on the connectivity between neighbouring neurons in the different layers. This significantly reduces the computation required since developed networks do not need to be functionally evaluated. Once evolution is complete, the functional performance of resulting structures is considered. Ultimately we intend to compare this approach with evolution based on functionality alone or a combination of both approaches.

To reduce the time taken to evolve solutions, a retina consisting of 36 cones, 13 bipolars and 16 horizontal cells is used. This is the smallest allowable retina to permit competitive interactions. The target architecture is illustrated in Figure 3. Edge-effects are negated by calculating the fitness value using only the central bipolar neuron and 4 central horizontal neurons.

Each layer of neurons possesses its own set of parameters, hence neurons in the same layer grow under the same developmental controls. Therefore, the parameters found on the small retina can be replicated and directly applied to larger retinas.

3.2 Pre-adaption

Pre-adaption is performed to restrict the search to particular regions of the parameter space, thereby reducing the time spent in search. For the retina model, cones intrinsically branch once, bipolars twice and horizontal neurons three times. This is similar to other models where syntactic constraints limit the number of neurons and branching frequency [Cangelosi et al., 1994, Kodjabachian and Meyer, 1998].

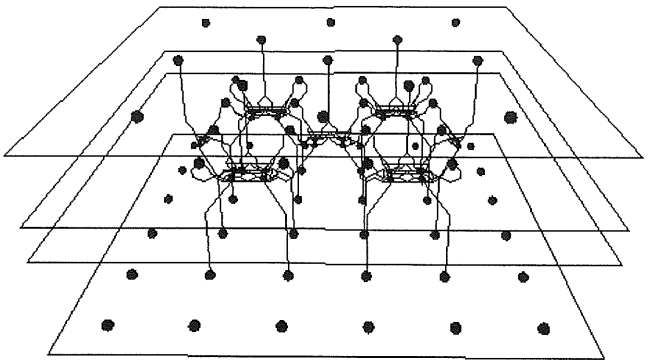
4 Results

Evolution was performed using the GENESIS genetic algorithm (GA) package [Grefenstette, 1990]. In all cases the population size was 50 with a mutation rate of 0.001. Selection was rank based and the elitist strategy was used. Once a stage of evolution was complete a 32x32 cone retina was grown (1024 cones, 481 bipolar neurons and 900 horizontal neurons) and functionality was investigated.

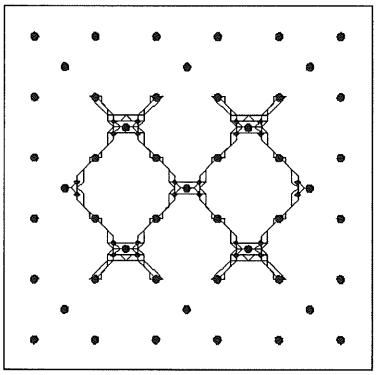
Figures 4(a) to (c) show that in the absence of any variability, intrinsic developmental rules can result in retina structures whose functional response (Figure 4(d)) matches the desired response (Figure 3(f)). However, if the positions of neurons are perturbed, the intrinsic rules fail to produce adequate functionality as illustrated in Figure 4(e). (Neuron coordinates were allowed to vary in all 3 directions by 1 unit with a 25% probability, where each unit represents a 10% displacement in position).

The developmental programme was made more robust to perturbations by incorporating rules permitting growing neurons to produce extra branches via interactions with the local developmental environment. Figures 5(a) to (c) show that the addition of the interactive overgrowth rules, results in a significant improvement in structure and hence functionality over intrinsic rules only. The target response is far more distinguishable in Figure 5(e) compared to Figure 4(e). However, black and white pixels indicate that those particular bipolar neurons are saturated due to having too many connections (see Figures 5(b) and (c)).

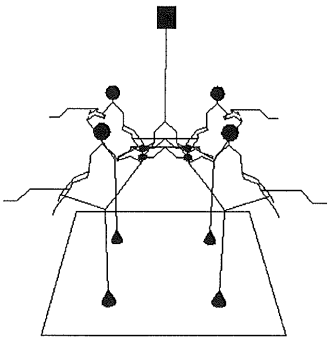
A further improvement in performance is achieved by incorporating interaction-based pruning rules, to control the extent of overgrowth, with the intrinsic and overgrowth rules. With the addition of the pruning parameters, the effects of noise on the functionality of the retina are again reduced, as seen in Figures 6(b), (c) and (e).



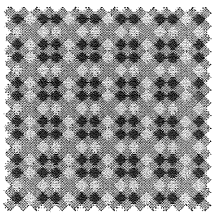
(a)



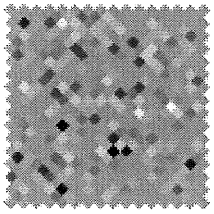
(b)



(c)

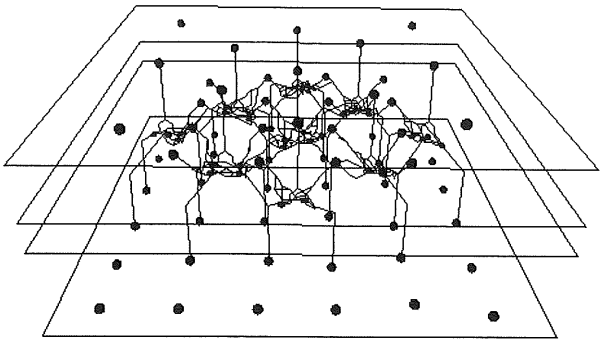


(d)

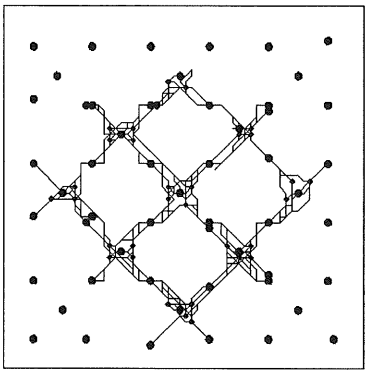


(e)

Figure 4: Retina grown using the parameters of the best evolved individual incorporating intrinsic developmental rules only. (a) 3D view of the evolved retina. (b) Plan view of (a) where, due to edge effects, only central neurons are shown. (c) Central bipolar neuron and associated connections extracted from (a). (d) Functionality of a symmetrical 32x32 retina. (e) Functionality of a perturbed 32x32 retina. Number of parameters evolved 20, genome length in bits 35, number of generations 2.



(a)



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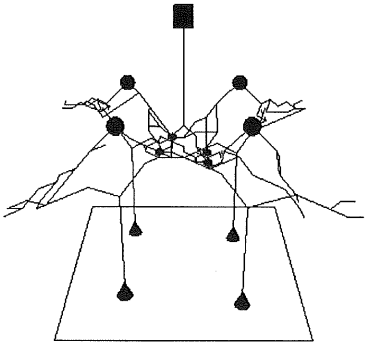

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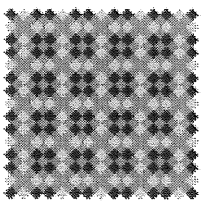

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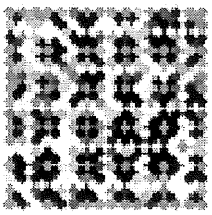
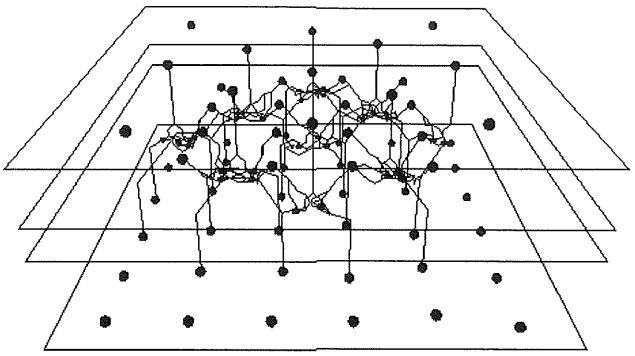
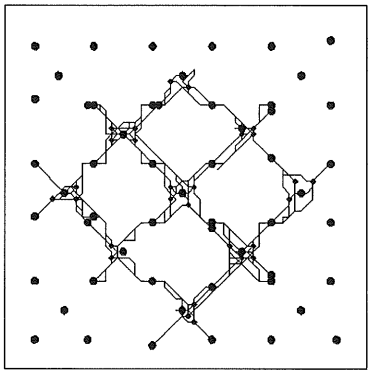


(e)

Figure 5: Retina grown using the parameters of the best evolved individual incorporating intrinsic and overgrowth rules. (a) and (b) are 3D and plan views of the evolved retina respectively. (c) Central bipolar neuron and associated connections extracted from (a). (d) Target functionality (see Figure 3(f)). (e) Actual functionality of a perturbed 32x32 retina. The new population was seeded using the best parameters from the symmetrical outgrowth case. The intrinsic parameters were allowed to vary but within a tighter range than previously permitted. To prevent the evolutionary process adapting to the characteristics of a single perturbed retina, each set of evolved parameters was used to create 3 retinas having different initial neuron positions. The average fitness of the grown networks was then compared to the target structure. The fitness function encouraged connectivity without harshly penalising multiple connections. Number of parameters evolved 25, genome length in bits 60, number of generations 48.



(a)



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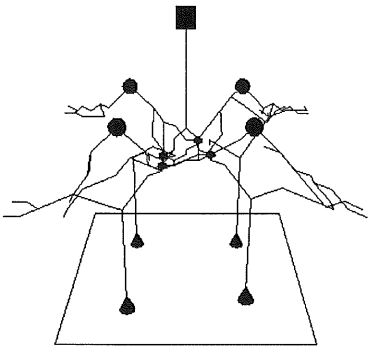
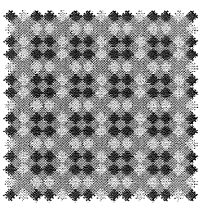


(c)



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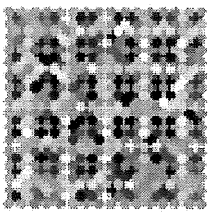

(e)

Figure 6: Retina grown using the parameters of the best evolved individual incorporating intrinsic, overgrowth and pruning rules. (a) and (b) are 3D and plan views of the evolved retina respectively. (c) Central bipolar neuron and associated connections extracted from (a). (d) Target functionality (see Figure 3(f)). (e) Actual functionality of a perturbed 32x32 retina. The best parameter set from the previous stage was again used to seed the new genome, also with restricted variability. Multiple retinas were again grown. Number of parameters evolved 33, genome length in bits 62, number of generations 55.

5 Discussion

The simulation results show that it is possible to evolve a correctly functioning retina from symmetrically placed neurons using a target structure and growth rules only. When neuron positions are inexact, the complexity of the developmental programme has to be increased through the addition of overgrowth and pruning, implemented using interactive self-organisation.

Evolution was carried out in stages, incorporating parameters from previous results and evolving them alongside new parameters. In this way the search space is increased in an orderly manner where evolution is channelled through developmental constraints. This contrasts with other models where all the developmental rules are co-evolved. Presenting such large, global search spaces can cause evolution to stall in the early generations [Dellaert and Beer, 1996]. If the search space is large then all the networks in a population may have the same fitness value. Evolution is therefore given no clear trajectory along which to progress. Other approaches to this problem have incrementally increased the complexity of the fitness function [Harvey et al., 1994] or subdivided a fitness function into a series of sub-tasks [Nolfi, 1998]. However, we feel that the approach described in this paper is more easily generalised and more biologically plausible.

The addition of overgrowth and pruning shows the developmental model to be robust under noisy conditions. This is best illustrated in Figure 4(c) and Figure 6(c). Under symmetrical conditions (Figure 4(c)) the triad junctions form in the same plane and the interconnections are regular in form. Figure 6(c) shows that although perturbations have produced triad junctions in non-symmetrical positions, the model is sufficiently robust such that the dendrites from the horizontal neurons still make the appropriate connections. This stage of connectivity development in ANN design is hence made to be less susceptible to errors caused by previous stages of artifical development, such as cell migration [Cangelosi et al., 1994, Kodjabachian and Meyer, 1998].

In this implementation, parameters are evolved based on layers of neurons. Adding neurons into layers therefore does not result in an increase in the length of the genome and to scaling problems. ANNs larger than the ones on which evolution operates can be grown. Developmental self-organisation results in neurons in the same layer having different morphologies through localised interactions.

6 Conclusion

Development allows a number of evolutionary parameters to operate on large numbers of cells. Cell-to-cell interactions during development allow robust development in-spite of the inevitable variations resulting from the qualitative nature of cellular development. Staged evolution of development offers an effective means of traversing the parameter search space and reducing the computational complexity of evolution. For an artificial retina, where functionality is directly related to structure, it is possible to use a target structure to evolve an edge detection capability even under noisy conditions, where neurons are subject to perturbations. Future work will focus on evolving ANNs where evolutionary progress is evaluated on functionality rather than structure.

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